ARTICLE

# ECOSPHERE

# The ecological role of native-plant landscaping in residential yards to birds during the nonbreeding period

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#### Abstract

Residential yards are a form of urban land use that cover a considerable amount of area in cities worldwide and provide important habitat for wildlife, especially when landscaped with native plants. Nevertheless, most native-plant landscaping and wildlife research in the northern temperate regions of the world has been conducted during the spring and summer breeding period, leaving a gap in our understanding of the importance of residential yards and native plants as habitats for animals during the nonbreeding period. To fill this gap, we quantified the ecological role of native-landscaped yards to avifauna throughout Greater Los Angeles (LA), California, during the winter nonbreeding period, which is a time of year when the region hosts a high abundance and diversity of migratory and resident birds. We surveyed birds and habitat features from October to March of 2020 and 2021 at 22 pairs of native- and non-native-landscaped yards plus 10 additional native-landscaped yards. We had three objectives for our study. First, we compared avifaunal communities, including feeding and nonfeeding behaviors, and habitat features between native and non-native-landscaped yards. Second, we quantified relationships between habitat features and bird richness, abundance, and feeding and nonfeeding behaviors-focusing on species affiliated with urban or natural terrestrial ecosystems of the region. Third, we documented feeding and nonfeeding behaviors by birds with native and non-native plants. Native-landscaped yards had a greater cover of native trees, shrubs, and herbaceous plants, and a higher cover of natural habitat elements, including leaf litter and bare-ground cover. Bird richness and abundance-especially bird species affiliated with tree- and shrub-dominated ecosystems-were greater in native than non-native-landscaped yards. Further, yards with a higher cover of native plants supported greater numbers of feeding birds, with individuals focusing their foraging behaviors on distinct native trees and shrubs, including Quercus spp. (oak), Heteromeles spp. (toyon), Arctostaphylos spp. (manzanita), and Salvia spp. (sage). Our results suggest that residential yards landscaped with native plants provide important habitat for birds during the nonbreeding

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period and are a viable approach for residents and cities if improving conditions for birds throughout the annual cycle is a goal.

KEYWORDS

avifauna, California, ecological landscaping, feeding, lawn, Los Angeles, native, non-native, shrubs, trees, urban

# INTRODUCTION

Urbanization is one of the most dominant forms of land use worldwide, and it poses a substantial threat to native ecosystems and biodiversity (Faeth et al., 2011; Forman, 2014; Grimm et al., 2008; McKinney, 2002). Urbanization is the process where land cover, whether natural or anthropogenic (e.g., agricultural lands or previous development), is converted into a built environment (Foley et al., 2005; Seto et al., 2010). In addition to habitat loss, urban development creates a complex, yet manicured ecosystem intended primarily for human habitation (Alberti et al., 2020; Grimm et al., 2008; Pickett et al., 2001). While cities can be hotspots for biodiversity, including rare species (Baldock et al., 2019; Ives et al., 2016; Kowarik, 2011; Spotswood et al., 2021), the general pattern is that urban ecosystems tend to harbor novel wildlife communities dominated by synanthropic species with few habitat specialists (Aronson et al., 2014; Blair, 1996; Callaghan et al., 2019; Groffman et al., 2014, 2017; Marzluff, 2001; McKinney, 2006, 2008; McKinney & Lockwood, 1999; Schwartz et al., 2006). Because of the changes in habitat and the shifts in species assemblages, urbanization is a primary factor in the decline of biodiversity, especially for animal populations (Aronson et al., 2014; Elmqvist et al., 2013; Faeth et al., 2011; Fattorini, 2011; Magle et al., 2021; Merckx & van Dyck, 2019; Piano et al., 2020; Wenzel et al., 2020). Moreover, as countries worldwide modernize and the global population expands, the amount of urban land cover will likely continue to grow, posing a critical challenge for biodiversity conservation (Angel et al., 2011; D'Amour et al., 2017; Güneralp & Seto, 2013; Seto et al., 2011, 2012).

One feature of urban ecosystems that has gained attention as potential habitat for wildlife is residential yards (or gardens) (Cannon, 1999; Gaston & Gaston, 2010; Goddard et al., 2010, 2013, 2017; Lerman et al., 2021; Lerman & Warren, 2011; Narango et al., 2017; Sperling & Lortie, 2010). Residential yards comprise a substantial percentage of land cover in many urban areas worldwide, and therefore, are a significant component of a city's greenspace (Gaston & Gaston, 2010; Ossola et al., 2019). The effect of residential yards in supporting wildlife is a pattern that has been uncovered in numerous cities across the globe (Gaston & Gaston, 2010). For example, yards landscaped with native plants tend to expand the volume of vegetation and produce resources that are beneficial to wildlife (Threlfall et al., 2017). On the other hand, landscaping in yards and gardens can also introduce substantial hurdles (Burghardt et al., 2009; Lerman et al., 2018; Narango et al., 2018). For example, in the United States, yard landscaping is often dominated by non-native plants, manicured lawns, and impervious surfaces that provide little benefit to wildlife (hereafter, conventional yards). Moreover, conventional yards have been associated with lower vegetation composition and complexity (Burr et al., 2018; Padullés Cubino et al., 2019), which can adversely affect various animal species (Threlfall et al., 2017). The reasons behind the preferences for plants that are non-native in their geographic origin to a region typically involve aesthetics, norms, nursery stock, and socioeconomic factors (Avolio et al., 2018; Burr et al., 2018; Locke et al., 2018; Padullés Cubino et al., 2020). Nevertheless, the landscaping decisions made by residents of a city can strongly filter the community assembly of urban wildlife species pools (Aronson et al., 2016; Goddard et al., 2010).

While landscaping with native plants in residential yards and urban areas generally benefits wildlife (e.g., DeGraaf, 2002; Tallamy, 2009; Tallamy et al., 2020), there remain key priorities for study. First, there is a general lack of knowledge of the value of native-plant landscaping in residential yards to avifauna during the nonbreeding period. The nonbreeding period for birds is devoted to feeding, resting, and focusing on safety (e.g., avoiding predators) to ensure preparedness for the spring migration and subsequent breeding season (Greenberg & Marra, 2005; Sillett & Holmes, 2002). A critical aspect of the nonbreeding period is ensuring body condition through food acquisition, which can carry over to influence breeding season fitness (Norris et al., 2006). Therefore, it is paramount for both individuals and populations of bird species to utilize habitats during the nonbreeding period that will provide the necessary resources to ensure fitness in all aspects of their life history throughout the annual cycle (Marra, Cohen, et al., 2015; Marra, Studds, et al., 2015). Most research on wildlife in yards has taken place during the breeding period, when resources in yards may have direct effects on the fitness of wildlife populations (e.g., Narango et al., 2017, 2018). While critical to understand how urban landscapes affect breeding wildlife, it may be equally as important to understand the role that urban habitats, including residential yards, play in supporting species during the nonbreeding period (e.g., Wood & Esaian, 2020).

Second, from a regional perspective, there is limited information regarding patterns of wildlife distribution in residential yards in coastal southern California (see Adams et al., 2020). Most of the globe's research on native-plant landscaping and wildlife has primarily been focused on the eastern or interior portions of the United States, Australia, and the United Kingdom (Burghardt et al., 2009; Daniels & Kirkpatrick, 2006; French et al., 2005; Lerman & Warren, 2011; Narango et al., 2017; Salisbury et al., 2015), with fewer studies from tropical cities (e.g., Akinnifesi et al., 2010). Coastal southern California, including Los Angeles (LA), the Inland Empire, Orange County, and coastal portions of San Diego County, has over 20 million residents and is an area famous for its suburban sprawl (Wolch et al., 2004). Since the turn of the century, the region has moved from one housing boom period to the next, with the development of single-family homes with yards built in nearly all low-lying areas (Pierson Doti & Schweikart, 1989). Yards with lawns and ornamental plants were a sign of prosperity and quickly became the norm for new developments (Reisner, 1987). Since the 1990s, the sprawl has slowed in the region (Moule & Polyzoides, 2005). However, the legacy of the development practices persists (Avolio et al., 2019). While there are incentive programs for property owners to convert their conventional yards to those with native plants (bewaterwise.com, 2021), most of the region continues to harbor yards dominated by lawns and exotic plants (Pincetl et al., 2019). Further, a new trend has emerged related to urban densification where property owners throughout LA are removing greenspace for the expansion of current buildings, or additional structures (Lee et al., 2017). Given the density of people and the vast cover of conventional yards in coastal southern California, coupled with the trend of increasing hardscape in the region, there is an urgent need to understand the ecological importance of native-landscaped yards and whether patterns from elsewhere in the world are consistent with the California southland.

Our goal was to quantify the ecological role of native-landscaped yards (hereafter, native yards) throughout LA to avifauna during the nonbreeding period. We had three objectives to support our goal. First, we used a paired-sampling design to compare avifaunal communities, including feeding and nonfeeding behaviors, and habitat features in native and conventional yards. We predicted that bird communities and feeding and nonfeeding behaviors would differ between native and conventional yards with a higher abundance and species richness, increased feeding and nonfeeding behaviors, and a distinct composition of species in native than conventional yards, following results during the spring and summer breeding period in the suburbs of southeastern Pennsylvania, Phoenix, Chicago, Illinois, and Washington, DC (Belaire et al., 2014; Burghardt et al., 2009; Lerman & Warren, 2011; Narango et al., 2017). Second, we quantified relationships between habitat features and bird richness, abundance, and feeding and nonfeeding behavioral patterns. We predicted that the abundance and richness of birds, especially those associated with natural terrestrial ecosystems of the region, and bird feeding rates would be higher in native yards with more native tree and shrub cover, given the importance of those habitat features to birds in urban areas (Lerman & Warren, 2011; Wood & Esaian, 2020). Third, we documented feeding and nonfeeding behaviors by birds with native and non-native plant species. We predicted that birds would concentrate their feeding activity on native plants following results from the Washington DC area where breeding Carolina Chickadees (Poecile carolinensis) preferentially foraged for invertebrate prey on native plants (Narango et al., 2017). Further, we predicted that native-landscaped yards would be a refuge for birds, as characterized by increased nonfeeding behaviors (e.g., perching)-similar to how birds congregate in parks in sections of cities (Vasquez & Wood, 2022).

### **METHODS**

### Study area

We surveyed birds and habitat features at 32 sites across LA, which contains numerous dense urbanized zones surrounded by suburban sprawl (Figure 1). Thirty sites were in LA County, while two were located within Orange County (Figure 1). The region is nestled within the California Floristic Province Biodiversity Hotspot and thus occupies a space that provides habitat for a great diversity of plants and wildlife, many of which are endemic to the area (Garrett et al., 2012; Higgins et al., 2019). In particular, the valley and foothill regions where present-day LA sits harbored large swaths of grassland, coastal sage scrub, chaparral, woodland, and wetland ecosystems (Ethington et al., 2020; Stein et al., 2007).

Our study was located within four primary sections of LA including the San Fernando, San Gabriel, and Pomona Valleys, and the LA basin (Figure 1). LA is surrounded by the San Gabriel Mountains to the



**FIGURE 1** Map of 32 study sites (black dots) throughout LA and Orange Counties. The blue shading highlights the urban extent of our study area in LA County, with city names labeled. The inset map highlights the location of the study area in California, and the photos depict a typical native- and conventional-landscaped yard of this study. GoogleMaps, Digital image (2019).

northeast, the Santa Monica and Santa Susana Mountains to the northwest, and the Pacific Ocean on its western and southern edges. Few patches of natural land remain within the boundaries of LA, such as Griffith Park, the Verdugo Mountains, foothills and canyons of the Palos Verdes Peninsula, the Punte, Montebello, and San Jose Hills, and the Ballona Wetlands. As a result, the study sites varied in distance to the nearest natural area from 27 m to 11.7 km. The climate in LA is Mediterranean, with hot, dry summers and mild, wet winters (Mooney & Zavaleta, 2016). Further, the climate varies considerably among study sites. In general, the coastal zones of the LA basin have more moderate temperatures and less rain. In contrast, the three valleys have more extreme temperatures with the potential for higher winter rainfall, especially in foothill communities.

### Study design

To accomplish our study goals, we established a paired-sampling design where each native yard was paired with a nearby conventional yard (Figure 1) (Burghardt et al., 2009). We only surveyed in front yards and omitted backyards as many were not landscaped with native plants or were unavailable for surveys. We considered yards "native" if they contained plant species that were generally native to coastal southern California ecosystems. including chaparral, coastal sage scrub, oak savanna and woodlands, and riparian (Appendix S1: Table S1) (Mooney & Zavaleta, 2016). However, there were plants in yards that were native to other regions of California (e.g., montane or desert ecosystems), or were cultivars (Appendix S1: Table S1). Further, nearly all native yards had individual plants that were non-native in geographic origin. Nevertheless, our selection captured yards where >79% of the plant cover included genera or species native to the region's dominant ecosystems (Appendix S1: Table S1). To identify paired conventional yards, we requested willing native-yard homeowners to introduce us to neighboring yards of similar size to their native yard, but with conventional landscaping. There were no native plants in any of the conventional yards of our survey (Figure 1). In total, we obtained permission to survey 22-paired conventional yards. The paired yards averaged 72.15 m from one another and generally did not show evidence of spatial autocorrelation of bird and habitat variables (Legendre & Fortin, 1989) (Appendix S1: Figure S1). Further, yard size did not vary significantly between native and conventional yards (paired t test, p = 0.20). Ten native yards were left unpaired because we were unable to identify willing homeowners for conventional yard surveys. In total, we included data from 54 yards surveyed at the 32 sites, including 22 pairs plus 10 unpaired native yards.

### Habitat features

We conducted vegetation and habitat surveys in each yard during the third round of surveys from January to March 2021. We used relevé methods to visually estimate the percent cover of vegetation at the ground, shrub, and tree canopy levels (Minnesota Department of Natural Resources, 2007; Wood et al., 2010). Further, we estimated the percent cover of bare soil, paved, leaf litter, mulch, and rock cover. In native yards only, we identified each plant at the shrub or tree level and visually estimated the area that each covered (Appendix S1: Table S1). We relied on homeowners to assist with identifying native plants. However, this practice was challenging as many individuals were difficult to identify to species (e.g., cultivars and exotic plants) (Appendix S1: Table S1). Thus, we collected data on plants based on the identification of a plant's genus (Appendix S1: Table S1).

Additionally, we used spatial analysis tools in ArcGIS to quantify habitat variables at the landscape scale in two ways (ESRI, 2016). First, we used the "measure" tool in ArcGIS to quantify the Euclidean distance from the centroid of each yard to the boundary of the nearest protected area (e.g., San Gabriel Mountains, Griffith Park, Bolsa Chica Ecological Reserve, Ballona Wetlands) and to the nearest urban greenspace (e.g., community gardens, urban parks, golf courses). We obtained boundaries for the protected areas and urban greenspaces from the "Countywide Parks and Open Space" layer, which are public data hosted by the County of LA (City of Los Angeles, 2016). We also hand-digitized polygons for the boundaries of all yards and calculated the area.

Second, to quantify habitat features to the extent of the surrounding neighborhood, we used a light detection and ranging (LiDAR) derived data product that provided urban-form data for every parcel in LA County (Galvin et al., 2016). Using a spatial join to merge with our sample locations, we included seven variables from the parcel-level data: the average land value and the average % cover of trees, grasses, bare soil, buildings, paved, and impervious surfaces. We included the land value of parcels to understand whether the "luxury effect" was an important driver of bird communities (Clarke et al., 2013; Hope et al., 2003; Leong et al., 2018). Further, we included the percent cover variables as each is influential in describing urban wildlife (Schell et al., 2020). We quantified the parcel-level data from all parcels within 200-m radii circular buffers of surrounding native yards to generally understand the effect of the adjacent urban habitat compared with habitat features within the native yards in influencing bird richness and abundance (Belaire et al., 2014). We selected data from the 200-m buffer as we assumed this spatial extent was the most biologically relevant to the birds of our study. The 200-m buffer captures an extent of 0.13 km<sup>2</sup>. The average "temporary home-range size" for a Yellow-rumped Warbler (Setophaga coronata), one of the most common birds in LA during the nonbreeding period when our

surveys were completed, used corridors and woodlands during fall migration in southeastern South Dakota that were 0.08 and 0.03 km<sup>2</sup> in area (Liu & Swanson, 2015). Therefore, we assumed that the 200-m extent adequately captured the potential habitat adjacent to the residential yards of our survey that may be important for filtering bird species composition of yards.

Our final tally included 22 predictor variables. Thirteen variables captured habitat features of each yard, including the size of yards, and the percent cover of trees, native trees, non-native trees, shrubs, native shrubs, non-native shrubs, herbaceous plants (nonlawn), native herbaceous plants, non-native herbaceous plants, bare ground, leaf litter, and lawn. Seven predictor variables captured conditions of the surrounding neighborhood, including the land value of parcels within the 200-m buffers of yards, and the % cover of trees, grass, bare soils, buildings, paved surfaces, and impervious surfaces within the 200-m buffers of yards. Lastly, two variables captured the geographic position of yards within the city and included the distance to the nearest protected area and the distance to the nearest urban greenspace. Thus, our predictor variables were designed to characterize conditions at three spatial extents: within yards ("yard extent," smallest), adjacent to vards ("neighborhood extent," medium), and proximity to natural and urban greenspaces ("geographic position extent," broad) that may influence avian communities within yards.

# Bird surveys and feeding and nonfeeding behavioral observations

We conducted three 20-min area-search bird surveys from October 2020 through March 2021 where we recorded the species and number of individuals using each yard (Watson, 2003). We completed surveys between 06:30 AM and 11:00 AM and visited both yards of each pair on the same day to minimize weather and seasonal biases. We alternated which yard was surveyed first between rounds and we did not conduct surveys during weather events such as high wind or rain. For each yard, we chose a series of vantage points outside of the yard's boundaries, typically the sidewalk, front porch, or driveway, where we stood and observed birds with binoculars. We did not count birds flying through a yard or in neighboring yards, as they were not directly utilizing vegetation or other resources within a yard. Thus, birds must have either landed on vegetation, the ground, or a structure or have exhibited active feeding behavior to be countable for our survey. To avoid double-counting individual birds between pairs, we kept track of individuals and only recorded birds when they were first detected. For example, if we detected a California Scrub-Jay (*Aphelocoma californica*) utilizing trees in various yards along a city block, we only included a detection in the first yard where we were surveying. While our method may have inadvertently overlooked smaller, more subtle species that may move between yards, such as a female House Finch (*Haemorhous mexicanus*), our approach provided a robust estimate of bird usage within and between yards.

Additionally, for each bird detected, we opportunistically recorded whether the individual was exhibiting feeding or nonfeeding behavior. Because most yards were small (Figure 1), after a bird was detected, we observed the individual, while continuing to count additional species. We then documented whether a bird exhibited feeding or nonfeeding behaviors while in the yard during surveys. Feeding behaviors included gleaning for prey items on the surfaces of plants, foraging on the ground, feeding on seeds or fruit, obtaining nectar from flowering plants, and aerial maneuvers (e.g., sallying) (Wood et al., 2012). For each observed feeding behavior, we recorded the behavior and the substrate-whether a plant, the ground, or an aerial maneuver from a plant. If birds fed on multiple substrates, we documented each behavior and substrate used during a foraging bout (Wood & Esaian, 2020). Quantifying feeding is critical as it indicates the direct use of resources and the potential for native yards to support bird populations during the nonbreeding period (Wood et al., 2012; Wood & Esaian, 2020). Nonfeeding behaviors included any activity other than feeding, including vocalizing, perching, or aggressive or defensive maneuvers. We assumed that nonfeeding behaviors suggested using the structural or natural features of yards, including plants, the ground, or built structures, for resting, moving during foraging, thermoregulating, or for cover from predators or potential competitors (Remsen & Robinson, 1990; Robinson & Holmes, 1982)-all of which are critical behaviors by birds during the nonbreeding period.

# Bird abundance estimation and habitat guilds

Detection probability, the probability of detecting a species if present at a survey location, is a concern with wildlife count data (MacKenzie et al., 2017). Thus, to account for detection probability, we calculated *N*-mixture models, which are hierarchical models that incorporate spatial replicates of raw abundance count data to estimate both detection probability and abundance for a given species (Royle & Nichols, 2003). First, we fitted the intercept-only *N*-mixture model, using the "pcount" function in the R package "unmarked," for 15 bird species with sufficient

Common name	Scientific name	Migratory	Category	Naïve	Det.	SE
Mourning Dove	Zenaida macroura	No	Urban	0.08	0.52	0.16
Anna's Hummingbird	Calypte anna	Yes	Natural lands	0.42	0.39	0.07
Allen's Hummingbird	Selasphorus sasin	No	Urban	0.56	0.39	0.07
Black Phoebe	Sayornis nigricans	No	Urban	0.17	0.62	0.11
California Scrub-Jay	Aphelocoma californica	No	Natural lands	0.10	0.48	0.14
Bushtit	Psaltriparus minimus	No	Natural lands	0.17	0.27	0.10
Ruby-crowned Kinglet	Corthylio calendula	Yes	Natural lands	0.35	0.30	0.10
Northern Mockingbird	Mimus polyglottos	No	Urban	0.33	0.24	0.10
House Finch	Haemorhous mexicanus	No	Urban	0.31	0.30	0.08
White-crowned sparrow	Zonotrichia leucophrys	Yes	Natural lands	0.27	0.30	0.07
California Towhee	Melozone crissalis	No	Natural lands	0.29	0.36	0.10
Orange-crowned Warbler	Leiothlypis celata	Yes	Natural lands	0.17	0.18	0.11
Yellow-rumped Warbler	Setophaga coronata	Yes	Natural lands	0.40	0.48	0.07
Lesser Goldfinch	Carduelis psaltria	No	Urban	0.23	0.37	0.09
House Sparrow	Passer domesticus	No	Urban	0.12	0.54	0.11

**TABLE 1** Naïve detections and detection probability (Det.) estimates and SEs of 15 bird species, characterized by habitat guild (natural lands and urban) and migratory status, included in the *N*-mixture models.

*Note*: Segments of Anna's and Allen's Hummingbird populations migrate. We assumed that Anna's Hummingbirds of our study were a mixture of migratory and nonmigratory individuals, whereas most Allen's Hummingbirds were likely nonmigratory in our system.

count histories for appropriate estimation (Table 1). We then estimated the posterior distribution of latent abundance from the N-mixture models for the 15 candidate bird species at each site using empirical Bayes methods, programmed within the "unmarked package" in R (function, "ranef") (Fiske & Chandler, 2011; R Core Team, 2017). A critical assumption for estimating detection probability within a season is "closure" (MacKenzie et al., 2017). While birds move frequently during the nonbreeding period, we assumed that the focal species of this study were present and available for detection throughout our surveys. The average naïve detection rate for the 15 focal species (unadjusted proportion of observations at yards) was 0.26 and ranged from 0.08 (Mourning Dove, Zenaida macroura) to 0.56 (Allen's Hummingbird, Selasphorus sasin; Table 1). The average detection probability was 0.39 and ranged from 0.17  $\pm$  0.11 (Orange-crowned Warbler, Leiothlypis celata) to  $0.62 \pm 0.11$  (Black Phoebe, Sayornis nigricans; Table 1). We detected a further 18 species (33 in total) that were rare (e.g., California Thrasher, Toxostoma redivivum) (Appendix S1: Table S2). It was not possible to fit N-mixture models for the rarer species. However, we did include the rare species in the cumulative richness metric (see below) and feeding and nonfeeding observation tallies (Appendix S1: Table S2).

To focus our analysis on segments of the bird population that we expected would respond positively or negatively to native yard habitat features, we aggregated the estimated abundance data from the 15 species into two

habitat guilds: natural lands and urban birds. The birds of natural lands are affiliated with natural ecosystems during the breeding period, whereas the urban birds are synanthropic species affiliated with human development and thus are commonly found throughout LA and other cities in coastal southern California (Billerman et al., 2021; Clark, 2017; Higgins et al., 2019) (Table 1). For either group, we summed the abundance of each bird within a group at each yard to come up with a guild-specific estimated abundance value. We also summed the total of all 15 bird species for total bird abundance. Five of the 15 species we included in our survey are migratory, and all were included within the natural lands group (Table 1). In addition to the total, natural lands, and urban bird abundances, we computed cumulative bird richness, which is the total of all bird species detected in a yard throughout the three surveys. Our surveys generally captured the accumulation of observable bird species, where after three visits, most species were likely detected in each yard that was present during the period of our surveys (Appendix S1: Figure S1).

### Statistical analysis

To address our first objective in comparing avifaunal communities, including feeding and nonfeeding behaviors, and habitat features in native and conventional yards, we conducted two analyses. First, we fit a series of paired sample *t* tests comparing bird metrics (abundance, richness, and feeding and nonfeeding behavioral counts) and the 22 predictor variables between native and conventional yards. We used Shapiro–Wilk's method to test for normality in the dataset. If the assumption of normality could not be met, we used a paired nonparametric Wilcoxon rank-sum test. We also calculated the effect size of each test to understand the magnitude of the difference of a variable between pairs using either a parametric Cohen's *d* or nonparametric *z*-score analysis (Zar, 1999).

We removed four pairs of yards from analyses in the first objective because either the native-landscaped or conventional yard had a bird feeder or a bird bath, which likely influenced numbers. We removed a further two pairs where we did not detect birds in one of the pairs on any visits. One yard was native and the other conventional. The native yard had freshly planted plants and was the smallest of our surveys, whereas the conventional yard had minimal plants. We assumed that the small yard size and possibly the growth stage of the newly planted plants in the yards likely were a factor in limiting the number of birds that may visit the yards. Therefore, we did not feel these two yards were comparable to the others in our study. We did include the native yards of the pairs in the final plant lists (Appendix S1: Table S1), simply as an indication of additional plants in native yards in our study areas. This left us with a total of 16 pairs (n = 32). All other yards had no bird feeders or baths, were similar in size, and also had mature vegetation (Figure 1). Thus, we assumed that the yards included in the analyses for the first objective were available to birds, which were attracted by the presence of plants and other habitat features.

Second, to identify the degree of dissimilarity in avian communities and habitat features between native and conventional yards, we conducted two, one-way analysis of similarities tests (ANOSIM) (Oksanen et al., 2019). The ANOSIM analyses assessed whether ranked dissimilarities of the avian community and habitat features within the native and conventional yards were more dissimilar than between yard types (Oksanen et al., 2019). We used the Bray-Curtis dissimilarity of the square-root transform of a matrix of the abundance values of the 15 bird species (first test) and the 13 within-yard predictor data for the habitat analysis (second test), grouped between native and conventional yards. To evaluate dissimilarity, we used 999 Monte Carlo permutations to generate the random test statistic, R, which ranges from -1 to 1. An *R* value near zero indicates that the avian community and habitat features did not differ between yard types, whereas R values further from zero indicated increasing dissimilarity. We computed the ANOSIM analysis using the "vegan" package (Oksanen et al., 2019).

To address our second objective in quantifying the relationships between the predictor variables and the avifaunal groups, we fitted generalized linear models (GLMs). We fitted GLMs using a negative-binomial error distribution using the "MASS" package in R (Venables & Ripley, 2002) because most models had clear evidence of overdispersion (Zuur et al., 2011). We fitted univariate models and used a model-selection framework in six model sets to determine which of the 22 predictor variables best explained each of the six avifaunal metrics (Burnham et al., 2011). In each model set, we also included the intercept-only model to understand whether predictor variables explained more variation than the response variable means. We ranked variable importance for each model set using Akaike information criterion (AIC) values, where the lowest  $\triangle$ AIC values indicated the best-fitting models (Burnham et al., 2011). Further, we calculated Kullback-Leibler-divergence-based values  $(R_{kl}^2)$  using the "rsq" package in R (Zhang, 2022). We generated the  $R_{kl}^2$  values by calculating the likelihood ratio index of a fitted model (Cameron & Windmeijer, 1997). In visual scatterplot inspections of a response variable against a predictor variable, there were some occasions of hump-shaped patterns. If this were the case, we fitted a model with a quadratic term included. We did not include data from the two sites in Orange County (two native yards and one conventional yard) as LiDAR data were not available outside of LA County. Additionally, we did not include nine yards that had bird feeders or baths (or their pair had a feeder or bath), or the two yards with no bird detections, resulting in a sample size of n = 40 for the objective 2 analyses.

To address our third objective, where we documented feeding and nonfeeding behaviors by birds with native and non-native plant species, we completed four analyses. First, we quantified patterns in bird-feeding observations on either shrubs or tree surfaces between native and conventional yards using a Wilcoxon rank-sum test and a z-score analysis. Second, we fitted six regression models using a similar GLM methodology to the second objective to quantify the relationships between the % cover of shrubs (total, native, and non-native) to the observations of birds feeding on shrubs. We then repeated this analysis for the % cover of trees (total, native, and non-native) to the observations of feeding birds on trees in native and conventional yards. We performed this series of analyses to understand whether native or non-native shrub or tree cover best explained directed feeding patterns on either substrate. Third, we computed a Wilcoxon rank-sum test and a z-score analysis to explore whether there were distinct patterns in bird-feeding observations between native and non-native plants. Fourth, we explored relationships, again using a similar GLM approach as described in

objective 2, between the % cover of distinct plants within native yards—including both native and non-native plants—to the number of bird feeding observations. For the third and fourth analyses, we relativized bird-feeding observations to suppress several unusually high-feeding observations by plant species. Our overarching intention with the analyses in the third objective was to understand whether bird feeding behavior was targeted in native yards and on native plants—an indication of potential food-web benefits of native landscaping.

### RESULTS

# Objective 1—Patterns of habitat and avifauna in native and conventional yards

Habitat features generally varied substantially between native and conventional yards. Overall, native yards harbored a higher cover of native trees, shrubs, native shrubs, native herbaceous plants, and bare ground and leaf litter than conventional yards (Table 2). The only habitat variables that were greater in conventional yards were non-native shrub cover and lawn cover (Table 2). Neighborhood and geographic position variables were similar between yard groups (Table 2). All avifaunal metrics were  $1.5 \times$  to  $3.5 \times$  greater in native yards with natural lands bird abundance (Cohen's d = -1.13), total bird abundance (Cohen's d = -0.99), and total feeding observations (Cohen's d = -1.00) having the greatest effect sizes, indicating strong differences between native and conventional yards (Table 2). Bird composition was similar between native and conventional yards (ANOSIM R = 0.04, p = 0.17). However, the mean within-group dissimilarity rank for native yards (294) was roughly two times greater than conventional yards (143). This result suggested conventional yards were composed of a less diverse and more homogenous assemblage of species than what we observed in native yards. There were unsurprisingly strong differences in the dissimilarities of habitat features between native and conventional vards (ANOSIM R = 0.91, p < 0.01). Interestingly, the within-habitat ranks were similar for native (105) and conventional (108) yards, which indicated a similar species pool within groups that were strongly different between groups.

# Objective 2—Relationships between habitat and birds

Variables at all three spatial extents were important in describing avifaunal patterns. The top model for explaining bird abundance in natural lands was the

distance to the nearest urban greenspace ( $R_{kl}^2 = 0.23$ , p < 0.01; Table 3). The relationship was negative, indicating the closer a yard was to an urban greenspace, the higher the likelihood of an increased abundance of birds affiliated with natural landscapes (Figure 2a). The top model for explaining both urban and total bird abundance was the cover of native trees ( $R_{kl}^2 = 0.23$ , 0.29, p < 0.01, respectively; Table 3). Both relationships were positive, suggesting that native trees within yards attracted a variety of species from the species pool utilizing a particular neighborhood (Figure 2b,c). Bird richness was best described by the size of yards  $(R_{kl}^2 = 0.18,$ p < 0.01; Table 3), which was a positive relationship indicating a potential species-area effect (Figure 2d). Bird-feeding observations were best explained by a positive relationship with leaf-litter cover  $(R_{kl}^2 = 0.29,$ p < 0.01; Table 3), which may indicate the value of this habitat element to ground-foraging birds and potentially as a surrogate for the amount of tree and shrub foliage available to birds and their food resources in a vard (Figure 2e). Lastly, nonfeeding observations were best described by the % cover of trees at the neighborhood extent ( $R_{kl}^2 = 0.23$ , p < 0.01; Table 3). This result was positive (Figure 2f), which may suggest yards embedded within lush neighborhoods are potentially an important refuge for birds based on surrounding habitat conditions.

# Objective 3—Feeding and nonfeeding behavior by birds

Bird feeding behavior was concentrated in native yards, where both shrub and tree feeding observations were upwards of  $2-3 \times$  higher. The effect was stronger for birds feeding on shrubs in native than conventional yards (z = 0.73, p < 0.01) than bird-feeding observations on trees in native than conventional yards (z = 0.49, p = 0.02; Figure 3a,e). These findings suggest the potential importance of shrubs and trees in native yards in supporting a robust food web involving birds and their prey items. Moving further, there was a positive relationship between the percent cover of shrubs and bird-feeding observations on shrubs ( $R_{kl}^2 = 0.39$ , p < 0.01; Figure 3b), and this relationship was governed by the percentage of native shrubs, which was also a positive relationship  $(R_{kl}^2 = 0.37, p < 0.01;$  Figure 3c). There was a weak negative trend with the percent cover of non-native shrubs and bird-feeding observations ( $R_{kl}^2 = 0.08$ , p = 0.13; Figure 3d). Bird-feeding observations on trees were positively related to the percent cover of trees  $(R_{kl}^2 = 0.11)$ , p < 0.01; Figure 3f). Importantly, this relationship was driven primarily by the stronger positive relationship between bird-feeding observations on native trees

	Native		Conver	Conventional			
Variable	Mean	SD	Mean	SD	Cohen's d	z	р
Avifauna							
Natural-lands bird abundance	7.4	3.5	4.5	2.7	-1.13		0.001
Urban bird abundance	5.2	2.9	3.6	1.6	-0.52		0.065
Bird abundance	12.7	5.1	8	3.4	-0.99		0.002
Cumulative bird richness	5	2.8	3.8	2.3	-0.55		0.051
Feeding	5.8	5.2	1.7	1.9	0.75		0.004
Nonfeeding	8.6	5.5	5.9	5.3	-0.50		0.076
Parcel features and yard habitat (yard	l extent)						
Size of yard (m <sup>2</sup> )	162	102	184	123	0.29		0.276
Tree cover (%)							
Total	23.2	11.5	18.3	15.8	-0.24		0.375
Native	11.8	12.3	0	0		0.71	0.006
Non-native	11.4	14	18.3	15.8		0.32	0.208
Shrub cover (%)							
Total	61.1	17.5	17	8.8	-2.03		0.000
Native	56.9	17.3	0	0		1.04	0.000
Non-native	4.2	5.3	17	8.8		0.80	0.000
Herbaceous cover (%)							
Total	11.8	16.5	3	4.1		0.49	0.059
Native	9.5	16.1	0	0		0.75	0.004
Non-native	2.2	4.2	3	4.1		0.13	0.623
Bare-ground cover (%)	14.7	9.9	4	2.8		0.70	0.006
Leaf-litter cover (%)	11.3	10.1	1	2.1		0.82	0.001
Lawn cover (%)	1	3.8	67	31		0.82	0.002
Adjacent features and neighborhood	habitat <sup>a</sup>						
Land value (US\$, 200 m)	389 k	212 k	395 k	208 k	0.04		0.869
Tree cover (%, 200 m)	29	11.6	29.9	11.3	0.14		0.605
Grass cover (%, 200 m)	21.5	4.5	21.5	4.7	0.07		0.803
Bare soil (%, 200 m)	1.9	1.9	1.8	1.6	-0.22		0.407
Building (%, 200 m)	30.5	7.2	30.5	6.6	0		0.990
Paved (%, 200 m)	16	6.2	15.9	6.1	-0.10		0.702
Impervious surface (%, 200 m)	46.7	11.4	46.7	10.8	-0.04		0.891
Geographic position extent							
Distance-protected area (m)	3668	150	3799	163	0.04		0.868
Distance urban greenspace (m)	673	406	713	392	0.40		0.181

**TABLE 2** Results of paired *t* tests and Wilcoxon rank-sum tests comparing avifauna, parcel features and yard habitat, adjacent features, and neighborhood habitat, and the geographic position of yards between native-landscaped and conventionally landscaped yard pairs.

*Note*: The Cohen's *d* (parametric) or *z* scores (nonparametric) measure the effect size, with values further from zero indicating increased effect. <sup>a</sup>Neighborhood extent is 200 m.

 $(R_{kl}^2 = 0.36, p < 0.01)$ , as there was only a very weak trend for a negative relationship between bird feeding on trees and non-native tree cover  $(R_{kl}^2 = 0.05, p = 0.17;$ Figure 3g,h). Bird-feeding observations in native yards were higher on native than non-native plants (z = 0.49, p = 0.05; Figure 4a). Native plants that were relatively common, including *Quercus* spp., *Heteromeles* spp., *Arctostaphylos* spp.,

**TABLE 3** Results of Akaike information criterion (AIC) model selection relating six bird response variables to habitat variables at three extents: Parcel features and yard habitat (finest extent), adjacent features and neighborhood habitat (medium extent), and geographic position of the yards concerning the nearest protected area or urban park (broadest extent).

Models	Natural lands	Urban	Abundance	Richness	Feeding	Nonfeeding	
Intercept-only	8.76	14.24	12.87	6.19	13.30	9.96	
Parcel features and yard habitat (yard extent)							
Size of yard (m <sup>2</sup> )	5.52	12.83	8.39	0	12.88	2.56	
Tree cover (%)							
Total	10.41	10.33	11.75	2.85	14.86	4.80	
Native	4.31	0	0	0.97	9.41	7.07	
Non-native	9.72	16.20	14.02	8.47	13.74	11.98	
Shrub cover (%)							
Total	6.29	15.38	10.93	7.46	8.06	12.00	
Native	5.99	14.19	9.70	7.68	7.85	11.83	
Non-native	9.25	11.77	11.13	8.48	12.97	11.70	
Herbaceous cover (%)							
Total	9.70	16.56	14.53	8.14	15.58	11.64	
Native	9.76	16.56	14.50	8.32	15.56	11.77	
Non-native	11.02	16.53	15.18	8.17	15.61	12.17	
Lawn cover (%)	11.05	15.40	14.71	8.45	10.49	12.16	
Bare-ground cover (%)	5.16	11.15	6.83	2.58	13.38	9.27	
Leaf-litter cover (%)	6.89	14.61	10.69	7.42	0	11.88	
Adjacent features and neighborhood habitat <sup>a</sup>							
Land value (US\$, 200 m)	10.27	16.18	15.12	8.47	15.20	12.27	
Tree cover (%, 200 m)	5.94	15.58	10.95	2.34	14.55	0	
Grass cover (%, 200 m)	10.64	16.55	14.95	8.43	15.20	12.27	
Bare soil (%, 200 m)	10.88	16.20	15.18	8.30	15.18	11.23	
Building (%, 200 m)	4.54	14.72	9.09	2.73	13.28	1.51	
Paved (%, 200 m)	10.52	16.55	14.96	7.21	15.61	8.76	
Impervious surface (%, 200 m)	7.25	15.99	12.21	4.11	14.87	3.05	
Geographic position extent							
Distance-protected area (m)	10.25	16.40	14.51	6.15	14.23	5.98	
Distance urban greenspace (m)	0	16.54	10.31	4.59	12.79	10.86	

*Note:* Each column corresponds to a model set for model selection. Values are  $\triangle$ AIC values. The best-supported model has a  $\triangle$ AIC value of 0, with competitive models having values of  $\triangle$ AIC < 2. Bird response variables are as follows: Natural lands, natural lands bird abundance; urban, urban bird abundance; abundance, total bird abundance; richness, cumulative bird richness; feeding, the total number of feeding behavioral observations; nonfeeding, the total number of nonfeeding behavioral observations.

<sup>a</sup>Neighborhood extent is 200 m.

Salvia spp., and *Eriogonum* spp., comprised the bulk of the feeding observations, thus driving a strong positive relationship between the cover of plants—in particular, native plants—and bird-feeding observations ( $R_{kl}^2 = 0.61$ , p < 0.01; Figure 4b). Importantly, each of the aforementioned plants was preferred by birds when comparing their feeding "use" versus the "availability" patterns of the plants, suggesting the strong role each has in influencing bird feeding networks in native yards (Appendix S1: Table S3).

# DISCUSSION

Over the past few decades, it has become clear that residential yards (or gardens) are important habitats for biodiversity throughout the world—especially for animals during the breeding period (Gaston & Gaston, 2010; Goddard et al., 2010). Nevertheless, a key gap in our understanding of the importance of residential yards to wildlife was whether they hold the same value



**FIGURE 2** Scatterplots with fitted lines and confidence intervals (gray shading) of the best-supported generalized linear models  $(\Delta AIC = 0)$  based on model selection between birds and habitat and parcel features in yards landscaped with native plants (native) and conventionally landscaped yards (conventional). The  $R^2$  values are the Kullback–Leibler-divergence-based  $R_{kl}^2$  values generated from calculating the likelihood ratio index of a fitted model. AIC, Akaike information criterion.

during the nonbreeding period—a time of the year when animals have distinct requirements and behaviors. We contributed information to fill this gap by quantifying the critical role that native-plant landscaping plays in providing key resources for avifauna during the winter months in coastal southern California. Residential yards of our



**FIGURE 3** Boxplots characterizing the number of bird-feeding observations on (a) shrubs or (e) trees between yards landscaped with native plants (native) and conventionally landscaped yards (conventional). We also display scatterplots with fitted lines and confidence intervals (gray shading) of generalized linear model outputs depicting the relationship between bird-feeding observations and the (b) percent cover of shrubs, (c) native shrubs, (d) non-native shrubs, (f) trees, (g) native trees, and (h) non-native trees. The *z* values in (a) and (e) are a measure of the effect size based on a paired Wilcoxon rank-sum analysis. The  $R^2$  values in (b–d) and (f–h) are the Kullback–Leibler-divergence-based  $R_{kl}^2$  values generated from calculating the likelihood ratio index of a fitted model.



**FIGURE 4** (a) Boxplot characterizing the number of bird-feeding observations (relativized) between native and non-native plants and (b) a scatterplot with fitted line and confidence interval (gray shading) derived from a generalized linear model (negative-binomial error structure) depicting the relationship between bird-feeding observations (relativized) and the relative area of plants, colored by whether they were native or non-native. The *z* value in (a) is a measure of the effect size based on a Wilcoxon rank-sum analysis and the  $R^2$  value in (b) is the Kullback–Leibler-divergence-based  $R_{kl}^2$  value generated from calculating the likelihood ratio index of the fitted model.

LA study area that were landscaped with native plants harbored habitat features that superficially resembled natural areas of the region and supported a greater diversity and abundance of wintering migratory and resident birds—particularly birds affiliated with the natural terrestrial ecosystems of coastal southern California. Additionally, birds were positively associated with key habitat features of yards, including native shrubs and trees, and a high cover of leaf litter, which highlights the importance of "natural" habitat elements to birds that utilize urban ecosystems during the winter. Moving further, we found that bird feeding was highly concentrated in yards landscaped with native plants, suggesting a central role that native plants have in structuring urban food webs that involve birds. Native plants belonging to a handful of genera, including both trees (e.g., Quercus spp.) and shrubs (e.g., Heteromeles spp.), supported the bulk of bird feeding opportunities, indicating the importance of landscaping decisions in influencing avian communities. Our study adds to the growing body of evidence of the ecological benefits of native landscaping to wildlife in urban areas (Berthon et al., 2021; Burghardt et al., 2009; Goddard et al., 2017; Jimenez et al., 2022; Lerman & Warren, 2011; Narango et al., 2017; Pardee & Philpott, 2014) and highlights the value of native-plant landscaping to birds during the nonbreeding period.

One of the most evident findings of our work was the stark difference in habitat features and avian communities between native and conventionally landscaped vards. While not surprising, the native-landscaped yards of our study had a far greater cover of native trees, native shrubs, native herbaceous plants, bare ground, and leaf-litter cover, whereas conventional yards harbored greater non-native shrub and lawn cover. Our results were like those from St. Louis, Missouri, and Melbourne, Australia, where native yards had increased vegetation composition and complexity (Burr et al., 2018) and greater understory vegetation (Threlfall et al., 2017). Regarding avifauna, our work mainly supported our initial predictions regarding a higher abundance, richness, and feeding and nonfeeding behaviors by birds in native than conventional yards, and generally mirrored results from Arizona and southeastern Pennsylvania where native birds, including species of conservation concern, were positively correlated with yards harboring native plants (Burghardt et al., 2009; Lerman & Warren, 2011). The consistency of results from Arizona and Pennsylvania during the breeding season along with our southern California study during the nonbreeding period bolsters the idea that native yards provide important resources that support avian communities throughout the year, including conditions supporting their feeding and nonfeeding behaviors.

We expected that avian communities between native and conventional yards would strongly differ, and our results did not support this. Interestingly, however, the within-group bird composition of native yards was substantially more diverse than in conventional yards. Our findings suggested that birds in all yards were likely a part of a larger, neighborhood species pool. Yet, the differences in within-group composition, along with abundance, richness, and feeding and nonfeeding behaviors indicated an important filter that native yards have on structuring aspects of the avian community. Further, our results strongly point toward important homogenizing effects of conventional yards—likely due to the limited resources available to birds when compared with native yards. Our findings underscore that increasing native landscaping throughout a city would likely contribute to conditions supporting a more heterogenous mix of avifauna than in a city dominated by conventional yards.

Our analysis highlighted key habitat elements both within and adjacent to yards that were related to bird abundance, richness, and feeding and nonfeeding behavioral patterns. Overall, habitat within yards rather than in the neighborhood or geographic position extents was the strongest predictor of avifaunal patterns, suggesting the important effect yards have on influencing urban biodiversity. One of the clearest features of yards in LA that attracted birds were native shrubs and native trees. Shrubs are the main components of two of the most dominant natural ecosystems in the region, chaparral, and coastal sage scrub. Trees are the main components of several natural ecosystems in the region, including riparian and woodland ecosystems, where Platanus racemosa (western sycamore) and Quercus agrifolia are dominant. P. racemosa and Q. agrifolia and numerous native shrubs common in the environments surrounding LA were commonly planted in the native yards of our study system.

The linkage between the native plants and birds suggests an important ecological adaptation of birds associating with plants in yards that were formally common on the landscape before intense urbanization. Our findings, along with those of others that focused on native-plant landscaping in yards (e.g., Adams et al., 2020; Narango et al., 2017) suggest an important future avenue for urban ecological research in further uncovering the role of remnant vegetation-or planted vegetation that previously dominated a region-in urban areas in supporting biodiversity. In addition to native trees, our work detailed the importance of associated habitat elements such as leaf-litter cover in supporting feeding birds. Leaf-litter cover is a potential surrogate for the cover of shrubs and trees and an indication of an important substrate for ground-feeding birds such as White-crowned Sparrows (Zonotrichia leucophrys), a migratory bird that winters in LA that we frequently observed feeding in the leaf litter under native shrubs. In sum, the native-landscaped yards of our study provided a mixture of structural and composition diversity, which are critical resources to birds during the breeding period in urban areas (Adams et al., 2020; Burghardt et al., 2009; Lerman et al., 2012; Narango et al., 2017; Wood & Esaian, 2020)—and, based on our work, also during the nonbreeding period.

It is common to find a strong influence of the adjacent habitat and socioeconomic factors in structuring wildlife communities in both natural and urban settings (e.g., Adams et al., 2020; Cohen et al., 2022; Lerman & Warren, 2011; Pardee & Philpott, 2014; Wood et al., 2011). However, this was generally not the case in our system. Yards with native plants were generally in affluent locations of LA, and therefore the land values of our study parcels were not highly variable and not a strong predictor of avifaunal patterns. We note, however, that we originally did intend to identify native yards in both high- and low-income areas of LA, and this was challenging in low-income areas. This suggests there likely is a strong luxury-effect pattern in where native landscaping in cities occurs. But we were unable to test this in our system—something that could be an important future avenue of research.

Regarding the role of adjacent habitat in structuring residential yard avian communities, our findings supported those from Chicago, which also did not find that habitat features at the neighborhood extent were as influential as those in yards (Belaire et al., 2014). Nevertheless, one potentially important finding of our work was the effect of tree cover at the extent of the neighborhood in structuring nonfeeding bird behavior in yards, such as vocalizing or resting. In a similar study in Phoenix, yards within neighborhoods with more desert trees and shrubs supported more native bird richness (Lerman & Warren, 2011). Further, in Fort Collins, CO, human-sensitive bird species, which resemble species in our natural-lands group, were positively related to tree canopy cover surrounding survey locations within residential open spaces (Jimenez et al., 2022). Potentially yards embedded within lush neighborhoods are an important refuge for birds that may be exposed to increased predation pressure, for example, Cooper's Hawks (Accipiter cooperii) nesting in dense urban tree canopy (Boal & Mannan, 2007). Further, yards may act as a spillover habitat based on density-dependent competition, where birds may move from overly dense urban habitats-such as lush neighborhoods (Wood & Esaian, 2020)---into less dense habitats (Fernandez-Juricic, 2001). Regardless of the potential mechanisms as to why tree cover at the extent of the neighborhood was the strongest predictor of bird nonfeeding observations, our work suggested that native yards provided important habitat (e.g., structural complexity) that supported a high concentration of nonfeeding bird behaviors. Given that birds exert substantial energy during the nonbreeding period in finding cover (Greenberg & Marra, 2005), our findings uncovered another potentially important mode of refuge that native landscaping provides birds during the winter months.

A tenet from the theory of island biogeography is that species richness will be greater on larger islands that are closer to a mainland (Molles & Sher, 2018). This also appears to be the case in urban ecosystems where the size of greenspace is consistently one of the primary correlates of wildlife diversity in cities across the world (Beninde et al., 2015; Cohen et al., 2022; la Sorte et al., 2020). Further, desert birds surveyed in the suburbs in Phoenix where large desert tracts were nearby were more diverse, suggesting potential neighboring effects likely due to ease of dispersal (Lerman & Warren, 2011). Patterns of bird richness and abundance in native yards in LA also follow the general principles from island biogeography, where we found a positive effect of yard size on the avifaunal richness and a positive effect on the distance (or nearness) to urban greenspaces for birds of natural lands. Our findings on the positive effect of yard area on species richness follow a species-area curve (Molles & Sher, 2018). Species-area curves are a common pattern found in the natural world and appear important for characterizing residential yard biodiversity. The biological linkage with our findings regarding nearness to surrounding urban greenspaces likely follows the neighboring effects uncovered in Phoenix (Lerman & Warren, 2011). While these were two clear patterns in our data that supported our predictions, there is also cause for concern. Greenspace on private residences in the LA area has drastically decreased over the past few decades, due to the development of mega mansions and increased hardscape on lots that were previously otherwise vegetated (Lee et al., 2017). Our results suggest decreases in vard size, even if dominated by exotic plants, will likely have a negative effect on urban wildlife, which would be exacerbated in neighborhoods further from natural lands and open spaces.

The most important finding from our work was the strong and positive effect that native landscaping had on bird feeding behavior. During the winter nonbreeding period, it was abundantly clear that birds fed in higher frequencies in native-landscaped yards than in neighboring conventional yards. The underlying driver behind the high-feeding behavior was likely the cover of native trees and native shrubs. Moving further, distinct genera of plants were primarily responsible for supporting the majority of feeding that we observed, including a mixture of trees, for example, Quercus spp., and Sambucus spp., and shrubs, for example, Heteromeles spp., Arctostaphylos spp., Salvia spp., and Eriogonum spp. Native plants in residential yards are important for supporting a high diversity and abundance of invertebrate prey which numerous birds, including nearly all migratory birds of this study, use as a food resource. For example, in residential yards in Washington DC, native plants supported higher biomass of caterpillars (Lepidoptera) than non-native plants (Narango et al., 2017). Further, native plants were highly preferred as foraging substrates by Carolina Chickadees and the birds' selectivity for native plants increased in yards with a higher proportion of non-native plants

(Narango et al., 2017). Additionally, in a related study, residential yards dominated by non-native plants were related to lower clutch sizes of Carolina Chickadees (Narango et al., 2018), suggesting the strong influence native plants have on influencing both individuals and populations. The studies from Washington, DC, and ours from LA support the notion that native plants in residential yards support robust food webs involving invertebrate prey, among other food resources, and birds during both the breeding and nonbreeding periods of the annual cycle. While we did not measure food resource availability on native and non-native plants in our study, doing so, in addition to piecing together food-web networks in residential yards would be an important future direction to better understand how urban ecosystems influence animal populations while also targeting important plant species to promote for maximizing wildlife habitat in cities (Narango et al., 2020).

Urbanized areas contain many unusable features for numerous species of birds, including buildings, impervious surfaces, and roadways (e.g., van Doren et al., 2021). What is interesting, however, is that within cities there are habitats-whether at the scale of a tree (Wood & Esaian, 2020), a yard (Burghardt et al., 2009), or a park (Vasquez & Wood, 2022) that provide important resources to birds. We extend the value of native landscaping to birds in yards from the breeding period (e.g., Narango et al., 2017) to the nonbreeding period. Set upon a fabric of conventionally landscaped yards, native vards cover a small proportion of the cityscape but punch far above their weight in supporting avifauna. Increasing yard conversions could vastly improve the capacity of LA in supporting birds during the winter months, thus minimizing the impact of urbanization on the region's biodiversity. More specifically, our findings provided clear support for landscaping residential yards with a high coverage of native shrubs and trees. Based on our results (see Figures 3 and 4), landscaping yards with greater than 20% of native tree cover and 40% of native shrub cover including plant species that feeding birds preferred, including Quercus spp., Heteromeles spp., and Arctostaphylos spp., or other native trees and shrubs that are structurally diverse and provide food resources will have the greatest impact on avifauna during the winter months in our LA study area. For plant suggestions for a particular region in the United States, see the National Audubon Society (2019). Further, our work points toward including natural habitat elements within yards, such as leaf litter and locations of bare ground that provide a variety of conditions for avifauna. While we omitted yards with feeders and baths to better isolate the effect of plants on birds, there are numerous studies detailing the role that feeders and baths have on birds and people (e.g., Cox & Gaston, 2016; Dayer et al., 2019; Fuller et al., 2008; Galbraith et al., 2015; Greig et al., 2017). Overall, we recommend that if providing habitat for birds is a goal for residents in urban areas, converting conventional to native yards and utilizing native-plant landscaping in new residential developments or other public spaces (e.g., parks, libraries, parking lots) will be beneficial. Further, we recommend governing agencies at the city, county, state, and federal levels to continue, adopt, or develop incentive programs such as bewaterwise (bewaterwise.com, 2021) and education programs that promote the use of native-plant landscaping that supports wildlife.

#### AUTHOR CONTRIBUTIONS

Noriko L. Smallwood and Eric M. Wood conceived the research; Noriko L. Smallwood and Eric M. Wood designed the study; Noriko L. Smallwood conducted fieldwork and data development; Noriko L. Smallwood and Eric M. Wood analyzed data and produced figures; Noriko L. Smallwood and Eric M. Wood wrote and edited the manuscript.

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#### **CONFLICT OF INTEREST**

The authors declare no conflict of interest.

### DATA AVAILABILITY STATEMENT

Data (Wood, 2022) are available from Dryad: 10.5061/ dryad.b2rbnzsk8.

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### REFERENCES

- Adams, B. J., E. Li, C. A. Bahlai, E. K. Meineke, T. P. McGlynn, and B. V. Brown. 2020. "Local- and Landscape-Scale Variables Shape Insect Diversity in an Urban Biodiversity Hot Spot." *Ecological Applications* 30: 1–14.
- Akinnifesi, F. K., G. W. Sileshi, O. C. Ajayi, A. I. Akinnifesi, E. G. de Moura, J. F. P. Linhares, and I. Rodrigues. 2010. "Biodiversity of the Urban Homegardens of São Luís City, Northeastern Brazil." Urban Ecosystem 13: 129–46.
- Alberti, M., E. P. Palkovacs, S. des Roches, L. de Meester, K. I. Brans, L. Govaert, N. B. Grimm, et al. 2020. "The Complexity of Urban Eco-Evolutionary Dynamics." *BioScience* 70: 772–93.

- Angel, S., J. Parent, D. L. Civco, A. Blei, and D. Potere. 2011. "The Dimensions of Global Urban Expansion: Estimates and Projections for All Countries, 2000–2050." *Progress in Planning* 75: 53–107.
- Aronson, M. F. J., F. A. la Sorte, C. H. Nilon, M. Katti, M. A. Goddard, C. A. Lepczyk, P. S. Warren, 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.
- Aronson, M. F. J., C. H. Nilon, C. A. Lepczyk, T. S. Parker, P. S. Warren, S. S. Cilliers, M. A. Goddard, et al. 2016. "Hierarchical Filters Determine Community Assembly of Urban Species Pools." *Ecology* 97: 2952–63.
- Avolio, M., D. E. Pataki, G. D. Jenerette, S. Pincetl, L. W. Clarke, J. Cavender-Bares, T. W. Gillespie, et al. 2019. "Urban Plant Diversity in Los Angeles, California: Species and Functional Type Turnover in Cultivated Landscapes." *Plants, People, Planet* 2: 144–56.
- Avolio, M. L., D. E. Pataki, T. L. E. Trammell, and J. Endter-Wada. 2018. "Biodiverse Cities: The Nursery Industry, Homeowners, and Neighborhood Differences Drive Urban Tree Composition." *Ecological Monographs* 88: 259–76.
- Baldock, K. C. R., M. A. Goddard, D. M. Hicks, W. E. Kunin, N. Mitschunas, H. Morse, L. M. Osgathorpe, et al. 2019. "A Systems Approach Reveals Urban Pollinator Hotspots and Conservation Opportunities." *Nature Ecology and Evolution* 3: 363–73.
- Belaire, J. A., C. J. Whelan, and E. S. Minor. 2014. "Having Our Yards and Sharing Them Too: The Collective Effects of Yards on Native Bird Species in an Urban Landscape." *Ecological Applications* 24: 2132–43.
- Beninde, J., M. Veith, and A. Hochkirch. 2015. "Biodiversity in Cities Needs Space: A Meta-Analysis of Factors Determining Intra-Urban Biodiversity Variation." *Ecology Letters* 18: 581–92.
- Berthon, K., F. Thomas, and S. Bekessy. 2021. "The Role of 'Nativeness' in Urban Greening to Support Animal Biodiversity." *Landscape and Urban Planning* 205: 103959.
- bewaterwise.com. 2021. https://www.bewaterwise.com/.
- Billerman, S. M., B. K. Keeney, P. G. Rodewald, and T. S. Schulenberg. 2021. *Birds of the World*. Ithaca, NY: Cornell Laboratory of Ornithology.
- Blair, R. B. 1996. "Land Use and Avian Species Diversity along an Urban Gradient." *Ecological Applications* 6: 506–19.
- Boal, C. W., and R. W. Mannan. 2007. "Nest-Site Selection by Cooper's Hawks in an Urban Environment." *Journal of Wildlife Management* 62: 864–71.
- Burghardt, K. T., D. W. Tallamy, and W. Gregory Shriver. 2009. "Impact of Native Plants on Bird and Butterfly Biodiversity in Suburban Landscapes." *Conservation Biology* 23: 219–24.
- Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. "AIC Model Selection and Multimodel Inference in Behavioral Ecology: Some Background, Observations, and Comparisons." *Behavioral Ecology and Sociobiology* 65: 23–35.
- Burr, A., D. M. Hall, and N. Schaeg. 2018. "The Perfect Lawn: Exploring Neighborhood Socio-Cultural Drivers for Insect Pollinator Habitat." *Urban Ecosystem* 21: 1123–37.
- Callaghan, C. T., R. E. Major, J. H. Wilshire, J. M. Martin, R. T. Kingsford, and W. K. Cornwell. 2019. "Generalists Are the

SMALLWOOD AND WOOD

most Urban-Tolerant of Birds: A Phylogenetically Controlled Analysis of Ecological and Life History Traits Using a Novel Continuous Measure of Bird Responses to Urbanization." *Oikos* 128: 845–58.

- Cameron, A. C., and F. A. G. Windmeijer. 1997. "An R-Squared Measure of Goodness of Fit for some Common Nonlinear Regression Models." *Journal of Econometrics* 77: 329–42.
- Cannon, A. 1999. "The Significance of Private Gardens for Bird Conservation." *Bird Conservation International* 9: 287–97.
- City of Los Angeles. 2016. "Countywide Parks and Open Space." https://geohub.lacity.org/datasets/0eb692c964734202860a211 fa6bbbee8\_12/explore?location=34.158028%2C-118.042778 %2C10.86.
- Clark, C. J. 2017. "eBird Records Show Substantial Growth of the Allen's Hummingbird (*Selasphorus sasin sedentarius*) Population in Urban Southern California." *The Condor* 119: 122–30.
- Clarke, L. W., G. D. Jenerette, A. Davila, D. G. Jenerette, A. Davila, G. D. Jenerette, and A. Davila. 2013. "The Luxury of Vegetation and the Legacy of Tree Biodiversity in Los Angeles, CA." Landscape and Urban Planning 116: 48–59.
- Cohen, H., M. Egerer, S. S. Thomas, and S. M. Philpott. 2022. "Local and Landscape Features Constrain the Trait and Taxonomic Diversity of Urban Bees." *Landscape Ecology* 37: 583–99.
- Cox, D. T. C., and K. J. Gaston. 2016. "Urban Bird Feeding: Connecting People with Nature." *PLoS One* 11128: 845–58.
- D'Amour, C. B., F. Reitsma, G. Baiocchi, S. Barthel, B. Güneralp, K. H. Erb, H. Haberl, F. Creutzig, and K. C. Seto. 2017. "Future Urban Land Expansion and Implications for Global Croplands." *Proceedings of the National Academy of Sciences of the United States of America* 114: 8939–44.
- Daniels, G. D., and J. B. Kirkpatrick. 2006. "Does Variation in Garden Characteristics Influence the Conservation of Birds in Suburbia?" *Biological Conservation* 133: 326–35.
- Dayer, A. A., C. Rosenblatt, D. N. Bonter, H. Faulkner, R. J. Hall, W. M. Hochachka, T. B. Phillips, and D. M. Hawley. 2019.
  "Observations at Backyard Bird Feeders Influence the Emotions and Actions of People that Feed Birds." *People and Nature* 1: 138–51.
- DeGraaf, R. M. 2002. *Trees, Shrubs, and Vines for Attracting Birds.* Lebanon: University Press of New England.
- Elmqvist, T., M. Fragkias, J. Goodness, B. Güneralp, P. J. Marcotullio, R. I. Mcdonald, S. Parnell, et al. 2013. Urbanization, Biodiversity and Ecosystem Services: Challenges and Opportunities. New York: Springer.
- ESRI. 2016. Arc GIS 10.5.1. Redlands, CA: Environmental Systems Research Institute.
- Ethington, P. J., B. MacDonald, G. Stein, W. Deverell, and T. Longcore. 2020. *Historical Ecology of the Los Angeles River Watershed and Environs: Infrastructure for a Comprehensive Analysis.* Los Angeles, CA: Spatial Sciences Institute, University of Southern California.
- Faeth, S. H., C. Bang, and S. Saari. 2011. "Urban Biodiversity: Patterns and Mechanisms." Annals of the New York Academy of Sciences 1223: 69–81.
- Fattorini, S. 2011. "Insect Extinction by Urbanization: A Long Term Study in Rome." *Biological Conservation* 144: 370–5.
- Fernández-Juricic, E. 2001. "Density-Dependent Habitat Selection of Corridors in a Fragmented Landscape." *Ibis* 143: 278–87.

- Fiske, I. J., and R. B. Chandler. 2011. "Unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance." *Journal of Statistical Software* 43: 1–23.
- Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, et al. 2005. "Global Consequences of Land Use." *Science* 309: 570–4.
- Forman, R. 2014. *Urban Ecology: Science of Cities*. Cambridge: Cambridge University Press.
- French, K., R. Major, and K. Hely. 2005. "Use of Native and Exotic Garden Plants by Suburban Nectarivorous Birds." *Biological Conservation* 121: 545–59.
- Fuller, R. A., P. H. Warren, P. R. Armsworth, O. Barbosa, and K. J. Gaston. 2008. "Garden Bird Feeding Predicts the Structure of Urban Avian Assemblages." *Diversity and Distributions* 14: 131–7.
- Galbraith, J. A., J. R. Beggs, D. N. Jones, and M. C. Stanley. 2015. "Supplementary Feeding Restructures Urban Bird Communities." *Proceedings of the National Academy of Sciences of the United States of America* 112: e2648–57.
- Galvin, M., J. O'Neil-Dunne, D. H. Locke, and M. Romolini. 2016. "Los Angeles County Tree Canopy Assessment." https://digit alcommons.lmu.edu/cgi/viewcontent.cgi?article=1005&contex t=cures\_reports.
- Garrett, K. L., J. L. Dunn, and B. E. Small. 2012. *Birds of Southern California*. Olympia, WA: R.W. Morse Company.
- Gaston, K., and S. Gaston. 2010. "Urban Gardens and Biodiversity." In *The Routledge Handbook of Urban Ecology*, edited by I. Douglas, D. Goode, M. C. Houck, and R. Wang, 450–8. London: Routledge.
- Goddard, M. A., A. J. Dougill, and T. G. Benton. 2010. "Scaling Up from Gardens: Biodiversity Conservation in Urban Environments." *Trends in Ecology and Evolution* 25: 90–8.
- Goddard, M. A., A. J. Dougill, and T. G. Benton. 2013. "Why Garden for Wildlife? Social and Ecological Drivers, Motivations and Barriers for Biodiversity Management in Residential Landscapes." *Ecological Economics* 86: 258–73.
- Goddard, M. A., K. Ikin, and S. B. Lerman. 2017. "Ecological and Social Factors Determining the Diversity of Birds in Residential Yards and Gardens." In *Ecology and Conservation* of Birds in Urban Environments, edited by E. Murgui and M. Hedblom, 371–97. Cham: Springer.
- GoogleMaps, Digital image. 2019. *Street View*. http://www.googlemaps.com.
- Greenberg, R., and P. P. Marra. 2005. *Birds of Two Worlds: The Ecology and Evolution of Migration*. Baltimore, MD: Johns Hopkins University Press.
- Greig, E. I., E. M. Wood, and D. N. Bonter. 2017. "Winter Range Expansion of a Hummingbird Is Associated with Urbanization and Supplementary Feeding." *Proceedings of the Royal Society B: Biological Sciences* 284: 1–9.
- Grimm, N. B., S. H. Faeth, N. E. Golubiewski, C. L. Redman, J. Wu, X. Bai, and J. M. Briggs. 2008. "Global Change and the Ecology of Cities." *Science* 319: 756–60.
- Groffman, P. M., M. Avolio, J. Cavender-Bares, N. D. Bettez, J. M. Grove, S. J. Hall, S. E. Hobbie, et al. 2017. "Ecological Homogenization of Residential Macrosystems." *Nature Ecology* and Evolution 1: 1–3.
- Groffman, P. M., J. Cavender-Bares, N. D. Bettez, J. M. Grove, S. J. Hall, J. B. Heffernan, S. E. Hobbie, et al. 2014. "Ecological

Homogenization of Urban USA." Frontiers in Ecology and the Environment 12: 74-81.

- Güneralp, B., and K. C. Seto. 2013. "Futures of Global Urban Expansion: Uncertainties and Implications for Biodiversity Conservation." *Environmental Research Letters* 8: 014025.
- Higgins, L. M., G. B. Pauly, J. G. Goldman, and C. Hood. 2019. Wild LA: Explore the Amazing Nature In and Around Los Angeles. Portland, OR: Timber Press.
- Hope, D., C. Gries, W. Zhu, W. F. Fagan, C. L. Redman, N. B. Grimm, A. L. Nelson, C. Martin, and A. Kinzig. 2003. "Socioeconomics Drive Urban Plant Diversity." *Proceedings of* the National Academy of Sciences of the United States of America 100: 8788–92.
- Ives, C. D., P. E. Lentini, C. G. Threlfall, K. Ikin, D. F. Shanahan, G. E. Garrard, S. A. Bekessy, et al. 2016. "Cities Are Hotspots for Threatened Species." *Global Ecology and Biogeography* 25: 117–26.
- Jimenez, M. F., L. Pejchar, S. E. Reed, and M. R. McHale. 2022. "The Efficacy of Urban Habitat Enhancement Programs for Conserving Native Plants and Human-Sensitive Animals." *Landscape and Urban Planning* 220: 104356.
- Kowarik, I. 2011. "Novel Urban Ecosystems, Biodiversity, and Conservation." *Environmental Pollution* 159: 1974–83.
- la Sorte, F. A., M. F. J. Aronson, C. A. Lepczyk, and K. G. Horton. 2020. "Area Is the Primary Correlate of Annual and Seasonal Patterns of Avian Species Richness in Urban Green Spaces." *Landscape and Urban Planning* 203: 103892.
- Lee, S. J., T. Longcore, C. Rich, and J. P. Wilson. 2017. "Increased Home Size and Hardscape Decreases Urban Forest Cover in Los Angeles County's Single-Family Residential Neighborhoods." Urban Forestry and Urban Greening 24: 222–35.
- Legendre, P., and M.-J. Fortin. 1989. "Spatial Pattern and Ecological Analysis." *Vegetatio* 80: 107–38.
- Leong, M., R. R. Dunn, and M. D. Trautwein. 2018. Biodiversity and Socioeconomics in the City: A Review of the Luxury Effect. London: The Royal Society.
- Lerman, S. B., A. R. Contosta, J. Milam, and C. Bang. 2018. "To Mow or to Mow Less: Lawn Mowing Frequency Affects Bee Abundance and Diversity in Suburban Yards." *Biological Conservation* 221: 160–74.
- Lerman, S. B., D. L. Narango, M. L. Avolio, A. R. Bratt, J. M. Engebretson, P. M. Groffman, S. J. Hall, et al. 2021. "Residential Yard Management and Landscape Cover Affect Urban Bird Community Diversity across the Continental USA." *Ecological Applications* 31: e02455.
- Lerman, S. B., and P. S. Warren. 2011. "The Conservation Value of Residential Yards: Linking Birds and People." *Ecological Applications* 21: 1327–39.
- Lerman, S. B., P. S. Warren, H. Gan, and E. Shochat. 2012. "Linking Foraging Decisions to Residential Yard Bird Composition." *PLoS One* 7: e43497.
- Liu, M., and D. L. Swanson. 2015. "Stopover Duration, Movement Patterns and Temporary Home Ranges of Fall Migrant Yellow-Rumped Warblers Setophaga coronata in Native and Anthropogenic Woodlands of the Northern Prairie Region, USA." Journal of Avian Biology 46: 452–61.
- Locke, D. H., R. Roy Chowdhury, J. M. Grove, D. G. Martin, E. Goldman, J. Rogan, and P. Groffman. 2018. "Social Norms,

Yard Care, and the Difference between Front and Back Yard Management: Examining the Landscape Mullets Concept on Urban Residential Lands." *Society and Natural Resources* 31: 1169–88.

- MacKenzie, D. I., J. D. Nichols, K. H. Pollock, J. A. Royle, L. L. Bailey, and J. E. Hines. 2017. Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. San Diego, CA: Academic Press.
- Magle, S. B., M. Fidino, H. A. Sander, A. T. Rohnke, K. L. Larson, T. Gallo, C. A. M. Kay, et al. 2021. "Wealth and Urbanization Shape Medium and Large Terrestrial Mammal Communities." *Global Change Biology* 27: 5446–59.
- Marra, P. P., E. B. Cohen, S. R. Loss, J. E. Rutter, and C. M. Tonra. 2015. "A Call for Full Annual Cycle Research in Animal Ecology." *Biology Letters* 11: 20150552.
- Marra, P. P., C. E. Studds, S. Wilson, T. S. Sillett, T. W. Sherry, and R. T. Holmes. 2015. "Non-Breeding Season Habitat Quality Mediates the Strength of Density-Dependence for a Migratory Bird." *Proceedings of the Royal Society B: Biological Sciences* 282: 197–241.
- Marzluff, J. M. 2001. Avian Ecology and Conservation in an Urbanizing World. New York: Springer Science & Business Media.
- McKinney, M. 2002. "Urbanization, Biodiversity, and Conservation." BioScience 52: 883–90.
- McKinney, M. L. 2006. "Urbanization as a Major Cause of Biotic Homogenization." *Biological Conservation* 127: 247–60.
- McKinney, M. L. 2008. "Effects of Urbanization on Species Richness: A Review of Plants and Animals." Urban Ecosystem 11: 161–76.
- McKinney, M. L., and J. L. Lockwood. 1999. "Biotic Homogenization: A Few Winners Replacing Many Losers in the Next Mass Extinction." *Trends in Ecology and Evolution* 14: 450–3.
- Merckx, T., and H. van Dyck. 2019. "Urbanization-Driven Homogenization Is more Pronounced and Happens at Wider Spatial Scales in Nocturnal and Mobile Flying Insects." *Global Ecology and Biogeography* 28: 1440–55.
- Minnesota Department of Natural Resources. 2007. A Handbook for Collecting Vegetation Plot Data in Minnesota: The Relevé Method. Biological Report 92. St. Paul, MN: Minnesota Department of Natural Resources.
- Molles, M. C., and A. Sher. 2018. *Ecology: Concepts and Applications*, 8th ed. New York: McGraw-Hill Education.
- Mooney, H. A., and E. S. Zavaleta. 2016. *Ecosystems of California*. Berkeley, CA: University of California Press.
- Moule, E., and S. Polyzoides. 2005. "LA's Sharp Turn from Sprawl." https://mparchitects.com/site/thoughts/las-sharp-turn-sprawl.
- Narango, D. L., D. W. Tallamy, and P. P. Marra. 2017. "Native Plants Improve Breeding and Foraging Habitat for an Insectivorous Bird." *Biological Conservation* 213: 42–50.
- Narango, D. L., D. W. Tallamy, and P. P. Marra. 2018. "Nonnative Plants Reduce Population Growth of an Insectivorous Bird." *Proceedings of the National Academy of Sciences of the United States of America* 115: 11549–54.
- Narango, D. L., D. W. Tallamy, and K. J. Shropshire. 2020. "Few Keystone Plant Genera Support the Majority of Lepidoptera Species." *Nature Communications* 11: 1–8.
- National Audubon Society. 2019. "Plants for Birds." https://www. audubon.org/plantsforbirds.
- Norris, D. R., P. P. Marra, G. J. Bowen, L. M. Ratcliffe, J. A. Royle, and T. K. Kyser. 2006. "Migratory Connectivity of a Widely

Distributed Songbird, the American Redstart (*Setophage ruticilla*)." Ornithological Monographs 61: 14–28.

- Oksanen, J., B. F. Guillaume, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, et al. 2019. "Vegan: Community Ecology Package." R Package Version 2.5-4. https://cran. r-project.org/web/packages/vegan/index.html.
- Ossola, A., D. Locke, B. Lin, and E. Minor. 2019. "Yards Increase Forest Connectivity in Urban Landscapes." *Landscape Ecology* 34: 2935–48.
- Padullés Cubino, J., M. L. Avolio, M. M. Wheeler, K. L. Larson, S. E. Hobbie, J. Cavender-Bares, S. J. Hall, et al. 2020. "Linking Yard Plant Diversity to homeowners' Landscaping Priorities across the U.S." *Landscape and Urban Planning* 196: 103730.
- Padullés Cubino, J., J. Cavender-Bares, S. E. Hobbie, S. J. Hall, T. L. E. Trammell, C. Neill, M. L. Avolio, L. E. Darling, and P. M. Groffman. 2019. "Contribution of Non-native Plants to the Phylogenetic Homogenization of U.S. Yard Floras." *Ecosphere* 10: e02638.
- Pardee, G. L., and S. M. Philpott. 2014. "Native Plants are the Bee's Knees: Local and Landscape Predictors of Bee Richness and Abundance in Backyard Gardens." Urban Ecosystems 17: 641–59.
- Piano, E., C. Souffreau, T. Merckx, L. F. Baardsen, T. Backeljau, D. Bonte, K. I. Brans, et al. 2020. "Urbanization Drives Cross-Taxon Declines in Abundance and Diversity at Multiple Spatial Scales." *Global Change Biology* 26: 1196–211.
- Pickett, S. T. A., M. L. Cadenasso, J. M. Grove, C. H. Nilon, R. V. Pouyat, W. C. Zipperer, and R. Costanza. 2001. "Urban Ecological Systems: Linking Terrestrial Ecological, Physical, and Socioeconomic Components of Metropolitan Areas." *Annual Review of Ecology and Systematics* 32: 127–57.
- Pierson Doti, L., and L. Schweikart. 1989. "Financing the Postwar Housing Boom in Phoenix and Los Angeles, 1945-1960." *Pacific Historical Review* 58: 173–94.
- Pincetl, S., T. W. Gillespie, D. E. Pataki, E. Porse, S. Jia, E. Kidera, N. Nobles, J. Rodriguez, and D. A. Choi. 2019. "Evaluating the Effects of Turf-Replacement Programs in Los Angeles." *Landscape and Urban Planning* 185: 210–21.
- R Core Team. 2017. R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/.
- Reisner, M. 1987. Cadillac Desert: The American West and its Disappearing Water. New York: Penguin Books.
- Remsen, J. V., and S. K. Robinson. 1990. "A Classification Scheme for Foraging Behavior of Birds in Terrestrial Habitats." *Studies in Avian Biology* 13: 144–60.
- Robinson, S. K., and R. T. Holmes. 1982. "Foraging Behavior of Forest Birds: The Relationships among Search Tactics, Diet, and Habitat Structure." *Ecology* 63: 1918–31.
- Royle, J. A., and J. D. Nichols. 2003. "Estimating Abundance from Repeated Presence–Absence Data or Point Counts." *Ecology* 84: 777–90.
- Salisbury, A., J. Armitage, H. Bostock, J. Perry, M. Tatchell, and K. Thompson. 2015. "Enhancing Gardens as Habitats for Flower-Visiting Aerial Insects (Pollinators): Should we Plant Native or Exotic Species?" *Journal of Applied Ecology* 52: 1156–64.

- Schell, C. J., K. Dyson, T. L. Fuentes, S. des Roches, N. C. Harris, D. S. Miller, C. A. Woelfle-Erskine, and M. R. Lambert. 2020.
  "The Ecological and Evolutionary Consequences of Systemic Racism in Urban Environments." *Science* 369: eaay4497.
- Schwartz, M. W., J. H. Thorne, and J. H. Viers. 2006. "Biotic Homogenization of the California Flora in Urban and Urbanizing Regions." *Biological Conservation* 127: 282–91.
- Seto, K. C., M. Fragkias, B. Güneralp, and M. K. Reilly. 2011. "A Meta-Analysis of Global Urban Land Expansion." *PLoS One* 6: e23777.
- Seto, K. C., B. Guneralp, and L. R. Hutyra. 2012. "Global Forecasts of Urban Expansion to 2030 and Direct Impacts on Biodiversity and Carbon Pools." *Proceedings of the National Academy of Sciences of the United States of America* 109: 16083–8.
- Seto, K. C., R. Sánchez-Rodríguez, and M. Fragkias. 2010. "The New Geography of Contemporary Urbanization and the Environment." *Annual Review of Environment and Resources* 35: 167–94.
- Sillett, T. S., and R. T. Holmes. 2002. "Variation in Survivorship of a Migratory Songbird throughout its Annual Cycle." *Journal of Animal Ecology* 71: 296–308.
- Sperling, C. D., and C. J. Lortie. 2010. "The Importance of Urban Backgardens on Plant and Invertebrate Recruitment: A Field Microcosm Experiment." Urban Ecosystem 13: 223–35.
- Spotswood, E. N., E. E. Beller, R. Grossinger, J. L. Grenier, N. E. Heller, and M. F. J. Aronson. 2021. "The Biological Deserts Fallacy: Cities in their Landscapes Contribute More than We Think to Regional Biodiversity." *BioScience* 71: 148–60.
- Stein, E. D., S. Dark, T. Longcore, N. Hall, M. Beland, R. Grossinger, J. Casanova, and M. Sutula. 2007. "Historical Ecology and Landscape Change of the San Gabriel River and Floodplain." Page Southern California Coastal Water Research Project Technical Report.
- Tallamy, D. W. 2009. Bringing Nature Home: How You Can Sustain Wildlife with Native Plants. Portland, OR: Timber Press.
- Tallamy, D. W., D. L. Narango, and A. B. Mitchell. 2020. "Do Non-Native Plants Contribute to Insect Declines?" *Ecological Entomology* 46(4): 729–42.
- Threlfall, C. G., L. Mata, J. A. Mackie, A. K. Hahs, N. E. Stork, N. S. G. Williams, and S. J. Livesley. 2017. "Increasing Biodiversity in Urban Green Spaces through Simple Vegetation Interventions." *Journal of Applied Ecology* 54: 1874–83.
- van Doren, B. M., D. E. Willard, M. Hennen, K. G. Horton, E. F. Stuber, D. Sheldon, A. H. Sivakumar, J. Wang, A. Farnsworth, and B. M. Winger. 2021. "Drivers of Fatal Bird Collisions in an Urban Center." *Proceedings of the National Academy of Sciences of the United States of America* 118: e2101666118.
- Vasquez, A. V., and E. M. Wood. 2022. "Urban Parks Are a Refuge for Birds in Park-Poor Areas of Cities." *Frontiers in Ecology* and Evolution 10: 958572.
- Venables, W. N., and B. D. Ripley. 2002. *Modern Applied Statistics with S*, 4th ed. New York: Springer US.
- Watson, D. M. 2003. "The "Standardized Search": An Improved Way to Conduct Bird Surveys." *Austral Ecology* 28: 515–25.
- Wenzel, A., I. Grass, V. V. Belavadi, and T. Tscharntke. 2020. "How Urbanization Is Driving Pollinator Diversity and Pollination—A Systematic Review." *Biological Conservation* 241: 108321.

- Wolch, J. R., M. Pastor, and P. Dreier. 2004. Up Against the Sprawl: Public Policy and the Making of Southern California. Minneapolis, MN: University of Minnesota Press. 401 pp.
- Wood, E. 2022. "The Ecological Role of Native-Plant Landscaping in Residential Yards to Birds During the Nonbreeding Period." Dryad. Dataset. https://doi.org/10.5061/dryad. b2rbnzsk8.
- Wood, E. M., and S. Esaian. 2020. "The Importance of Street Trees to Urban Avifauna." *Ecological Applications* 30: 1–20.
- Wood, E. M., M. D. Johnson, and B. A. Garrison. 2010. "Quantifying Bird-Habitat Using a Relevé Method." *Transactions of the Western Section of the Wildlife Society* 46: 25–41.
- Wood, E. M., A. M. Pidgeon, C. Gratton, and T. T. Wilder. 2011. "Effects of Oak Barrens Habitat Management for Karner Blue Butterfly (*Lycaeides samuelis*) on the Avian Community." *Biological Conservation* 144: 3117–26.
- Wood, E. M. M., A. M. M. Pidgeon, F. Liu, and D. J. J. Mladenoff. 2012. "Birds See the Trees inside the Forest: The Potential Impacts of Changes in Forest Composition on Songbirds during Spring Migration." Forest Ecology and Management 280: 176–86.

- Zar, J. H. 1999. *Biostatistical Analysis*. Englewood Cliffs, NJ: Prentice-Hall.
- Zhang, D. 2022. "rsq: R-Squared and Related Measures." R Package Version 2.5. https://CRAN.R-project.org/package=rsq.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2011. *Mixed-Effects Models and Extensions in Ecology with R*. New York: Springer US.

#### SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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