The more things change: species losses detected in Phoenix despite stability in bird–socioeconomic relationships

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Abstract. The science of urban ecology has increasingly grappled with the long-term ramifications of a globally urbanized planet and the impacts on biodiversity. Some researchers have suggested that places with high species diversity in cities simply reflect an extinction debt of populations that are doomed to extinction but have not yet disappeared. The longitudinal studies conducted to date have found species composition shifting with urbanization but have not always documented continued species extirpations post-urbanization. We used long-term monitoring data on birds from the greater metropolitan area of Phoenix, Arizona, to measure changes in residential bird communities, species–habitat relationships, and human perceptions of bird species diversity over a five-year period. Bird richness, occupancy, and abundance decreased, as did the percentage of respondents satisfied with bird variety in their neighborhoods. As in previous analyses for this region, we found that desert specialist species were associated with neighborhoods with xeric landscaping consisting of gravel groundcover, and drought-tolerant, desert-adapted vegetation. These species were also found in neighborhoods with high per capita income rates and lower percentages of renters and Hispanic/Latinx residents. Non-native species were positively associated with neighborhoods containing mesic yards with grass and other water-intensive vegetation. The proportions of yards in our surveyed neighborhoods with these distinct landscaping types likewise remained relatively stable over five-year period. Although habitat–species relationships remained unchanged, we detected significant loss of species across the sampling period. Declines were not confined to desert specialist species but included generalist and invader species as well. The parallel reduction in residents’ satisfaction suggests that people perceive some aspect of this environmental degradation. Further investigation into the mechanisms underlying these species losses may reveal options for retaining some desert specialist species, and the uniqueness they contribute to urban fauna.

Key words: biodiversity; bird; Central Arizona–Phoenix Long-Term Ecological Research; mesic; residential yard; satisfaction; socioeconomic; xeric.

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INTRODUCTION

The science of urban ecology has increasingly grappled with the long-term ramifications of a globally urbanized planet and the impacts on biodiversity (Grimm et al. 2008, Seto et al. 2012). Studies have simultaneously characterized urbanization as a key threat to biodiversity (McKinney 2002, Grimm et al. 2008) and cities as places that can support surprisingly high levels of species
diversity (Aronson et al. 2014, Marzluff et al. 2016, Andrade et al. 2018). The retention of native vegetation (Turner 2003, Donnelly and Marzluff 2004, Burghardt et al. 2009), or at least vegetation structure resembling native plant communities (Lerman and Warren 2011), has been proposed as a means to retain native fauna, particularly in moderately urbanized settings (e.g., suburbs; Lepczyk et al. 2008, Marzluff and Rodewald 2008). Yet, knowledge about the persistence of species in urban landscapes over time is limited (Fidino and Magle 2017).

Studies provide diverse findings, with some species exhibiting higher rates of productivity (Rodewald and Shustack 2008a, Chamberlain et al. 2009) or survival (Evans et al. 2015) and experiencing or perceiving lower rates of predation (Ryder et al. 2010, Lerman et al. 2012) in urban settings compared to rural or wildland ones. For other species, urbanization brings increased exposure to hazards and suppressed reproductive success (Rodewald and Shustack 2008b, Loss et al. 2012, Bonnington et al. 2013). To date, the longitudinal studies conducted have found species composition shifting with urbanization but have not always documented continued species extirpations post-urbanization (Shultz et al. 2012, Nemésio et al. 2014, Strohbach et al. 2014, Fidino and Magle 2017). Building on a previous study of bird communities in residential yards in Phoenix, Arizona, USA (Lerman and Warren 2011), this study examines change over time in bird communities in light of regional trends in bird populations, habitat relationships, potential societal drivers, and human responses to the local bird community.

The majority of community composition studies are of short duration (1–2 yr; Marzluff et al. 2001, Kampichler et al. 2014), but a growing body of longitudinal studies of urban biotic communities is emerging. A recent review found 34 studies of urban birds that encompass five or more years of sampling (Fidino and Magle 2017). A common limitation to these studies is spatial replication, wherein temporal depth is traded off against the number of study sites (Campbell et al. 2012, Osenkowski et al. 2012, Shultz et al. 2012, Porzíg et al. 2014, Fidino and Magle 2017), with potential limitations to the generalizability of the findings (Ballard et al. 2003, Fahey et al. 2015). Large-scale volunteer-driven bird surveys in North America and Europe provide a major exception to this common tradeoff, with nationwide surveys conducted over multiple decades (Butcher et al. 1990, Sanderson et al. 2006, Hewson and Noble 2009, Laaksonen and Lehikoinen 2013, Murthy et al. 2016). However, these nationwide surveys are conducted at a relatively coarse spatial grain, with each sampling unit aggregating over large areas (e.g., 1 × 1 km squares) and including a mixture of land use types (King et al. 2007, Gagné et al. 2016). In addition, most longitudinal studies of urban biotic changes include little or no evaluation of the extent to which changes are a function of regional trends, local environmental change, or stochastic processes.

Region-wide trends such as species range shifts or new species invasions may contribute to species turnover in cities (Shochat et al. 2010, Strohbach et al. 2014). In Cambridge, Massachusetts, a 150-yr record of breeding birds registered regional changes like reforestation of New England in the early to mid-twentieth century, reductions in populations of insectivores from use of DDT, the subsequent rebounding of insectivorous species, and northward range expansions due to climate change (Strohbach et al. 2014). In missing these effects, synoptic studies likely underestimate the potential for species turnover in urban areas (Shultz et al. 2012, Strohbach et al. 2014, Fidino and Magle 2017). Likewise, longitudinal studies may overemphasize the effect of local-scale environmental changes, for example, urban intensification at the parcel or neighborhood scale, on species gains and losses without referencing concurrent population trends at broader scales.

As the majority of green space in cities is found in private yards (Nowak et al. 2001, Chamberlain et al. 2004, Loram et al. 2007), environmental changes in residential areas represent a significant force in shaping the distribution and abundance of habitat for birds (Goddard et al. 2013). Local-scale change in urban neighborhoods can take the form of urban intensification (e.g., through lot subdivision or redevelopment; Sushinsky et al. 2013) or alterations to landscaping at the scale of individual yards (Cook et al. 2012). Previous studies in Phoenix have identified associations between species of birds and other taxa and particular landscape arrangements (e.g., desert birds associating with desert-like landscaping; Kinzig
et al. 2005, Bang and Faeth 2011, Lerman and Warren 2011, Ackley et al. 2015). Attributes like income, ethnicity, and education have been shown to be the primary drivers of these landscape choices across multiple studies (Larsen and Harlan 2006, Larson et al. 2009, Zhou et al. 2009, Meléndez-Ackerman et al. 2014). For instance, residents in wealthier portions of Phoenix and many other cities have greater access to diverse communities of regionally distinctive bird species (Hope et al. 2003, Kinzig et al. 2005, Lerman and Warren 2011, Leong et al. 2018). Our previous studies in Phoenix also found increased satisfaction of residents in neighborhoods with greater desert bird diversity (Lerman and Warren 2011). This and other studies suggest there may be important ramifications for human well-being of species gains or losses (Luck et al. 2011, Dallimer et al. 2012). Thus, an examination of how urban bird communities change over time should evaluate concurrent changes in both local-scale environmental and social factors.

Five years after our initial study documenting associations among bird communities, landscape design, and socioeconomic factors, we revisited the same sites to evaluate changes in bird species composition in the context of regional trends in bird populations, local-scale environmental change in habitat and land use, neighborhood-scale socioeconomic change, and residents’ self-reported satisfaction. Specifically, we examined (1) which species have persisted in residential landscapes in Phoenix over time, (2) whether desert bird species continue to associate with more desert-like landscape types, (3) whether socioeconomic inequalities in access to bird diversity continue to exist, and (4) whether these inequalities are reflected in local satisfaction with bird variety.

**Methods**

**Study area**

Home to a population of 4.5 million (U.S. Census Bureau 2017), the greater metropolitan area of Phoenix, Arizona, is located in the Salt River Valley, within the northern limits of the Sonoran Desert in the southwestern United States. Perennial vegetation is dominated by *Ambrosia deltoidea* (bursage), *Encelia farinosa* (brittle bush), *Larrea tridentata* (creosote bush), *Olmeya tesota* (desert ironwood), *Parkinsonia floridana* (blue palo verde), and *Prosopis juliflora* (mesquite; Martin et al. 2004). Phoenix is landscaped with a range of different designs, from mesic yards (i.e., turf groundcover with a mixture of shrubs and leafy trees that are highly water-dependent) to xeric yards (i.e., crushed gravel ground cover with drought-tolerant or desert-adapted plants and trees). A third, prevalent landscape design, typically referred to as oasis, mixes features from both mesic and xeric (some grass and some crushed stone with plants, shrubs, and trees; Larson et al. 2017).

**Study design**

We conducted our study within the Central Arizona–Phoenix Long-Term Ecological Research (CAP LTER) site. The CAP LTER study area covers 6400 km² and consists of 204 long-term monitoring sites, including residential, commercial, agricultural, and desert land uses. The 204 sites were selected using a dual-density, randomized, tessellation-stratified design, and measure plant, bird and arthropod diversity, air and water quality, and human activity (Hope et al. 2003). This study included only the residential sites co-located with the 40 neighborhoods sampled for the Phoenix Area Social Survey (PASS; Harlan et al. 2007, 2017a, b, Lerman and Warren 2011), a CAP LTER longitudinal household survey that investigates residents’ perceptions and practices including environmental satisfaction and landscape choices (Larson et al. 2009), as further discussed below (*Habitat characteristics* section). For sampling purposes, we defined a neighborhood as a U.S. Census Block Group (CBG; Logan and Molotch 1987), and neighborhoods were stratified by income and distance from Central Phoenix. We omitted one neighborhood because only a small percentage of the area in that neighborhood was residential, for a final sample size of 39 neighborhoods (Fig. 1). Each set of samples (birds, household surveys, land use) occurred during two distinct time periods, separated by 5 yr. Sampling period 1 encompassed 2006–2008, and sampling period 2 encompassed 2011–2013.

**Bird surveys**

We surveyed birds at a randomly selected point in each of the 39 PASS neighborhoods within the long-term monitoring site (Bateman
et al. 2017). Point count locations were located on publicly accessible places within residential areas (Bateman et al. 2017), and previous research has established that habitat characteristics are relatively homogeneous at the neighborhood (census block group) scale (Lerman and Warren 2011). A trained observer stood at plot center and recorded all birds seen and heard within a 40 m radius for a 15-min count period (Ralph et al. 1995). The bird surveys were conducted in two seasons per year (winter and spring), and in two years per time period. Since winter sampling takes place in December and January, some bird counts are technically in the previous calendar year. For sake of clarity and simplicity, we refer to the winter sampling by the calendar year of the January portion of these counts. Spring counts take place from March to
early May. Thus, for the bird surveys, sampling period 1 encompassed 2007–2008 and sampling period 2 encompassed 2012–2013. Two different observers visited each site once per season per year, for a total of eight visits per site for each sampling period. To ensure observed birds were using the local habitat, we only included birds seen within 40 m of plot center and omitted all birds flying through the plot. Over the eight visits for each sampling period, we combined the bird community data and calculated the maximum number of each species recorded per site to accurately portray the year-round bird community (Melles 2005). We then classified the bird community into three major distribution categories based on Birds of North America distribution maps (Rodewald 2015): invaders, generalists, and desert specialists. As in our previous study (Lerman and Warren 2011), globally distributed species—including nonnative or alien species introduced by humans and predominantly urban specialists—were termed “invaders.” Widespread generalist species found in a variety of land use types throughout the United States, Mexico, and Canada were termed “generalists.” Regionally specific birds, including predominantly native Sonoran Desert species, were termed “desert” species.

**Habitat characteristics**

For the two sampling periods, we used survey responses to characterize the landscape type as mesic, xeric, or oasis from the PASS to characterize the habitat in the neighborhoods where bird monitoring was done. Based on our previous study, these landscape types serve as surrogates for key habitat characteristics, such as vegetation structure and composition, which have direct implications for structuring the bird community (Lerman and Warren 2011). The Institute for Social Science Research at Arizona State University administered the PASS from April through September 2006 (coinciding with sampling period 1 bird surveys), and May 2011 through January 2012 (coinciding with sampling period 2 bird surveys). The survey team contacted 40 households within each of the 39 PASS neighborhoods with a response rate of 51% for sampling period 1 (n = 811 households) and 43% for sampling period 2 (n = 806 households), 365 of which (45%) were repeat households from sampling period 1 and 441 were new houses surveyed in sampling period 2. Surveys were taken on the Internet, by telephone, and in personal interviews. Individual respondent identifiers were used to join data from the two sampling periods to compare the responses over time. Since the bird surveys were conducted at the neighborhood scale, we focus on aggregated neighborhood level survey results (11–20 respondents per neighborhood).

The PASS asked respondents to select what type of landscape design resembled their front and backyards (two separate questions). The landscape types were described as mesic, xeric, and oasis, with the definitions of these different designs described as: a yard with grass, some shrubs, and leafy trees (mesic); a yard with crushed stone and native desert plants and trees (xeric); a yard with some grass and some crushed stone with plants, shrubs, and trees (oasis). We aggregated the front yard and backyard categories into a single parcel categorization (mesic, xeric, oasis; Appendix S1: Fig. S1). We verified that these classifications were consistent at the neighborhood scale with the ground classifications of landscape types conducted in 2007 and 2008. We then conducted a linear regression analysis within a general linear model (GLM) framework to test whether the proportions of self-reported yard type closely aligned with the proportions of observed yard types. We report that the self-reported yard types were strong predictors of the observed yard types at the neighborhood scale for front yard xeric, parcel xeric, and front yard (r² = 0.53, df = 37, t = 5.87, P < 0.0001; r² = 0.40, df = 37, t = 4.40, P < 0.0001; r² = 0.36, df = 37, t = 4.57, P < 0.0001, respectively). The model for front yard oasis had the weakest relationship (r² = 0.08, df = 37, t = 1.79, P < 0.08). These preliminary results provide confidence in using the self-reported landscape type for modeling relationships with the bird community.

**Neighborhood demographics**

We incorporated CBG data to characterize neighborhood demographics (co-located with the bird monitoring neighborhoods). To quantify demographic features of the PASS neighborhoods, we summarized the CBGs that were co-located with the 39 PASS neighborhoods. U.S. Census Block Group variables included percent...
of the CBG that is Hispanic or Latinx (see discussion of this terminology in Watkins and Gerrish 2018), per capita income of the CBG, percent of the homes classified as owner occupied (vs. renters), population density, age (percent of householders older than 65), and education level (percent of households with a bachelor’s degree). We examined demographic characteristics of the survey respondents to test whether the survey sample changed between the two sampling periods (Appendix S1: Table S1).

**Land use change**

We tested whether land use changes occurred at broader spatial scales. We obtained the Existing Land Use file database from the Maricopa Associations of Government (MAG) to identify the land use patterns in and around the 39 PASS neighborhoods for the two sampling periods. Maricopa Associations of Government data were available for 2004 (sampling period 1) and 2012 (sampling period 2). The Existing Land Use database, created as a joint effort of MAG and MAG member agency staff, is comprised of a number of sources including aerial imagery recognition, MAG member agency land use data, developer information, newspaper articles, and Maricopa County Assessor data. Existing Land Use components are classified into 100+ land use categories that identify both the type and intensity of land use. The data are vector with parcel data as the primary inputs. We generated a 1-km buffer around each bird monitoring location and summed the area within each buffer for each land use category for the two sampling periods. There were 24 different land use categories. Because we were primarily interested in whether residential development increased at the expense of open space (defined by MAG as either active open space or passive/restricted open space), we focused on these two land use categories, comparing changes in total area (m²) between the two sampling periods using an ANOVA.

**Environmental satisfaction**

For both sampling periods, PASS survey respondents were asked a series of closed-ended questions regarding satisfaction with neighborhood amenities. Here, we focus on one environmental satisfaction question on bird biodiversity. Respondents were asked to indicate their satisfaction with the variety of birds in their neighborhood. A four-point ordinal response scale included (1) very satisfied, (2) somewhat satisfied, (3) somewhat dissatisfied, and (4) very dissatisfied; respondents were also given the option “don’t know” or “refuse to answer.” We calculated neighborhood satisfaction with bird variety as the percent of respondents within each of the 39 PASS neighborhoods who were either “very satisfied” or “somewhat satisfied” with bird variety (see descriptive statistics in Appendix S1: Table S1).

**Statistical analysis**

*Bird community changes over time.*—We used an occupancy modeling framework to test whether bird community composition changed between the two sampling periods. We fit models with a logit link and compared the two bird sampling periods for each bird species. We only included species with occurrence in at least 10% of all sites in either sampling period to ensure rare species do not have a disproportionate influence on our results (McCune and Grace 2002, McGarigal et al. 2013). We determined whether each bird species’ probability of occupancy (ψ) changed between the two surveys using Program Mark (single-species occupancy model; White and Burnham 1999). We pooled bird surveys within each season (winter and spring) across two observers into one detection period for each sampling period, giving us a total of four detection periods (a winter and spring detection period for sampling period 1 and a winter and spring detection period for sampling period 2). Single-season analyses would not provide a robust estimate of detectability, and all but six species in this analysis are resident. For each single-species model, we set the detection probability (p) to be constant between the two sampling periods and tested the null hypothesis that probability of occupancy did not change (null model: p(0) × ψ(0)). We compared the null model with models whose occupancy changed between the two sampling periods (change model: p(0) × ψ(1)). We ranked models based on Akaike information criterion score (Burnham and Anderson 2002); when the change model was higher ranked than the null model, we treated this as a case of change; when the null model was ranked higher, we treated it
as a case of no change. Since occupancy modeling only assesses changes in presence–absence, we also evaluated whether abundance for each species changed between the two sampling periods using paired t tests. In addition, we compared mean species richness per season between sampling period 1 and sampling period 2 using a t test to determine whether total richness of desert specialists changed between the two sampling periods.

*Bird and landscape type/bird and socioeconomic relationships.*—We performed two redundancy analyses (RDA) to assess (1) the relationships between the bird community and the landscape design, and (2) the bird community and socioeconomic variables. We included time (sampling periods 1 and 2) as a constraining factor in the analysis. Redundancy analysis is a constrained ordination technique that explains the variation found in ecological communities and is driven by environmental constraints (ter Braak 1986). We employed RDA due to the linear response of bird abundance (DCA1 axis length = 2; ter Braak 1986). Only bird species present in more than one site (5% of total sites) were included in the analysis; rare species were omitted due to their disproportionate weight (McCune and Grace 2002, McGarigal et al. 2013). Bird abundance was square root transformed and standardized using a row relativization prior to analysis (Legendre and Gallagher 2001). First, we calculated the proportion of total inertia present in the constrained axis to determine the bird community variation explained for each ordination. Then, for each of the ordinations, we used a Monte Carlo global permutation procedure to test the significance of (1) the overall ordination, (2) each axis, and (3) the individual terms constraining community variation (Hope 1968). We then conducted a variance partitioning analysis to test the exclusive and shared effects of time, landscape type, and socioeconomic variables (Tuomisto and Ruokolainen 2006, Legendre and Gauthier 2014). We used the vegan package in R (Oksanen et al. 2016).

We conducted a paired t test to determine whether satisfaction with desert bird variety changed between the two sampling periods within the sampled neighborhoods. We then performed a logistic regression with a binomial distribution in a generalized linear model framework to test whether satisfaction with variety of desert birds accorded with actual bird variety for each sampling period based on the bird surveys as described above. To do so, respondents that were highly dissatisfied or somewhat dissatisfied were classified as 0 and respondents that were highly satisfied or somewhat satisfied were classified as 1. Responses were aggregated for each neighborhood separately for each sampling period. We then regressed this response variable as a function of the number of desert species observed at each neighborhood. If a household respondent selected “don’t know” or “refuse to answer” in either sampling period, then the respondent was omitted from the analysis. We used the predict function to fit lines to our data to display the probability scale of respondents satisfied with bird variety given the actual desert bird richness. We used the base r package in R, using glm(family = binomial, link = logit) and predict function.

**RESULTS**

**Bird community changes over time**

Average bird occupancy decreased between the two sampling periods by 9% (46.7% in sampling period 1 to 37.8% in sampling period 2). The majority of desert specialists declined in occupancy (6 out of 11 species), while half of generalist species (8 out of 17 species) and invader species (2 out of 4 species) did not change (Table 1). Only four species increased in neighborhood occupancy over time: one desert species (White-winged Dove, *Zenaida asiatica*), a generalist species (Brown-headed Cowbird *Molothrus ater*), and two invaders (European Starling *Sturnus vulgaris* and Eurasian Collared Dove *Streptopelia decaocto*). Meanwhile, during the same time period, desert bird richness declined by almost three species per neighborhood (t test: \( t = 2.86, df = 38, P < 0.006; \) Appendix S1: Table S1). The majority of species experienced declines in abundance between the two sampling periods, regardless of category (Fig. 2; Appendix S1: Table S2). The exceptions included Eurasian Collared Dove (an invader) and White-winged Dove (desert specialist), both of which increased in abundance.

**Longitudinal bird and landscape relationships**

Yards exhibited no significant change in landscape types between the two sampling periods.
Table 1. Results of the modeled individual species occupancy estimates between the two sampling and the raw percent of sites where species occurred for the two sampling periods.

| Common name by species guild | Species code | Occupancy (SD) | Best fit | Direction of change | Percentage of occurrence |
|------------------------------|--------------|---------------|----------|---------------------|-------------------------|
|                              |              | Period 1      | Period 2  |                     |                         |
|                              |              | (Occupancy)   | (Occupancy) |                     |                         |
|                              |              | Period 1      | Period 2  |                     |                         |
| Desert                       |              |               |           |                     |                         |
| Albert’s Towhee†             | ABTO         | 0.84 (0.12)   | 0.58 (0.11) | p(1) × ψ(1)        | Dec                     | 0.62 0.46               |
| Anna’s Hummingbird           | ANHU         | 0.93 (0.04)   | 0.76 (0.07) | p(1) × ψ(1)        | Dec                     | 0.9 0.74                |
| Curve-billed Thrasher†       | CBTH         | 0.77 (0.08)   | 0.59 (0.09) | p(1) × ψ(1)        | Dec                     | 0.69 0.51               |
| Gilded Flicker†‡             | GIFF         | 0.21 (0.05)   | 0.02 (0.05) | p(1) × ψ(1)        | Dec                     | 0.18 0                  |
| Say’s Phoebe                 | SAPH         | 0.19 (0.05)   | 0.11 (0.04) | p(1) × ψ(1)        | Dec                     | 0.33 0.21               |
| Verdin†‡                     | VERD         | 0.97 (0.04)   | 0.8 (0.07)  | p(1) × ψ(1)        | Dec                     | 0.95 0.79               |
| White-winged Dove           | WWDO         | 0.04 (0.04)   | 0.34 (0.16) | p(1) × ψ(1)        | Inc                     | 0.03 0.18               |
| Cactus Wren†‡                | CACW         | 0.31 (0.06)   | 0.31 (0.06) | p(1) × ψ(1)        | NC                      | 0.33 0.21               |
| Costa’s Hummingbird         | COHU         | 0.24 (0.07)   | 0.21 (0.07) | p(1) × ψ(1)        | NC                      | 0.21 0.21               |
| Gambel’s Quail†‡             | GAQU         | 0.32 (0.05)   | 0.32 (0.05) | p(1) × ψ(1)        | NC                      | 0.36 0.28               |
| Gila Woodpecker             | GIWO         | 0.81 (0.07)   | 0.73 (0.08) | p(1) × ψ(1)        | NC                      | 0.77 0.69               |
| Generalist                   |              |               |           |                     |                         |
| Great-tailed Grackle        | GTGR         | 0.93 (0.04)   | 0.76 (0.07) | p(1) × ψ(1)        | Dec                     | 0.92 0.74               |
| Killdeer                     | KILL         | 0.3 (0.26)    | 0 (0)     | p(1) × ψ(1)        | Dec                     | 0.13 0                  |
| Lesser Goldfinch             | LEGO         | 0.67 (0.21)   | 0.18 (0.1)  | p(1) × ψ(1)        | Dec                     | 0.36 0.1                |
| Northern Mockingbird        | NOMO         | 0.86 (0.06)   | 0.69 (0.08) | p(1) × ψ(1)        | Dec                     | 0.82 0.64               |
| Northern Rough-winged Swallow| NRWS         | 0.2 (0.05)    | 0 (0.04)   | p(1) × ψ(1)        | Dec                     | 0.15 0                  |
| Orange-crowned Warbler      | OCWA         | 0.46 (0.21)   | 0.14 (0.81) | p(1) × ψ(1)        | Dec                     | 0.23 0                  |
| Yellow-rumped Warbler       | YRWA         | 1 (0)         | 0.84 (0.08) | p(1) × ψ(1)        | Dec                     | 0.87 0.72               |
| Brown-headed Cowbird        | BHCO         | 0.08 (0.04)   | 0.16 (0.04) | p(1) × ψ(1)        | Inc                     | 0.03 0.1                |
| American Kestrel            | AMKE         | 0.16 (0.04)   | 0.11 (0.04) | p(1) × ψ(1)        | NC                      | 0.1 0.08                |
| House Finch                 | HOFI         | 0.99 (0.03)   | 0.92 (0.05) | p(1) × ψ(1)        | NC                      | 0.97 0.9                |
| Mourning Dove               | MODO         | 0.1 (0)       | 0.92 (0.04) | p(1) × ψ(1)        | NC                      | 0.97 0.92               |
| Northern Flicker            | NOFL         | 0.35 (0.33)   | 0.35 (0.33) | p(1) × ψ(1)        | NC                      | 0.1 0.1                 |
| Ruby-crowned Kinglet        | RCKI         | 0.45 (0.2)    | 0.3 (0.15)  | p(1) × ψ(1)        | NC                      | 0.18 0.15               |
| Rock Wren                   | ROWR         | 0.09 (0.07)   | 0.17 (0.11) | p(1) × ψ(1)        | NC                      | 0.05 0.1                |
| Red-winged Blackbird        | RWBL         | 0.17 (0.11)   | 0.09 (0.07) | p(1) × ψ(1)        | NC                      | 0.1 0.05                |
| White-crowned Sparrow       | WSCP         | 0.55 (0)      | 0.36 (0)   | p(1) × ψ(1)        | NC                      | 0.41 0.28               |
| Inca Dove                   | INDO         | 0.76 (0.08)   | 0.49 (0.09) | p(1) × ψ(1)        | Dec                     | 0.69 0.44               |
| Invader                     |              |               |           |                     |                         |
| Eurasian Collared Dove      | EUCD         | 0.26 (0.08)   | 0.6 (0.1)  | p(1) × ψ(1)        | Inc                     | 0.23 0.54               |
| European Starling           | EUST         | 0.52 (0.08)   | 0.7 (0.07)  | p(1) × ψ(1)        | Inc                     | 0.67 0.51               |
| House Sparrow               | HOEP         | 0.98 (0.02)   | 0.95 (0.03) | p(1) × ψ(1)        | NC                      | 0.97 0.95               |
| Rock Pigeon                 | ROPI         | 0.61 (0.08)   | 0.49 (0.08) | p(1) × ψ(1)        | NC                      | 0.62 0.49               |

Notes: Individual species occupancy models whose occupancy changed between sampling periods (p(1) × ψ(1) × ψ(1)) were ranked against the null model (p(1) × ψ(1)) using Akaike information criterion scores. Species codes correspond to the redundancy analysis. Direction of change abbreviations are Dec, decreased; Inc, increased; NC, no change.

† Designates a species as a U.S.–Canada Stewardship Species due to their restricted distribution and considered to have continental importance (Panjabi et al. 2012).

‡ Designates a species of continental importance either on a watch list or a common bird undergoing steep declines (Rosenberg et al. 2016).

Numerically, mesic parcels slightly decreased (20% vs. 18%) and oasis parcels slightly increased (27% vs. 29%), while the percentage of xeric parcels remained constant (53%; see Appendix S1: Table S1). Residents were more likely to change their backyards than the front ones (Appendix S1: Fig. S1).

The landscape design variables in the landscape RDA explained 27.5% of the variation in the Phoenix bird communities (constrained inertia; Fig. 3a, Table 2). The ordination was significant (df = 73, F = 6.9077, P < 0.001), as were the first two axes; therefore, we interpreted both axes on the triplots (Fig. 3a, Table 2). We found that
Fig. 2. Species abundances in the two sampling periods. Bars and whiskers indicate mean and standard errors for abundance of the maximum count per species per site for all birds included in the occupancy analysis. Comparisons between sampling periods 1 and 2 are significant by t tests (Appendix S1: Table S2).
Fig. 3. Redundancy analysis ordination diagram of bird species distributed in site space (species locations closer to one another indicate similarity in ordination space) in relation to (a) parcel landscape variables and (b) in
mesic and xeric yards significantly influenced the orientation of species groups. In general, desert species increased in abundance in neighborhoods with higher percentages of xeric yards compared to neighborhoods with higher percentages of grassier landscapes (mesic yards), whereas the majority of invader birds increased their abundance in the mesic yards (Fig. 3a, Table 2). By controlling for sampling period (i.e., Year in the RDA; Fig. 3a, Table 2), we determined that the relationships between the bird community and landscape types remained consistent over time, yet we also documented that the bird community shifted between the two sampling periods irrespective of the bird–landscape relationship ($F = 18.6185, P < 0.001$).

**Bird and socioeconomic relationships**

We detected no changes in education or income level of the survey respondents during the two sampling periods but did detect a shift in reported ethnicity. The respondents were typically in their late forties to fifties, with an average per capita income of $26,000–34,000 (Appendix S1: Table S1). Across the two sampling periods, the ethnicity of the Phoenix sample shifted toward more Hispanic/Latinx respondents and fewer Anglo ones, which reflects a growing minority population in the region. Overall, the sample represents a diversity of residents in terms of demographics and location throughout the region (Harlan et al. 2007, 2017a, b).

The socioeconomic variables in our RDAs explained 32.2% of the variation in Phoenix bird communities (constrained inertia; Fig. 3b, Table 2). The ordination was significant ($df = 70, F = 4.756, P < 0.001$), as were the first two axes; therefore, we interpreted both axes on the triplots (Fig. 3b). We found household income, percent of the neighborhood with owner occupancy and with a bachelor’s degree, and percent of the neighborhood identifying as Hispanic/Latinx were significant in explaining local bird populations (Table 2). These variables significantly influenced the orientation of species groups. Desert birds had higher abundance in higher income neighborhoods, whereas invader species were more abundant in neighborhoods with a higher percent of Hispanic/Latinx residents, denser populations, and lower income levels (Fig. 3b). By controlling for sampling period (i.e., Year in the RDA; Fig. 3b, Table 2), we determined that the relationships between the bird community and socioeconomic variables remained consistent over time, yet we also documented that the bird community shifted between the two sampling periods, irrespective of the relationships with the social variables ($F = 18.6126, P < 0.001$).

The shared variation explained by the landscape design variables, socioeconomic variables, and time was 37% with independent variation for each variable at 9% (landscape design), 14% (socioeconomic factors), and 19% (time). Thus, the decline in bird species/change in composition is driven by factors other than changing demographics or landscapes.

**Land use change**

Land use did not significantly differ between the two sampling periods. Specifically, the amount of open space did not decline ($F = 0.0075, P = 0.93$), and the amount of residential development did not increase ($F = 0.1329, P = 0.7164$). Persisting patterns of satisfaction with birds.—The majority of Phoenix-area residents reported they...
were satisfied with the variety of birds in their neighborhood in both sampling periods 1 and 2 (72.27% and 62.75%, respectively; Appendix S1: Table S1). The percentage of respondents satisfied with bird variety decreased by 10% between the two time periods ($t$ test: $t$ value = 4.7254, $P < 0.001$). One of the largest drivers of this trend was the decrease in households that were somewhat satisfied and the increase in “don’t know” responses.

As reported previously for sampling period 1 (Lerman and Warren 2011), neighborhood satisfaction was positively correlated with actual richness of birds unique to southwestern deserts (desert specialists). We found similar patterns for sampling period 2 though the correlation was weaker (logistic regression: $\beta = 0.304$, $z = 6.483$, $P < 0.001$; $\beta = 0.195$, $z = 3.597$, $P = 0.003$, sampling periods 1 and 2, respectively). However, the strength of the relationship declined between the two sampling periods ($\beta = 0.304$, 0.195 sampling periods 1 and 2, respectively).

### DISCUSSION

This study aimed to measure changes in bird communities, their associations with local habitat and socioeconomic conditions, and human responses over a five-year period. Overall, we found that species richness and bird abundance declined in Phoenix yards, though the distribution of species relative to yard type and socioeconomic status has not changed over the five-year sampling window. Desert landscaping still supported desert birds, and wealthier residents still had greater access to diverse, desert-like bird communities. Resident satisfaction with bird diversity declined over time, though again, the relationship between satisfaction and actual bird diversity remained unchanged. These relationships suggest feedbacks in that humans alter urban habitat through landscape designs, birds respond to these changes, and in turn, humans respond to the biodiversity in their neighborhoods.

Levels of species losses similar to those we report here were detected in a 12-yr study conducted in riparian areas in Phoenix, Arizona, USA (Banville et al. 2017). However, our findings are in sharp contrast to several other long-term analyses of bird and other animal community changes in urban settings. Bird diversity in three sites in Cambridge, Massachusetts, in an Ohio woodlot, and on the University of California at Berkeley campus remained remarkably stable over multiple decades post-urbanization (Horn 1985, Shultz et al. 2012, Strohbach et al. 2014), though considerable turnover in species composition was detected in all of these studies. Similarly, orchid bee communities exhibited species turnover but diversity remained highly stable over a seven-year study of a single urban park in Belo Horizonte, Brazil (Nemésio et al. 2014).
These studies differ in important ways from ours, such as the land use and spatial extent of sampling, but also in the biogeographic context and growth form of the cities in which they were conducted, all of which are factors that may influence the pace and direction of long-term trends (Fidino and Magle 2017). It is difficult to say how unique our findings in Phoenix are since change in species composition within already urbanized land uses is not examined as often as changes in composition as a result of conversion from wildland to urban land uses (Fidino and Magle 2017).

Why do we see these declines for some species (primarily desert specialists) yet increases for other species (predominantly invaders) in Phoenix? Declines detected in Phoenix might simply reflect regional trends of species declines due to broad-scale factors, such as climate oscillations or habitat loss on wintering grounds (Ballard et al. 2003, Sanderson et al. 2006, Koenig et al. 2017). Other possible mechanisms for bird declines include the emerging effects of an extinction debt that existed at the time of initial surveys in Phoenix or the effects of further urban intensification. The actions required to slow or reverse species losses differ as a function of which explanation is most likely (Hahs et al. 2009, Banville et al. 2017). Next, we evaluate evidence for these two possible mechanisms, concordance with regional trends and local-scale change, as well as the potential feedbacks to human experience of biodiversity.

Regional trends for Phoenix birds

Which species are declining and why?—Almost all species declined in abundance (Fig. 2), but about half declined in occupancy (Table 1). The species experiencing a decline in occupancy between the two sampling periods include a mix of broadly distributed desert birds, as well as species known to be sensitive to urbanization (Table 1; Lerman and Warren 2011). The bulk of the species for which we detected a decline in occupancy in Phoenix (10 out of 14) are listed as increasing or stable at regional and global scales and are classified as under no threat of extinction (Table 1; Rosenberg et al. 2016). Some of these regionally stable species are generalist species with broad continental distributions include Great-tailed Grackle (Quiscalus mexicanus), Yellow-rumped Warbler (Setophaga coronata), Lesser Goldfinch (Spinus psaltria), and Inca Dove (Columbina inca). Others are more specialized, including some desert specialists still regarded as
common species, such as Anna’s Hummingbird (Calypte anna) and Say’s Phoebe (Sayornis saya). An eighth species, Northern Rough-winged Swallow (Stelgidopteryx serripennis), is categorized as under no threat though its population is experiencing slight to moderate declines (Rosenberg et al. 2016). Thus, for most species we can rule out the simple explanation that decline in occupancy of birds in Phoenix is due to regional trends or broad-scale factors. Instead, the best explanations for these declines are likely to involve impacts of urbanization.

We documented six desert species with declines in occupancy in Phoenix, four of which are matched by declines or threats at regional and global scales (Rosenberg et al. 2016). We also documented an additional four desert species with no change in occupancy including two species of conservation concern. Species with the highest threat levels according to the Partners in Flight (2017) Science Committee database, a network of bird conservation partners in the Western Hemisphere, include Gilded Flicker Colaptes chrysoides (a species of continental conservation concern), Cactus Wren Campylorhynchus brunneicapillus, and Verdin Auriparus flaviceps (both Common Birds in Steep Decline, though Cactus Wrens appear stable in Phoenix). Five desert species were grouped as a U.S.–Canada Stewardship Species due to their restricted distribution and considered to have continental importance. These include Curve-billed Thrasher Toxostoma curvirostre, Abert’s Towhee Melozone aberti, and Verdin, all experiencing a decline in occupancy in our study (Table 1). Interestingly, the list also includes two species for which we did not detect a change in occupancy, Gambel’s Quail Callipepla gambelii and Cactus Wren (Table 1). Although we detected declines in abundance for both of these species, the changes were not significant (Table 1).

The aim of the Stewardship designation is to bring attention to the plight of declining species and to inspire conservation action toward protecting and enhancing their habitats (Panjabi et al. 2012). Results from our RDAs, namely that desert birds increased in abundance in neighborhoods with desert-like landscaping, suggest that expanding xeric landscapes in developed and future residential yards could continue to provide habitat necessary for supporting these and other desert specialists. Broadly throughout the region, there has been a push for xeric landscaping in recent years (McGlade 2015), with some evidence that use of xeric landscaping may be increasing (Martin et al. 2003, Frost 2016). Further, the Partners in Flight conservation assessment is based on Christmas Bird Counts and Breeding Bird Surveys and does not fully incorporate surveys in private yards. Thus, our research in private yards fills an important gap, and, given the large area covered by residential land (Loram et al. 2007), suggests a potential contribution that private yards may serve for regional conservation and habitat for Cactus Wren and Gambel’s Quail.

Colonization of a new species.—During the two bird survey periods, our data documented the invasion of Eurasian Collared Dove S. decaocto, which more than doubled its occupancy and mean abundance (Table 1). The trends we detected were similarly documented in eBird, a citizen science online depository and database for birders to submit observations (Sullivan et al. 2009). Eurasian Collared Dove was introduced to Florida, USA, in the 1980s and quickly spread west, reaching California by 2005 (Bled et al. 2011, Romagosa 2012). Although Eurasian Collared Dove was one of the most abundant birds recorded during the second bird survey, the species was restricted to yards with mesic landscaping. The replacement of exotic vegetation with desert plantings thus has the potential to discourage the continued invasion of Eurasian Collared Dove. It is unclear whether Eurasian Collared Dove is having negative impacts on other dove species but has the potential to compete with Mourning Doves and White-winged Doves (Romagosa and McEneaney 1999).

Local-scale change
Are species losses due to ongoing urban intensification or vegetation cover change?.—Urban intensification is an increasing trend, even in relatively densely populated portions of existing cities (Song and Knaap 2004, Tratalos et al. 2007, Delmelle et al. 2014). Across Great Britain, species richness initially increases with housing density, but then declines sharply at higher housing densities for most species of birds, including those classified as urban indicator species (Tratalos et al. 2007). A modeling exercise for
Brisbane, Australia, projects declines in occupancy of birds classified as urban-sensitive species, a reasonable parallel to the desert species in our sample, under a scenario that includes densification of residential neighborhoods (Sushinsky et al. 2013). In our study, however, we detected no significant changes in land use or land cover change in our sample neighborhoods in Phoenix. The amount of residential development at the neighborhood scale did not alter significantly across the two time periods. Likewise, the land area of remnant desert patches within 1 km of our study sites did not significantly change over the course of the study. Thus, while some portions of Phoenix are undergoing redevelopment and densification (Collins and Grineski 2007, Kittrell 2012), it appears this either (1) the trend is not widespread enough to account for the species losses we detected across the 5-yr sampling window of our study or (2) the sampled neighborhoods are not sufficiently representative to detect urban intensification. The latter explanation is unlikely since the sample was selected to be representative of key socioeconomic, demographic, and urbanization factors, such as distance from the urban fringe (Harlan et al. 2017b).

Vegetation cover as indicated by yard types (mesic vs. xeric) in resurveyed households also showed no significant change though some front yards became more xeric while backyards more mesic (Appendix S1: Fig. S1). Our analyses indicate that residents’ self-reported yard types are strongly correlated with the actual vegetation structure and composition in these yards. The lack of change in yard types over the sampling period suggests that land cover change is not responsible for the species losses, though finer scaled changes in vegetation may have occurred.

If losses are not due to local-scale change, then what?—Using several different measures of land use and land cover change, we see more stability than change in bird habitat in Phoenix residential areas. But the possibility remains that changes in an unmeasured factor are at the root of the species losses detected here. We also acknowledge that this five-year study may not be sufficiently long term to determine whether bird communities will ultimately stabilize as they appear to have done at sites in Cambridge and Berkeley (Shultz et al. 2012, Strohbach et al. 2014). However, we found similar declines in species richness in riparian sites in Phoenix across a longer period of time (12 yr; Banville et al. 2017). One additional possibility is that the species losses are a result of extinction debts coming due in this relatively young and rapidly growing city.

Evidence for urban extinction debts has been presented in a global analysis of extinction rates in emergent plant communities (Hahs et al. 2009), particularly in newer cities. Phoenix has developed rapidly over the past few decades and in a non-linear fashion. Much of the city was converted to urban land use in the 1990s and 2000s (Kane et al. 2014). Even for older neighborhoods, rapid land use change was ongoing during that time period in the landscapes surrounding them (Shrestha et al. 2012). Thus, it is possible that the species detected at our initial sampling time (2006–2007 for this study; 2000–2012 for Banville et al. 2017) reflect an extinction debt from initial urbanization. However, additional mechanistic and demographic studies are necessary to resolve the question of extinction debt and to identify the mechanisms underlying species losses in Phoenix.

**Human landscape decisions and potential feedbacks**

*Native landscaping for native birds.*—Landscape choices and their management have long been proposed as a means to support diverse, native communities and complex food webs in urbanized areas (Germaine et al. 1998, Goddard et al. 2010, 2017, van Heezik et al. 2013). A growing number of observations support this contention for both birds and arthropods at the scale of neighborhoods and individual yards (Burghardt et al. 2009, Lerman and Warren 2011, Pardee and Philpott 2014, Narango et al. 2017, but see Gaston et al. 2005, Matteson and Langellotto 2011). At a city scale, reduced extinctions of native species for plants and birds in urban settings are also strongly associated with retention of native vegetation in cities (Hahs et al. 2009, Aronson et al. 2014). Over the five-year period of our study, avian communities tended to assort themselves consistently, with desert specialists associated with xeric, gravel-covered yards (i.e., desert landscaping) and broadly distributed generalist and invader species associated with mesic, lawn-covered yards, dominated by non-native plant
species (Fig. 3a). While the stability of these associations reinforces the call for native landscaping to support native species, the species losses detected across Phoenix, even in xeric yards and neighborhoods, suggest that this tactic alone is not sufficient to support native species in the longer term.

Landscape designs for yards change over time, and these patterns tend to be reflected in differences among neighborhoods in major vegetation types depending on the decade in which a yard was established (Whitney and Adams 1980, Martin et al. 2003, Daniels and Kirkpatrick 2006, Gillespie et al. 2012). This pattern suggests a high degree of inertia in yard type within a neighborhood over time. That is indeed what we found in our sample of Phoenix yards, despite several decades of incentives for homeowners to convert yards to xeriscape (Martin et al. 2003) and reports that xeriscaping is increasing in the region (McGlade 2015, Frost 2016). Households surveyed in both sampling periods exhibited no significant changes between mesic and xeric yard types (N = 365 households; see Appendix S1: Fig. S1). Studies of yard preferences suggest this may be true over even longer periods, since respondents frequently indicate a mismatch between their preferred yard type and the one they have (Larsen and Harlan 2006, Larson et al. 2009). In general, research has shown that multiple factors constrain landscape change in residential areas, often referred to as legacy effects, based on long-lasting social norms in neighborhoods and the lack of individual efforts to change landscapes—especially in front yards (Larson et al. 2017).

Persistent income inequalities in access to native species.—Previous research has found significant disparities in the distribution of urban nature relative to the socioeconomic status and racial composition of urban neighborhoods (Hope et al. 2003, Martin et al. 2004, Strohbach et al. 2009, Davis et al. 2012, Leong et al. 2018). General patterns emerging suggest that the inequalities to access fall along economic lines, whereby higher income sections of cities support higher species diversity (Hope et al. 2003, Kinzig et al. 2005, Melles 2005, Warren et al. 2010). Higher income neighborhoods in Phoenix, Arizona, USA, supported more native birds and lizards (Lerman and Warren 2011, Ackley et al. 2015), and in the city of Waco, Texas, tree-dwelling bats increased their abundance in more affluent neighborhoods (Li and Wilkins 2014). These and other studies imply a mediating influence of vegetation, whether it be higher tree canopy cover (Li and Wilkins 2014, Locke and Baine 2015), mature garden vegetation (Hand et al. 2016), or cooler temperatures (Jenerette et al. 2007). In Phoenix, the vegetation structure of higher income neighborhoods, particularly the greater abundance of shrubs and succulents, has been cited as important underlying factors in bird distributions (Martin et al. 2004, Kinzig et al. 2005, Lerman and Warren 2011). Regardless of the mechanisms, our study continues to reinforce the importance of socioeconomic variables in accounting for urban biodiversity patterns (Fig. 3b). In particular, we note that these relationships appear remarkably stable, despite species losses being detected across all neighborhoods in our study. In addition, the two sampling periods encompass a major economic recession that altered patterns of vegetation, particularly for annual plants (Ripplinger et al. 2016). Our study further reinforces the finding that equalizing access of urban residents to species diversity can be difficult to achieve (Danford et al. 2014) and is likely to require active interventions.

Do people notice losses of bird species?.—Studies testing whether people notice biodiversity or loss of species in their yards have mixed findings (Dahmus and Nelson 2014). A study in Sheffield, UK, found a strong concordance between people’s perceptions and actual plant and bird species richness (Fuller et al. 2007), but others found weak or no relationships between those measures (Shwartz et al. 2014, Belaire et al. 2016). Given limited and mixed results, additional research is needed to understand how people interact with their environments and the implications for biodiversity. Both the current study and our previous study in Phoenix, Arizona, showed that satisfaction with bird variety was positively related to desert species richness (Lerman and Warren 2011). We note that satisfaction with birds was correlated with other neighborhood measures and may not indicate a true recognition of species losses by Phoenix residents. The consistency of the relationship between resident satisfaction and species diversity, however, reinforces the notion that biodiversity affects human...
well-being—that is, since satisfaction declined along with species declines.

Understanding patterns of species persistence and loss are critical for managing people’s exposure to biodiversity. Alarm has been raised over the extinction of experience for an increasingly urban population (Miller 2005, Soga and Gaston 2016). The spatial inequalities in residents’ access to regionally distinctive fauna we have documented here may exacerbate this effect. Yards supporting higher levels of biodiversity may lead to positive feedbacks within residential areas, wherein positive experiences with backyard wildlife can lead to more wildlife friendly landscape choices in the future (Goddard et al. 2013, Belaire et al. 2016).

CONCLUSIONS

We documented significant losses in species richness and abundance, particularly for desert specialist species across a five-year period in Phoenix residential areas. However, some of the obvious mechanisms of regional population trends or local-scale environmental change do not appear to account for these losses, raising the possibility of an extinction debt. The bird community appears to have responded gradually to the initial development of Phoenix, with some desert species unable to adjust to the novel ecosystem during the re-equilibration phase (Kuussaari et al. 2009, Ramalho and Hobbs 2012). Similar non-linear effects of urbanization have been found in forested regions as well (Pidgeon et al. 2014). Further investigation into the mechanisms underlying these species losses may reveal options for retaining some desert specialist species, and the uniqueness they contribute to a region’s fauna.

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