

Historical racial redlining and contemporary patterns of income inequality negatively affect birds, their habitat, and people in Los Angeles, California

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ABSTRACT

The Home Owners' Loan Corporation (HOLC) was a U.S. government-sponsored program initiated in the 1930s to evaluate mortgage lending risk. The program resulted in hand-drawn "security risk" maps intended to grade sections of cities where investment should be focused (greenlined areas) or limited (redlined zones). The security maps have since been widely criticized as being inherently racist and have been associated with high levels of segregation and lower levels of green amenities in cities across the country. Our goal was to explore the potential legacy effects of the HOLC grading practice on birds, their habitat, and the people who may experience them throughout a metropolis where the security risk maps were widely applied, Greater Los Angeles, California (L.A.). We used ground-collected, remotely sensed, and census data and descriptive and predictive modeling approaches to address our goal. Patterns of bird habitat and avian communities strongly aligned with the luxury-effect phenomenon, where green amenities were more robust, and bird communities were more diverse and abundant in the wealthiest parts of L.A. Our analysis also revealed potential legacy effects from the HOLC grading practice. Associations between bird habitat features and avian communities in redlined and greenlined zones were generally stronger than in areas of L.A. that did not experience the HOLC grading, in part because redlined zones, which included some of the poorest locations of L.A., had the highest levels of dense urban conditions (e.g., impervious surface cover), whereas greenlined zones, which included some of the wealthiest areas of the city, had the highest levels of green amenities (e.g., tree canopy cover). The White population of L.A., which constitutes the highest percentage of a racial or ethnic group in greenlined areas, was aligned with a considerably greater abundance of birds affiliated with natural habitat features (e.g., trees and shrubs). Conversely, the Hispanic or Latino population, which is dominant in redlined zones, was positively related to a significantly greater abundance of synanthropic birds, which are species associated with dense urban conditions. Our results suggest that historical redlining and contemporary patterns of income inequality are associated with distinct avifaunal communities and their habitat, which potentially influence the human experience of these components of biodiversity throughout L.A. Redlined zones and low-income residential areas that were not graded by the HOLC can particularly benefit from deliberate urban greening and habitat enhancement projects, which would likely carry over to benefit birds and humans.

Keywords: avifauna, ethnicity, HOLC, Los Angeles, legacy effect, luxury effect, race, socioeconomic

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LAY SUMMARY

- Redlining was a racially biased investment and lending practice established in the 1930s and applied in 239 cities across the United States.
- The program was terminated in 1968 but has since been linked with strong segregation of human communities, wealth, and green amenities in cities nationwide.
- In Greater Los Angeles, California, redlining continues to be negatively related to avian community patterns, their habitat and the people who may experience them.
- Luxury-effect patterns, where biodiversity is positively associated with affluence, largely predicted avifaunal patterns in Greater Los Angeles.
- Legacy-effect patterns due to historical redlining also showed strong relationships and patterns of bird habitat and community composition, suggesting the practice is potentially a powerful force structuring contemporary urban avifauna and human communities.
- Careful yet deliberate action in urban greening could likely benefit birds and humans in redlined zones and other low-income areas of Greater Los Angeles.

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La discriminación racial histórica en la delimitación de zonas y los patrones contemporáneos de desigualdad de ingresos afectan negativamente a las aves, su hábitat y a las personas en Los Ángeles, California.

RESUMEN

La Corporación de Préstamos para Propietarios de Hogares (HOLC, por sus siglas en inglés) fue un programa patrocinado por el gobierno de EEUU, iniciado en la década de 1930, para evaluar el riesgo en la concesión de hipotecas. El programa resultó en la creación de mapas de “riesgo de seguridad” dibujados a mano, destinados a clasificar secciones de ciudades donde la inversión debería centrarse (áreas resaltadas en verde) o limitarse (zonas marcadas en rojo). Los mapas de seguridad han sido ampliamente criticados posteriormente por ser inherentemente racistas y se han asociado con altos niveles de segregación y niveles más bajos de comodidades verdes en ciudades de todo el país. Nuestro objetivo fue explorar los posibles efectos heredados de la práctica de calificación de HOLC en las aves, su hábitat y en las personas que podrían experimentarlos, en toda una metrópolis donde los mapas de riesgo de seguridad se aplicaron ampliamente, el Gran Los Ángeles, California (L.A.). Utilizamos datos recopilados en el terreno, obtenidos de forma remota y censales, junto con enfoques descriptivos y de modelado predictivo, para abordar nuestro objetivo. Los patrones de hábitat de las aves y de las comunidades de aves se alinearon fuertemente con el fenómeno del efecto de lujo, en el que las comodidades verdes fueron más sólidas y las comunidades de aves fueron más diversas y abundantes en las partes más ricas de L.A. Nuestro análisis también reveló posibles efectos heredados de la práctica de calificación de HOLC. Las asociaciones entre las características del hábitat de las aves y las comunidades de aves en las zonas marcadas en rojo y verde fueron generalmente más fuertes que en las áreas de L.A. que no experimentaron la calificación de HOLC, en parte porque las zonas marcadas en rojo, que incluían algunas de las ubicaciones más pobres de L.A., tuvieron los niveles más altos de condiciones urbanas densas, como la cobertura de superficie impermeable, mientras que las zonas marcadas en verde, que incluían algunas de las áreas más ricas de la ciudad, tuvieron los niveles más altos de comodidades verdes, como la cobertura de dosel arbóreo. La población blanca de L.A., que constituye el mayor porcentaje de un grupo racial o étnico en las áreas resaltadas en verde, se correspondió con una abundancia considerablemente mayor de aves afiliadas a características de hábitat natural (e.g., árboles y arbustos). Por el contrario, la población hispana o latina, que es dominante en las zonas marcadas en rojo, estuvo relacionada positivamente con una abundancia significativamente mayor de aves sinantrópicas, que son especies asociadas con condiciones urbanas densas. Nuestros resultados sugieren que la discriminación histórica en la delimitación de zonas y los patrones contemporáneos de desigualdad de ingresos están asociados con comunidades de avifauna distintas y con sus hábitats, lo que potencialmente influye en la experiencia humana de estos componentes de la biodiversidad en todo L.A. La delimitación de zonas marcadas en rojo y las áreas residenciales de bajos ingresos que no fueron calificadas por HOLC pueden beneficiarse especialmente de proyectos dirigidos al enverdecimiento urbano y a la mejora de hábitat, que probablemente a su vez beneficiarán a las aves y los humanos.

Palabras clave: avifauna, efecto de lujo, efecto heredado, etnicidad, HOLC, Los Ángeles, raza, socioeconómico

BACKGROUND

In 1933, the U.S Federal Home Loan Bank Board initiated a program named the Home Owners’ Loan Corporation (HOLC), which was intended to assist homeowners who were in default on their mortgages to avoid foreclosure as well as to identify prime areas for real estate investments (Hillier 2003, Aaronson et al. 2018, Mitchell and Franco 2018). The decline in homeownership during the Great Depression was a major concern for political and financial leaders as high homeownership rates in the U.S. were considered a cornerstone of American national identity and a bulwark against radicalism (Leuchtenberg 2009). Another aspect of the HOLC was to evaluate mortgage lending risk to stabilize the nation’s mortgage lending system, which was in disarray following the Great Depression (Mitchell and Franco 2018). To identify prime areas for lending, the HOLC hand drew “security risk” maps with four color-coded zones intended to indicate areas where investment, via lending, should be focused and where it should also be limited. The graded zones were colored green (“best,” HOLC grade = A), blue (“still desirable,” HOLC grade = B), yellow (“definitely declining,” HOLC grade = C), and red, which is the notion of redlining where areas were labeled as “hazardous” for lending (HOLC grade = D). The HOLC security risk maps were drawn and applied in 239 cities throughout the U.S. in the early to mid-portions of the 20th century before the practice was formally halted in 1968 when the Fair Housing Act was passed (Squires 1992).

It has been debated whether the HOLC security-risk maps were intended for secret use or whether they were planned to be shared and utilized by appraisers in making decisions regarding lending (Hillier 2003). Nevertheless, the drawn boundaries of the security maps were inherently racially

biased. The security maps were based on “Area Descriptions,” and the ratings of these descriptions were based, in part, on the race or ethnicity of the inhabitants rather than on the physical qualities or amenities of the neighborhoods (Ethington 2001). This was especially true for Black or African American communities, among other communities of color, and neighborhoods dominated by older and poorer households (Mitchell and Franco 2018). Despite the stated objectives of rescuing homeowners from default on their mortgages, the racially biased method of evaluating property values has been related to patterns of racial injustice and economic inequality in cities across the U.S. (Squires 1992, Rothstein 2017, Aaronson et al. 2018, Swope et al. 2022). For example, redlining is negatively correlated with numerous urban functions, including climate mitigation (Wilson 2020), public health (Krieger et al. 2020, Nardone et al. 2020b, d), subjection to freeway development (Stermon and Lukinbeal 2021), and uneven distribution of greenness (Locke et al. 2021, Nardone et al. 2021, Nowak et al. 2022, Burghardt et al. 2022) throughout most major cities in the U.S. It is important to note that redlining was one of the numerous forms of systemic racism that occurred throughout the 20th century in the U.S. (e.g., racial housing covenants, blockbusting, and single-family zoning; Sadler and Lafreniere 2017, Menendian et al. 2022) that continues to affect the structure of urban centers (Schell et al. 2020). Nevertheless, it remains uncertain whether the legacy of redlining is associated with the current distribution of urban wildlife and their habitat (Schell et al. 2020).

Our goal was to explore the potential legacy effects of the HOLC grading practice on birds, a ubiquitous component of wildlife, a provider of ecosystem services, and an indicator of biodiversity in most cities worldwide (Marzluff et al. 2001,

Whelan et al. 2008, Lepczyk et al. 2017), their habitats, and the people who may experience them throughout Greater Los Angeles, California (L.A.). We present our analysis as a case study, where we used the conceptual frameworks of the “luxury”- and “legacy-effect” hypotheses to test whether modern patterns of income inequality have led to stronger effects on L.A.’s avifauna and their habitat compared with historical patterns of disinvestment throughout the city. The luxury-effect hypothesis posits that there is a positive relationship between affluence and biodiversity in cities (Leong et al. 2018)—with a focus on green amenities (e.g., tree cover, Schwarz et al. 2015) and wildlife diversity and abundance (Wood and Esaian 2020). The luxury effect applies in many cities worldwide (Chamberlain et al. 2019, 2020) and is our baseline for measuring the potential legacy effects of redlining on urban biodiversity. The legacy-effect hypothesis suggests that environmental changes result from historical human activities (Schell et al. 2020). Legacy effects are common explanatory pathways for patterns found in natural communities (Foster et al. 2003) and have gained attention in urban ecosystems when focused on relationships between development patterns and biodiversity (Clarke et al. 2013, Grove et al. 2018, Ziter and Turner 2018). Our analysis was thus designed to understand whether avifauna, their habitat, and human communities in L.A. were related to the luxury effect and then if patterns and effects were stronger in redlined zones (legacy effects) due to the historical barriers to lending compared with sections of the city that the HOLC did not grade. We organized our analysis into the following five objectives.

Objective No. 1: Patterns of Residential Housing Variables, Urban Habitat, and Avifauna

We documented patterns of residential housing variables, urban habitat, and distributions of birds in the nonbreeding season, hereafter nonbreeding birds, related to the HOLC grading scheme in L.A. We also measured habitat and avifauna in non-graded zones throughout L.A. to compare the effects between the HOLC-graded zones and areas of the city that were not part of the practice. We predicted that there would be distinct bird habitat and avian communities, with greater green amenities in “best” and “still desirable” zones (hereafter A and B zones) compared with “definitely declining” and “hazardous” (or redlined) areas (hereafter C and D zones), which is in line with patterns found for tree cover across numerous cities in the U.S. (Hoffman et al. 2020, Namin et al. 2020, Locke et al. 2021, Nowak et al. 2022). Further, we predicted that habitat features and avifauna in non-graded affluent areas would align with A and B zones, and non-graded lower-income areas would align with C and D zones, following luxury-effect patterns in L.A. (Wood and Esaian 2020).

Objective No. 2: Relationships Between Residential Housing and Habitat Variables and Avifauna

We quantified relationships between a collection of residential housing and habitat variables and nonbreeding bird abundance with HOLC-graded and non-graded zones. We predicted that nonbreeding birds affiliated with natural ecosystems during the breeding period would be positively related to tree cover and street-tree density (Belaire et al. 2014, Wood and Esaian 2020), which would be greater in A and B

zones (Locke et al. 2021, Nowak et al. 2022) and non-graded affluent areas. Natural ecosystems refer to any non-urban terrestrial ecosystem which contains trees, shrubs, and grasses. The nonbreeding birds in our system, except for synanthropic species, typically breed in forests, woodlands, shrublands, or grasslands. We focus our habitat associations on the breeding period as most are well understood and carry over to the nonbreeding period (Billerman et al. 2021). Further, we predicted negative relationships with nonbreeding birds affiliated with natural ecosystems to built features of the urban landscape (e.g., building density; Lepczyk et al. 2008, 2017), which would be more common in C and D zones and non-graded low-income areas (Nardone et al. 2021). Lastly, we predicted synanthropic bird species would show opposite relationships due to their associations with human development (Marzluff 2001, Wood et al. 2014, 2015).

Objective No. 3: Predictions of Bird Abundance throughout Greater Los Angeles

We compared patterns from HOLC-graded and non-graded zones based on predictions of nonbreeding bird abundance throughout L.A. to understand how pervasive potential patterns are throughout the city. We predicted that C and D zones would harbor a higher predicted abundance of synanthropic species and a lower abundance of nonbreeding birds affiliated with natural ecosystems during the breeding period (e.g., forest-breeding birds), with opposite relationships for A and B zones, similar to our expectations for objective two. We also predicted that zones not part of the HOLC grading practice that are currently wealthy or poor would show similar patterns in predicted nonbreeding bird abundance to either A and B (assumed wealthy) or C and D (assumed poor) zones.

Objective No. 4: Human Population Patterns of Race and Ethnicity in Relation to HOLC Grading

Because redlining was a racist practice, we explored how race and ethnicity have shifted among HOLC-graded zones and non-graded areas from the 1940s, just after the HOLC practice went into effect in L.A., to the current time. We expected to find the White population to dominate in A and B zones and the Black and Hispanic or Latino population to dominate in C and D zones (Perry and Harshbarger 2019). Furthermore, we expected that race and ethnicity patterns would change drastically from the 1940s to the present, with the White population declining within the study area across time and the Hispanic or Latino population surging, following patterns from the decadal census (“US Census 2020” 2022) and detailed by Perry and Harshbarger (2019).

Objective No. 5: Relationships Between Race and Ethnicity and Urban Avifauna

We were interested in how the current racial and ethnic makeup of L.A. related to patterns of nonbreeding avifauna and habitat features. We generally expected to find differences in parcel land values, tree canopy coverage, and the distribution of distinct components of the nonbreeding avian community throughout L.A. concerning race and ethnicity, following patterns during the nonbreeding and breeding period from Phoenix, Arizona, a city with a similar demographic makeup (Kinzig et al. 2005, Lerman and Warren 2011). More specifically, we predicted that areas of L.A. with a greater proportion of the White population

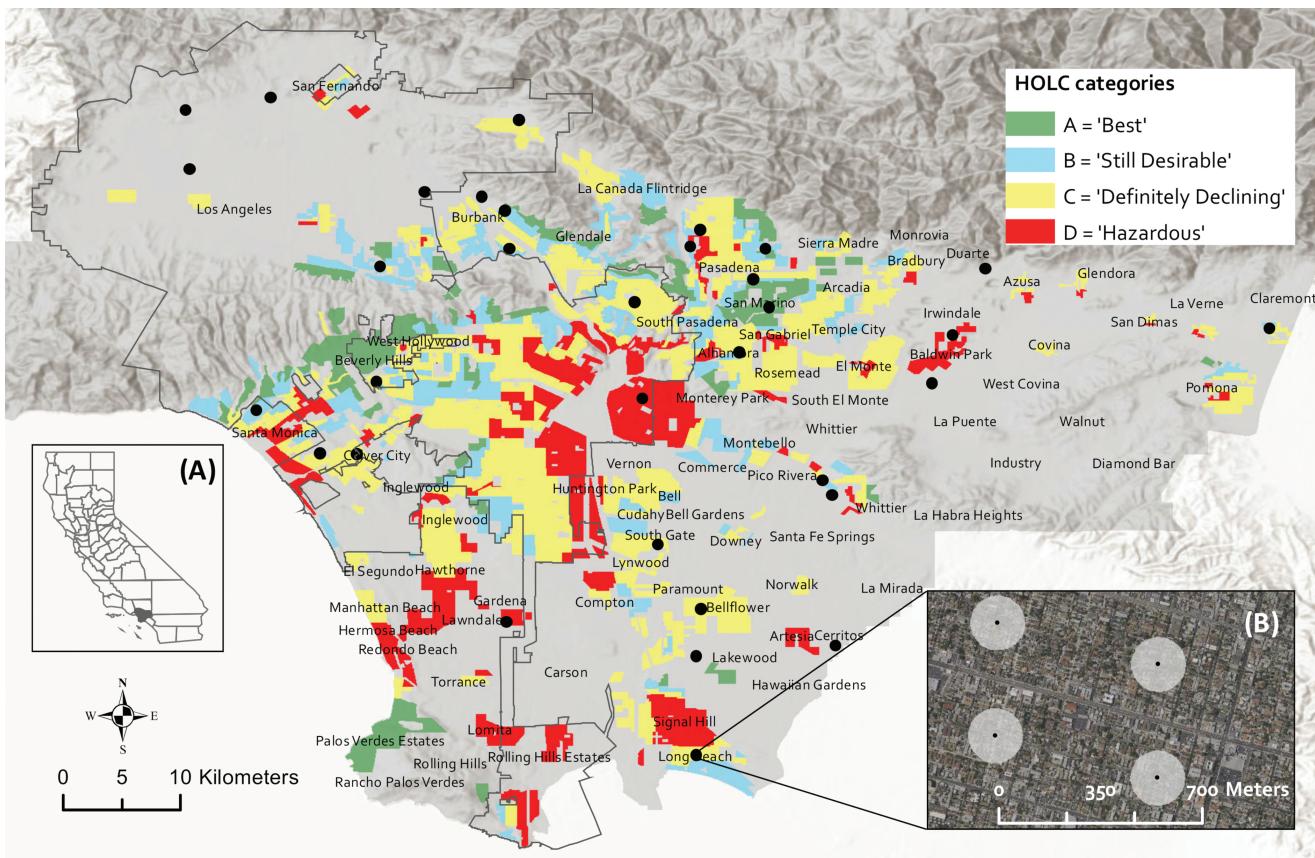


FIGURE 1. Distribution of 33 survey locations (black dots) within residential neighborhoods among HOLC-graded and non-graded zones across (A) Greater Los Angeles, CA. (B) The inset map depicts the sampling design at each survey location, where we established 4 locations, that were >350 m from one another for bird and habitat surveys.

would have higher parcel land values with greater tree coverage and subsequently harbor more nonbreeding birds associated with natural ecosystems during the breeding period (e.g., forest birds) than synanthropic birds. Additionally, we predicted that the Asian population, which generally has a high median household income in L.A. (Asante-Muhammad and Sim 2020), would show similar patterns as the White population. We expected opposite patterns for the Black or African American and Hispanic or Latino populations. Our expectations were derived from patterns of the distribution of urban forest cover and access to nature with race and ethnicity patterns in cities across the U.S. (Gerrish and Watkins 2018, Grade et al. 2022).

METHODS

Study Area and Sampling Design

To address objectives nos. 1 and 2, we used an established sampling design of bird and habitat survey locations in 33 residential communities throughout L.A. (Wood and Esaian 2020; Figure 1, Supplementary Material Figure 1). Within the 33 residential communities, we located four sample points > 350 m from one another ($n = 132$ total) for bird and habitat assessment (Figure 1). Because of potential issues with spatial autocorrelation, we aggregated bird, remote sensing, and street-tree data within each cluster of 4 sample points (see below). Twenty-four of the 33 clusters were in each of

the 4 categories of the HOLC security maps: A ($n = 3$), B ($n = 9$), C ($n = 8$), and D ($n = 4$). To address limitations in sample size, we combined data from zones A and B, as these were areas where lending was more likely and plentiful by the HOLC ($n = 12$, hereafter: AB). Additionally, we combined data from zones C and D, as these were areas where lending was historically limited ($n = 12$, hereafter: CD). We obtained spatial boundaries for the HOLC-graded zones from the “Mapping Inequality Project” at the University of Richmond (Nelson et al. 2020). Nine clusters were located in areas that were non-graded by the HOLC and were developed primarily in the 1960s (median parcel age, 1961). Parcels in the AB and CD zones were developed in the 1930s and 1940s (median parcel age, 1933 and 1943, respectively). The median housing price for parcels in the non-graded zones of our study in 2018 was \$644,000 USD, compared to \$607,000 for CD zones, and \$1,030,000 for AB zones (Redfin 2018). Thus, data from the 9 non-graded zones provided a measure of how newer developments on the lower socioeconomic spectrum compared with the AB and CD zones.

Data from 13 of our 33 aggregated point-count locations had conflicting overlapping boundaries with the spatial extents of the HOLC boundaries. For each aggregated set of HOLC and non-graded data, we assigned a designated HOLC grade based on the point-count locations that were embedded within. In three instances, we aggregated data from point-count locations that were within A and B zones; and in

another case, we combined data from point-count locations within C and D zones, which we deemed acceptable as we grouped these categories for analysis (see above). In 3 cases, we combined conflicting groups. In the first 2 cases, which included 1 cluster where there were 3 point-count locations in the B zone and one in the D zone of the San Rafael Hills and Rose Bowl sections of Pasadena, and another cluster in central Claremont with 3 point-count locations in the B zone and 1 point-count location in the C zone, we opted for combining in the AB category, as each area currently has high median income values (Wood and Esaian 2020). For the third cluster (Glendale, Riverside Rancho), 2 point-count locations fell within C-graded zones and 2 point-count locations were in B-graded zones but had overlapping 100-m radius boundaries with the C zones. We combined these point-count locations into the CD category. In 6 cases, we grouped data from non-graded zones with HOLC-graded zones. We did so because current conditions in the non-graded sections of neighborhoods superficially resembled those of the HOLC-graded sections. This happened in Baldwin Park where 1 point-count location was graded as D and 3 were non-graded. We categorized the Baldwin Park cluster in the CD category. There were 2 clusters in Whittier, where in 1 cluster, 3 point-count locations were graded as B and another was non-graded; whereas in the other cluster, 1 point-count location was graded as B and 3 were non-graded. We added the Whittier clusters to the AB category. In Carson, there was a cluster where 3 point-count locations fell within the D-graded zone with the fourth point-count location in a non-graded zone. In Southgate, 2 point-count locations of the cluster were graded as C, and 2 were non-graded; and in Venice, the cluster included 3 point-count locations that were graded as C and 1 that was non-graded. We added the Carson, Southgate, and Venice clusters in the CD category.

Residential Housing and Habitat Variables

To investigate the influence of residential housing and habitat features on avifauna, we used 3 data sources. First, we quantified habitat features remotely using a light detection and ranging (LiDAR) derived data product that yielded data on a suite of variables for every parcel in the L.A. region (hereafter: “parcel data”; Galvin et al. 2016). We considered 6 variables from the parcel data that characterized residential housing patterns, including the year parcels were built, the building density, the land value, the last sale amount, the number of bedrooms and bathrooms, and the square footage of parcels. Further, we included 5 cover variables that we expected would describe patterns of urban avifauna, including the % cover of the tree canopy, grass, impervious surfaces, buildings, and paved areas. For each variable, we computed the sum (building density), median (year parcels were built, the land value, the last sale amount, the number of bedrooms and bathrooms, and the square footage of parcels), or mean (cover variables) across all parcels within 100-m circular buffers of the 132 sample points, and then further aggregated using the sum, median, and mean as described above for the associated metrics within the 33 clusters. Our justification for our approach is that we first needed to compute the parcel data metrics within the range of our 100-m circular bird sampling locations. We then needed to match the extent of the predictor data with that of the aggregated bird data (see below).

Second, we included street-tree data from all sampling locations, which strongly affects bird-feeding behavior in L.A. (Wood and Esaian 2020). We measured the diameter at breast height of all street trees within sample points and the walking routes linking sample points (7,126) and identified each species as described in Wood and Esaian (2020). We then calculated relative street tree density, relative street tree dominance, and the importance values of all street tree species along a walking route (Wood et al. 2012). For further information on the street tree data used in this analysis, please refer to Wood and Esaian (2020). We used street-tree data along the walking routes linking sample points to generally capture street-tree conditions of the neighborhood where we completed bird surveys.

Third, we quantified the geographic position of sample points within L.A. to 6 green space features adjacent to and within the city. We determined the Euclidean distance using the *Near* tool in ArcGIS (ESRI 2016) from the centroid of each of the 33 clusters to the nearest (A) natural areas and wildlife sanctuaries (e.g., Angeles National Forest); (B) ecological sites (e.g., locations within Santa Monica Mountains); (C) regional parks and gardens (e.g., the Huntington Gardens); (D) golf courses; (E) cemeteries; and (F) beaches and marinas, assuming each may be influential in providing habitat for birds that may utilize residential areas in L.A. The distance variable for beaches and marinas was intended to generally capture climatic trends that may influence bird communities, whereas the other distance variables captured the geographic position in the city of sampling locations in relation to green spaces within and adjacent to L.A. We obtained boundaries for the green spaces from the “Countywide Parks and Open Space” layer, which are public data hosted by the County of Los Angeles (Los Angeles County 2016).

Avian Point Counts, Abundance Estimation, Habitat Guilds, and Richness Calculations

We conducted standardized 5-min 100-m radius point counts at the 132 sample points for 2 field seasons (2 visits per season) from October to March 2016–2018 (Ralph et al. 1995) to characterize the nonbreeding bird community in L.A. (Garrett et al. 2012). The data from 2016 to 2018 represent the training data for our spatial models (see below). We then revisited a subset of sample points ($n = 88$ sample points, $n = 22$ clusters) during the winter season of 2019–2020 as testing data for the spatial models (see below). We followed identical counting protocols for the testing and training data. One observer collected the training data (SE) and another the testing data (CB).

To account for detection probability, we calculated N-mixture models (Royle and Nichols 2003). We fitted the intercept-only N-mixture model, using the *pcount* function in the R package *unmarked* for 30 bird species, including individuals belonging to one family group (*Amazona* spp.) (hereafter, 31 species) (Fiske and Chandler 2011; Supplementary Material Table 1). We combined avian observation data for the training dataset across the 2 winter seasons for a database composed of 4 visits (2 per count season). 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 species included in this study were present and available for detection during the winter months throughout our

surveys. To account for potential season-to-season differences in species abundance in the training models, we allowed for detection probability to be estimated by a distinct intercept between seasons. From the intercept-only models, we then estimated the posterior distribution of latent abundance for the 31 candidate bird species at each sample point from either the training or testing datasets using empirical Bayes methods from the unmarked package function *ranef* (Fiske and Chandler 2011).

We computed the intercept-only estimated abundance, which we used in further analyses, for 3 reasons. First, our exploratory analyses indicated substantial overdispersion in fitted models, and thus we needed to use a negative binomial error structure. *N*-mixture models perform poorly when fit using negative binomial errors (Kéry 2018). Abundance was a key metric that we desired to model in our analysis. Therefore, we first estimated latent abundance in the *N*-mixture models using a Poisson distribution, from which we then used the abundance estimates as response variables in negative binomial generalized linear models (GLMs; see below). We display the errors of our models in **Supplementary Material Table 1**. Second, we desired to create avian habitat guilds based on the species-specific abundance estimates. We explored coding our data to sum counts of all individuals within a guild and then run the *N*-mixture models; however, this was a problem when considering further modeling routines due to the potential overdispersion in our data. Third, we desired species-specific estimates of the abundance of the avian community based on our count data (a matrix with rows as sample-point clusters and columns of the abundance values of each species), which we used in our multivariate analyses (see statistical analysis). We were unable to fit *N*-mixture models for 14 of the 31 species because detection probabilities were low (mean detection probability, $P = 0.05$) leading to unreliable estimates **Supplementary Material Table 1**. Nearly all the 14 bird species were common, synanthropic species that were essential to our analysis. Therefore, we included the raw abundance (unmodeled, high count across visits) for each **Supplementary Material Table 1**. The raw abundance data were highly correlated with the estimated abundance data ($r > 0.9$) for species in which we could fit the *N*-mixture models. Thus, when we present the bird abundance results, we refer to the *N*-mixture or raw abundance values summed among sample points within the 33 sample-point clusters.

To focus components of our analysis on segments of the bird community that may have variable responses to urban habitat features, we aggregated (total sum) the estimated abundance data from the 31 species into 7 groups: 4 habitat-specific groups (forest and woodlands [forest], shrub, natural lands, and synanthropes), 1 group based on geographic origin (exotic), and 2 groups based on migratory behavior (migratory or resident) (**Supplementary Material Table 2**). The forest and shrub birds are affiliated with forested or shrubland ecosystems during the breeding period (Allen et al. 2016, Billerman et al. 2021). We also created a composite variable called “natural-lands birds,” which was the summed values of the forest and shrub bird groups. The synanthropes are species affiliated with human development and commonly found throughout L.A. (Billerman et al. 2021). The exotic species are those with geographic origins outside our coastal Southern California study area (Billerman et al. 2021). Lastly, the migratory and resident birds are those that migrate from

L.A. to nesting locations farther north during the breeding period (migratory), or those that generally remain in the L.A. area throughout the year (resident) (Garrett et al. 2012, Allen et al. 2016, Billerman et al. 2021). In addition to abundance measures, we also computed cumulative species richness for all birds and each of the groups described above.

Race and Ethnicity Data

To quantify the spatial distribution of race and ethnicity throughout our study area, related to objectives nos. 4 and 5, we used 3 data sources. First, we incorporated race and ethnicity data for census tracts using a decadal census product from 1940 to 2000, which were based on the 2000 census tract outlines (Ethington et al. 2000). From these data, we quantified the percentage of the population within each census tract that was Black or African American (hereafter “Black”), Hispanic or Latino (hereafter “Hispanic”), or Non-Hispanic White (hereafter “White”), which were generally the racial or ethnic groups affected by the HOLC grading practice. We used race and ethnicity names given by the Office of Management and Budget Standards in the 2020 U.S. Census (U.S. Census 2022). To complete the time series from 2000 to 2020, we used 2 additional data sources. We incorporated comparable data (i.e., the percentage of the population of the race and ethnic groups described above from the 2010 census) with the 1940–2000 dataset (U.S. Census 2010). Lastly, we included additional data on the race and ethnicity groups from estimates derived from the American Community Survey (ACS) for 2015–2019 (“ACS,” U.S. Census 2020) as a measure of trends in census data towards 2020 (hereafter “2020 data”). In addition to focusing on the Black, Hispanic, and White populations, we included the Asian population from the ACS dataset to characterize the current and dominant race and ethnicity patterns in L.A. (U.S. Census 2020, 2022). For the 2010 and 2020 data, we merged boundaries using an intersect with the 2000 census tract outlines to compile a time series spanning from 1940 to 2020. Thus, the 1940 to 2020 time series were used in an analysis to characterize shifts in race and ethnicity in L.A. over the past 80 years, following the application of the HOLC security maps, the halting of the practice, and general immigration and emigration patterns of the city (see Statistical Analysis, objective no. 4). The 2020 data were used in exploring relationships between race and ethnic groups and bird and habitat variables (see Statistical Analysis, objective no. 5).

STATISTICAL ANALYSIS

Objective No. 1: Patterns of Residential Housing Variables, Urban Habitat, and Avifauna

To address our first objective of documenting patterns of residential housing variables, urban habitat, and bird distributions with regard to the HOLC grading scheme in L.A., we completed 3 analyses. First, we explored differences in the means or medians of the predictor and response variables among AB, CD, and non-graded zones. We used either a one-way analysis of variance (ANOVA) or a Kruskal–Wallis test, depending on whether assumptions for parametric models were satisfied, with the AB, CD, or non-graded groups as the categorical factor. When ANOVA or Kruskal–Wallis tests were significant, we conducted a multiple comparisons routine using

either a parametric Tukey Kramer or nonparametric multiple comparisons routine (*nparcomp* package in R; Konietschke 2011). We evaluated pairwise comparisons among groups using a Bonferroni-adjusted alpha value ($0.05/3 = 0.02$). We also computed parametric Cohen's d or non-parametric z -scores to quantify the effect sizes between pairwise comparisons (Zar 1999).

Second, to identify the degree of dissimilarity in residential housing and habitat variables and the bird community in relation to the redlining practice, we conducted a one-way analysis of similarities test (ANOSIM) (Oksanen et al. 2019), using the Bray–Curtis dissimilarity of the square-root transform of residential housing, habitat, and bird abundance data, grouped into AB, CD, and non-graded zones. The ANOSIM analyses assessed whether ranked dissimilarities of the residential housing and habitat variables and the bird community within the AB, CD, and non-graded zones were greater than among zones (Oksanen et al. 2019). 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 habitat and bird community variables did not differ among the AB, CD, and non-graded zones; whereas R -values farther from zero indicated increasing dissimilarity. Because we made 3 comparisons among the AB, CD, and non-graded zones, we used a Bonferroni adjustment to the alpha value of $0.05/3 = 0.02$ to assess significance. We computed the ANOSIM analysis using the *vegan* package (Oksanen et al. 2019) in R (R Core Team 2017). For all other analyses, we also used the R statistical software package. For graphics, we used either base R capabilities, *ggplot2* (Wickham 2016), or the *ggbubr* packages (Kassambara 2020) in conjunction with Adobe Illustrator software (Adobe Inc. 2019).

In a third analysis related to our first objective, to further quantify dissimilarities in the avian community among the AB, CD, and non-graded zones, we conducted a non-metric multidimensional scaling (NMDS) analysis. We used the Bray–Curtis dissimilarity of the square-root transform of the abundance data of the 31 bird species to compute an ordination graph of the 2-D representation of the avian community using the *vegan* package. Further, we overlaid residential housing and habitat vectors on the ordination using the *envfit* function in *vegan* to quantify general associations between the bird community and predictor variables (Oksanen et al. 2019). The *envfit* function assessed the correlation between residential housing and habitat vectors and avian species vectors with the first two axes of the ordination (Oksanen et al. 2019). The resulting output thus provided a measure of continuous change in the avian community concerning residential housing and habitat variables across the AB, CD, and non-graded zones.

Objective No. 2: Relationships Between Residential Housing and Habitat Variables and Avifauna

To address our second objective of quantifying relationships between residential housing and habitat variables and bird abundance in relation to redlining practices, we fit a series of linear regression models. We structured our analysis to understand the relationships between predictor and response variables both among and within AB, CD, or non-graded groups. To quantify the among-group relationships, we first fit 7 model sets, in which each set consisted of 1 of the 7 bird abundance response variable groups, 20 predictor variables,

and the intercept-only model. Many predictor variables were highly correlated (Supplementary Material Figure 2). We intended, however, to understand the strength of the relationship of each variable to bird abundance as all are important for urban ecological studies and city planning. Therefore, we included all predictors as univariate models in each set and compared them using the Akaike information criterion (AIC). We performed an identical analysis for the bird richness groups.

We assessed all assumptions of linear models, including normality, heteroscedasticity, and independence (Legendre and Fortin 1989, Zar 1999; Supplementary Material Figure 3). In a few cases, we transformed our predictor data using natural logarithmic transformations and refit models to adhere to model assumptions (e.g., normality of the residuals of a fitted model). For the shrub-bird abundance group, we could not meet assumptions for either linear models or Poisson GLMs due to overdispersion in our data. Thus we fitted models using negative binomial GLMs to account for the non-normal distribution of the residuals of fitted models (MASS package; Venables and Ripley 2002). We checked for overdispersion and the overall fit of the negative binomial models using chi-square (χ^2) goodness-of-fit tests, which revealed adequate fits. We fitted the models with a quadratic term when initial visualizations of model fit indicated hump-shaped patterns. To evaluate the fit of the models within each set relative to one another, we used a model-selection framework, with models having ΔAIC values < 2 indicating substantial support (Burnham and Anderson 2002).

To quantify the within-group relationships, we fit a similar set of models where we included the interaction term between a predictor variable, a response variable, and the AB, CD, and non-graded zones as groups. The purpose of the within-group analysis was to understand whether relationships were similar between a predictor and response variable (similar slopes) among the 3 groups. If we detected similar slopes, especially between CD and non-graded zones, this would provide support that the CD and non-graded zones yielded similar data, and thus fail to provide support for legacy-effect patterns concerning redlining. In visual inspections of our within-group data, there were no instances that suggested quadratic fits or the application of GLMs. Similar to the among-group analysis, we assessed all assumptions for each model.

Objective No. 3: Predictions of Bird Abundance Throughout Greater Los Angeles

To address our third objective of comparing patterns of bird abundance from HOLC-graded and non-graded zones, we created spatial predictions of bird abundances for the forest- and synanthropic-bird groups. We focused on abundance patterns as they were similar yet stronger than richness patterns (see results). Forest-bird abundance was correlated with the natural lands ($r = 0.95$), shrub ($r = 0.66$), and migratory-bird group abundances ($r = 0.92$, all $P < 0.01$). Synanthropic-bird abundance was correlated with exotic ($r = 0.70$) and resident-bird abundances ($r = 0.70$, both $P < 0.01$).

To create the spatial predictions, we developed area-weighted averages of the land value and tree cover of all parcels within a 200-m buffer centered on the centroid of each parcel, assigning the average values to the center parcel ($n = 1,377,068$ parcels). We focused on the parcel land-value data because this variable directly measured the luxury effect and

possible disparities in affluence among HOLC-graded zones. Furthermore, parcel land value was the top predictor for the forest-bird guild and highly correlated with the top variable for the synanthropic-bird group, which was parcel square footage ($\rho = 0.82$, $P < 0.01$) (see results). We also included the percent tree cover because this is a common variable of focus in other redlining and urban vegetation studies (Locke et al. 2021, Nowak et al. 2022). We used the 200-m buffers of each parcel because our bird surveys encompassed four sample points with 100-m radius circles, which cover an area of $A = 125,664 \text{ m}^2$. The area of a 200-m radius circle is identical ($A = 125,664 \text{ m}^2$), thus providing an appropriate match for our spatial predictions given our field sampling design. Our approach was similar to a moving window analysis in smoothing unusually high or low parcel values within the dataset while quantifying the average land and tree cover values within residential zones of L.A. We then created a prediction for forest- and synanthropic-bird abundances for every parcel, using the coefficients from a multiple linear regression model including both land value and percent tree cover as predictor variables regressed against forest- or synanthropic-bird abundance, and wrote the outputs of each model prediction for every parcel to a shapefile for analyses. Tree-canopy cover and land value were moderately correlated ($r = 0.54$, $P < 0.01$). However, we included both in the multiple regression given the substantial amount of variation that was uncharacterized. For the forest-bird abundance model, the adjusted R^2 was 0.72, $P < 0.01$, and for the synanthropic-bird abundance model, the adjusted R^2 was 0.56, $P < 0.01$. We completed all spatial data processing steps using the *sf* package in R (Pebesma 2018).

Following the creation of the spatial predictions, we quantified the average predicted abundances of each bird group within graded zones of the redlining practice (A, B, C, and D), as well as high-, medium-, and low-income areas of non-graded zones. We used census tracts based on the 2000 census boundaries (see methods, Race and ethnicity data) to delineate a spatial reference boundary for the high-, medium-, and low-income non-graded areas. We then quantified the average land value of all parcels within census tracts that were not part of the HOLC grading criteria and then calculated the lower, middle, and upper 33% of the parcel land value. We then performed ANOVA analyses of the average predicted bird abundances among the HOLC grading criteria as well as high-, medium-, and low-income non-graded zones. The purpose of this analysis was to understand whether HOLC-graded zones across L.A. consistently harbored distinct avian communities and whether potential patterns were similar to non-graded high- and low-income areas of the city. This analysis is in line with objective no. 1 and our expectations regarding the luxury- and legacy-effect hypotheses but is designed to assess the influence of redlining across the entirety of L.A.

To validate our predictive maps, we used the testing dataset (see avian counts) (Guisan and Zimmermann 2000). At each of the $n = 88$ sample points, we calculated the abundance of forest and synanthropic birds following identical methods to the training dataset. We then aggregated these data (summed abundances) within each cluster for a sample size of 22. We then extracted the predicted forest- and synanthropic-bird abundances based on the spatial models at all 88 sample-point locations and averaged the predicted values within clusters. While it is customary to use testing data that are

spatially distinct from training data, our approach provided a measure of the model error, across seasons, and thus an adequate validation of the predictive maps. We completed 2 analyses comparing predictions to the abundance estimates from the testing data. First, we calculated a chi-square analysis, comparing observed and predicted data (Guisan and Zimmermann 2000). Second, we fitted Pearson's correlations of observed and predicted data (Guisan and Zimmermann 2000). For the chi-square analysis, a P -value of >0.05 would indicate that the expected outcome of the observed and predicted data were similar providing support for the model predictions. Further, if we noticed significant correlations with a similar positive slope between observed and predicted data, we assumed that the spatial predictions adequately characterized bird abundance patterns (Guisan and Zimmermann 2000).

Objective No. 4: Human Population Patterns of Race and Ethnicity in Relation to HOLC Grading

To address our fourth objective of understanding how race and ethnicity have shifted among HOLC-graded zones and non-graded areas since the 1940s, just after the HOLC practice went into effect in L.A., to 2020, we completed 2 analyses. First, we used linear mixed models to quantify the shift in the proportion of the Black, Hispanic, or White populations in the HOLC-graded and non-graded zones. We fitted the linear mixed models, with year as an ordinal fixed factor, the percentage of a racial or ethnic group within a census tract as a continuous response variable, and the census tract number as a random effect, which allowed for a random shift in the intercept based on the repeated sampling at a census tract across years. To align census tract boundaries with HOLC-graded zones, we used an intersect of the 2000 census tract boundaries with the HOLC boundaries. Our resolution for analyses related to objectives nos. 4 and 5 was the census-tract boundary; thus if there were multiple HOLC-graded polygons within a given census tract, we assigned a HOLC grade based on the security-risk map category covering the most area within a census tract boundary. To compare pairwise differences in the percentage of the population that was a given race or ethnicity between decadal time steps, in a forward direction (e.g., 1940 to 1950, etc.), we computed the least-squares means of the percentage data based on the estimates from the linear mixed model analysis, and subsequently computed a Tukey-Kramer test. We fitted the mixed models and the P -values using the *lmer* and *lmerTest* packages (Bates et al. 2015, Kuznetsova et al. 2017), and the least-squares means and Tukey-Kramer test using *lsmeans* (Lenth 2016).

Second, we fitted ANOVA models to compare differences in the mean percentage of a racial or ethnic group within HOLC categories and non-graded zones based on 2020 census data. If ANOVA models were significant, we fitted a Tukey-Kramer test to quantify pairwise comparisons of race and ethnicity among HOLC and non-graded zones. We checked all assumptions for fitted models, which indicated parametric models were appropriate. Our intention with this analysis was to understand which segments of the human population currently reside in HOLC and non-graded zones. As we made nine pairwise comparisons in the Tukey-Kramer analysis, we used a Bonferroni adjusted P -value of $0.05/9 = 0.006$ to assess significance.

Objective No. 5: Relationships Between Race and Ethnicity and Urban Avifauna

To address our fifth objective, in which we sought to test the relationship between the current racial and ethnic make-up of L.A. and the patterns of avifauna and residential housing and habitat features, we completed 2 analyses. First, we compared patterns of parcel land values, tree canopy cover, and forest- and synanthropic-bird abundance among racial and ethnic groups. Because many census tracts in L.A. are composed of a highly diverse human population, we computed the majority of a racial or ethnic group within each census tract (>55% of the population) and assigned whichever race or ethnic group was the majority to that census tract. If there was no majority >55% in a census tract, we omitted that census tract from this analysis. We then used ANOVA and Tukey-Kramer analyses, to test for patterns in the means and variances of the predictor variables among racial and ethnic groups within the categorized census tracts.

Second, we fitted negative binomial GLMs including the predictor variables of the percentage of the Asian, Black, Hispanic, or White population in a census tract from the 2020 census data regressed against the response variables of predicted forest- or synanthropic-bird abundance (average values within census tracts). Like our objective two regression analysis, we completed this analysis both among- and within-HOLC categories. For the within-HOLC category analysis, many of the fitted relationships required quadratic terms. Thus, due to complications with fitting interactions with quadratic functions, we omitted this approach from our analysis and instead simply explored general similarities in the slopes and model fits within the HOLC categories for each racial or ethnic group. For both among and within HOLC-category analyses, we checked for overdispersion between fitted Poisson and negative binomial regression models and chose the latter which was appropriate for our dataset. We calculated R^2 values using the Kullback-Leibler-divergence-based R_{KL}^2 values, which were generated from calculating the likelihood ratio index of fitted models (Cameron and Windmeier 1997). Further, if there were apparent hump-shaped effects in the among-group models from initial inspections of scatterplots, we fitted models including a quadratic term.

RESULTS

Objective No. 1: Patterns of Residential Housing Variables, Urban Habitat, and Avifauna

The residential housing and habitat variables associated with income and greenness were strongly skewed towards the AB zones (Figure 2). Outside of building density, which was significantly greater in CD than in AB zones, the land value, the last sale price, the number of bedrooms and bathrooms, and the square footage of parcels were all roughly two times greater in AB than in CD zones (Table 1, Figure 2A and B). Like the bird-response data, the non-graded zones were generally similar to the CD zones, indicating in some cases that patterns associated with contemporary income levels can resemble those from the HOLC-graded zones. The notable exception was the square footage of homes, which was 22% smaller in CD zones than in non-graded zones indicating that newer developments on the lower-income side were larger, whereas parcels in CD zones were the smallest in all of L.A.

Distance variables to the green habitat features, including natural areas and wildlife sanctuaries, ecological sites, regional parks and gardens, golf courses, cemeteries, and beaches and marinas were not significant among zones. However, the percentage of tree cover was significantly greater in AB than in CD and non-graded zones (30% greater; Table 1, Figure 2C); whereas the cover of impervious surfaces, buildings, and pavement was upwards of 30% greater in CD and non-graded zones (Table 1, Figure 2D). Street-tree variables trended towards higher values in AB zones (upwards of 24% greater) (Table 1).

Forest, shrub, natural lands, and migratory birds trended towards greater abundance in AB than in CD or non-graded zones (Table 1, Figure 2E, Supplementary Material Table 3). Forest birds were upwards of 24% more abundant in AB zones; whereas migratory birds were 17% more abundant, followed by natural lands (15%) and shrub birds (8%) (Table 1). Compared with AB zones, the most abundant birds in the CD and non-graded zones were synanthropic (upwards of 22% greater abundance), exotic (38%), and resident (11%) species (Table 1, Figure 2F). Importantly, we detected greater effect sizes for synanthropic and exotic birds in CD than in non-graded zones when compared with AB zones (Table 1, Figure 2F).

Bird richness patterns somewhat mirrored abundance patterns with a few notable exceptions (Table 1). The richness of synanthropic birds was similar across AB, CD, and non-graded zones, suggesting that L.A. can generally be characterized by a similar synanthropic bird community throughout, though with highly variable abundance patterns depending on location in the city. Importantly, however, the richness of natural-lands birds was greater in AB zones, suggesting these residential communities provide amenities that attract species affiliated with natural ecosystems (Table 1).

Bird composition was significantly dissimilar among AB, CD, and non-graded zones (ANOSIM $R = 0.14$, $P < 0.01$). This pattern was primarily driven by more substantial dissimilarities in the bird community between AB and CD zones (ANOSIM $R = 0.26$, $P < 0.01$), followed by a weaker dissimilarity of avifauna between AB and non-graded zones (ANOSIM $R = 0.09$, $P = 0.10$). Avian communities were similar between CD and non-graded zones (ANOSIM $R = 0.04$, $P = 0.21$), whereas predictor variables were similar across AB, CD, and non-graded zones (ANOSIM $R = 0.04$, $P = 0.18$). The mean ranked within-group dissimilarity was greatest in AB zones (337) and was 1.9 times greater than in CD (179.5) and 2.4 greater in non-graded zones (139.5) (Figure 3). The greater within-group dissimilarity for survey locations within the AB zones suggested a broader composition of bird species among the AB residential communities. The CD and non-graded zones were often in valley locations that have been heavily developed, and therefore, potentially harbor a narrower range of species acclimated to the dense urban areas.

The NMDS analysis revealed important distinctions in residential housing and habitat variables and avian communities among HOLC-graded and non-graded zones (Figure 3). Overall, axis 1 characterized a gradient of affluence. The affluence gradient was positively associated with AB zones and negatively with CD and non-graded low-income zones. Bird species aligned predictably with this gradient, with forest and shrubland species, positively associated with AB zones and likely attracted to the larger lot sizes and denser green

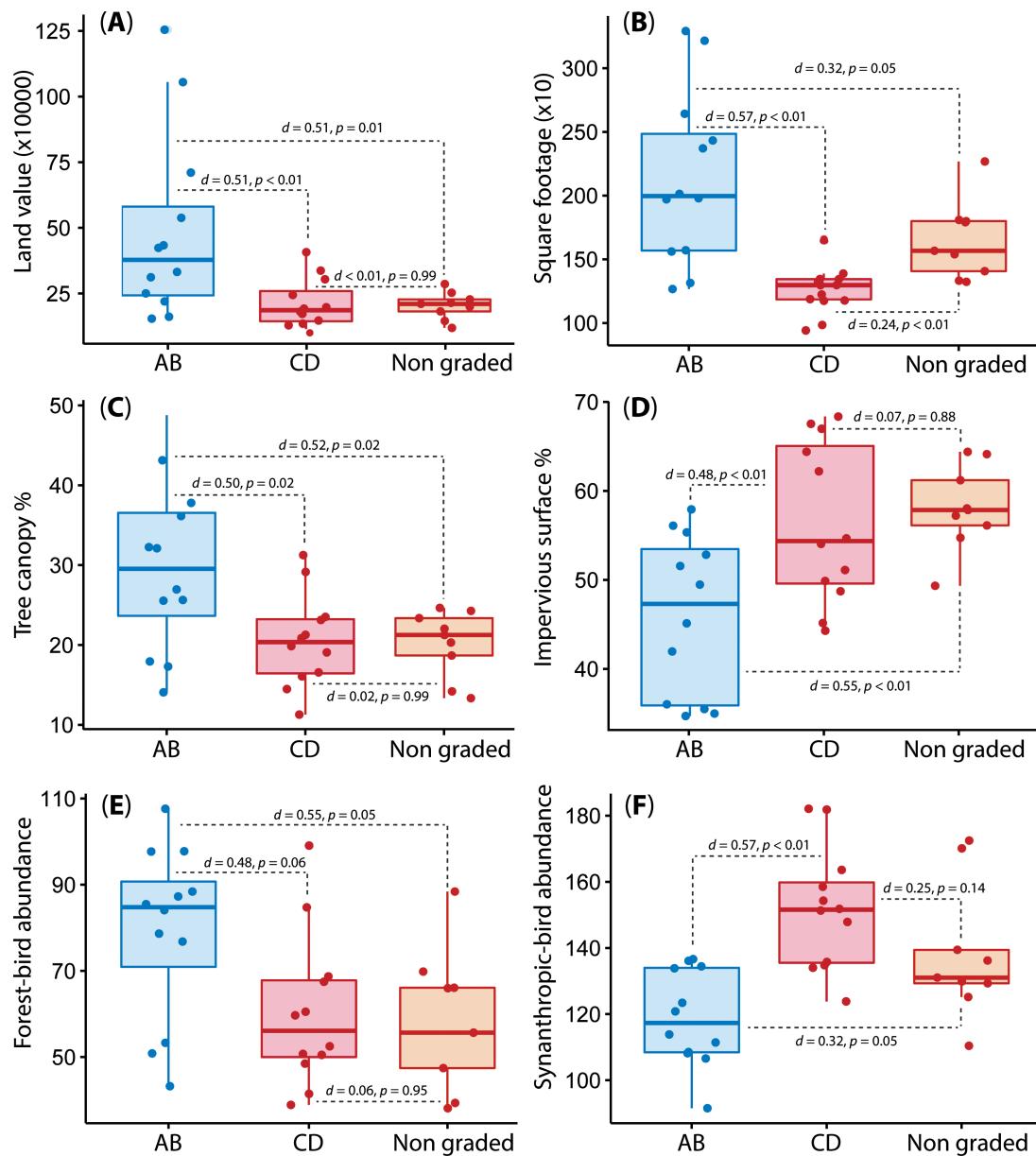


FIGURE 2. HOLC-graded AB zones (best and still desirable) contained a higher abundance of (A) forest birds, a lower abundance of (B) synanthropic birds, greater (C) land values, larger (D) parcels (square footage), higher (E) tree canopy cover, and lower (F) impervious surface cover than HOLC-graded CD (definitely declining and hazardous) and lower-income non-graded zones. These data are from field-collection (bird) and remote sensing efforts (residential housing and habitat cover variables) at 33 residential community locations within the HOLC-graded and non-graded zones throughout L.A. The d scores are Cohen's d values and are a measure of effect size. Values further from zero indicate an increasing effect. The P -values were computed based on a Tukey's post hoc test following a significant one-way analysis of variance test.

cover—both in street trees and yard vegetation. On the other hand, synanthropic species were affiliated with dense urban conditions (i.e., the CD zones and ungraded low-income zones; Figure 3). There were fewer notable patterns with axis 2, which somewhat characterized a gradient of affluence as well as geographic position in the city (Figure 3)

Objective No. 2: Relationships Between Residential Housing and Habitat Variables and Avifauna

The top-fitting model for explaining patterns of bird abundance among HOLC categories was overwhelmingly parcel land value, which was the top model in 5 of the 7 model sets (Supplementary Material Table 4). Parcel land value was

strongly and positively related to the abundance of forest, shrub, natural lands, and migratory birds, and negatively with synanthropic and exotic birds (Figure 4A and B), explaining upwards of 70% of the variability in bird abundance (Figure 5A–D). The only bird groups where land value was not the top-performing variable were synanthropic and resident birds, where the parcel square footage was the top explanatory variable (Figure 5A–D, Supplementary Material Table 4). Other important predictor variables that were related to bird response groups were the square footage of parcels, tree-canopy cover, distance to golf courses, and street-tree importance values (Figures 4C–H and 5B,C). All were correlated with parcel-land values (Supplementary Material Figure 2).

TABLE 1. Mean \pm SE summaries of 20 predictor variables associated with residential housing, habitat cover, street-tree metrics, or distance measures and the abundance and richness of birds within 33 residential communities throughout Los Angeles.

	AB		CD		Non-graded	
Residential housing variables						
Building density	130	\pm	6.46	155	\pm	6
Year built	1935 ^A	\pm	1.32	1938 ^A	\pm	2.2
Land value, \$	487K ^A	\pm	61K	213K ^B	\pm	15K
Last sale price, \$	1,765K	\pm	3,405K	1,434K	\pm	3,158K
Bedrooms and bathrooms	5.67 ^A	\pm	0.21	4.2 ^B	\pm	0.1
Square footage	2163 ^A	\pm	118.02	1279 ^B	\pm	28.2
Cover variables						
Tree canopy cover, %	29.8 ^A	\pm	1.85	20.5 ^B	\pm	0.9
Grass cover, %	23.3	\pm	0.77	21.7	\pm	0.8
Impervious cover, %	46 ^A	\pm	1.57	56.4 ^B	\pm	1.5
Building cover, %	31.5 ^A	\pm	0.84	36.5 ^B	\pm	0.8
Paved surface, %	14.2 ^A	\pm	0.92	19.8 ^{AB}	\pm	1.1
Street trees						
Street-tree density	3.2	\pm	0.23	2.4	\pm	0.2
Street-tree dominance	3.3	\pm	0.35	2.5	\pm	0.3
Street-tree importance value	3.3	\pm	0.26	2.5	\pm	0.2
Distance (km)						
Natural areas and wildlife sanctuaries	1.7	\pm	0.2	2	\pm	0.2
Ecological sites	3.7	\pm	0.4	5.4	\pm	0.8
Regional parks and gardens	0.7	\pm	0.1	0.7	\pm	0.1
Golf courses	1.6	\pm	0.2	2.5	\pm	0.2
Cemeteries	2.7	\pm	0.2	2.4	\pm	0.2
Beaches and marinas	28.1	\pm	2.4	19.6	\pm	2.2
Bird abundance						
Forest abundance	79.3 ^A	\pm	3.5	60 ^{BC}	\pm	3.1
Shrub abundance	90.5	\pm	2.2	83.5	\pm	3.4
Natural-lands abundance	170	\pm	5.3	144	\pm	6.1
Synanthrope abundance	119 ^A	\pm	2.5	152 ^B	\pm	3.2
Exotic abundance	36.7 ^A	\pm	1.9	60.5 ^B	\pm	3.6
Migratory abundance	84.1	\pm	2.9	70	\pm	2.9
Resident abundance	190 ^A	\pm	2.2	214 ^B	\pm	2.4
Bird richness						
Cumulative richness	20.2	\pm	0.6	20.5	\pm	0.5
Forest richness	7.9 ^A	\pm	0.3	5.6 ^{AB}	\pm	0.4
Shrub richness	4.4 ^A	\pm	0.2	3.3 ^B	\pm	0.2
Natural-lands richness	10.8 ^A	\pm	0.3	7.9 ^B	\pm	0.5
Synanthrope richness	9.4	\pm	0.3	10.1	\pm	0.2
Exotic richness	2.6	\pm	0.2	2.6	\pm	0.2
Migratory richness	5.3 ^A	\pm	0.2	4.1 ^{AB}	\pm	0.3
Resident richness	15.5	\pm	0.3	14.8	\pm	0.3

(1) The HOLC group AB is a combination of “best,” HOLC grade = A and “still desirable” HOLC grade = B zones. The CD group is a combination of “definitely declining,” HOLC grade = C, and red, HOLC grade = D zones. The non-graded zones are sections of L.A. that were not subjected to the HOLC grading system.

(2) Variables with the same superscript letter do not differ significantly among groups (AB = best and still desirable; CD = definitely declining and hazardous) and non-graded zones based on a one-way ANOVA with Tukey-Kramer test, or Kruskal-Wallis test with nonparametric multiple comparisons procedure, with Bonferroni adjusted P -value: $0.05/3 = 0.02$.

(3) Birds were grouped by whether they are associated with forest and woodland (forest), shrub, urban (synanthrope), or natural lands (forest and shrub combined) during the breeding period, whether they are non-native in their geographic origin to our Southern California study area (exotic), or whether they are nonbreeding migratory birds (migratory) or resident breeders to the L.A. study area (see [Supplementary Material Table 2](#) for further details).

The within-group regression analyses revealed important relationships between predictor and response variables ([Supplementary Material Appendix 1](#)). In general, slopes were similar within groups for the distance and street-tree variables explaining patterns of bird abundance, which mirrored patterns from the among-group analysis. Concerning the parcel

land value, the slopes for AB and CD zones were also similar for the abundance of most bird response groups ([Figure 6A](#)). Notably, for the relationships between parcel land value and synanthropic-bird abundance, there was a significant interaction between non-graded zones and AB and CD zones. The slope for the non-graded zones dropped off steeply compared

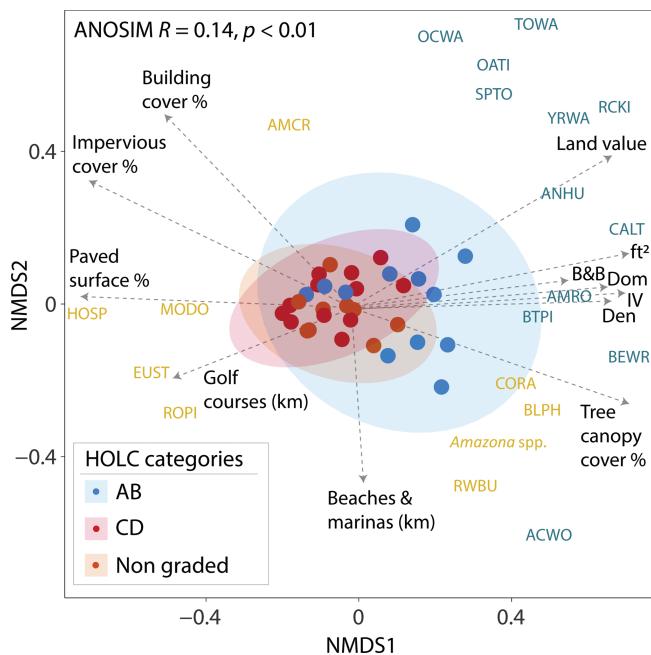


FIGURE 3. Two-dimensional non-metric, multidimensional scaling ordination (NMDS) indicating the shifts in avian species composition (N -mixture estimated or raw abundance per species) among HOLC and non-graded zones within 33 residential communities across L.A. Avian communities in HOLC-graded AB zones (best and still desirable) were composed of a higher abundance of forest birds (teal font) and were distinct from CD (definitely declining and hazardous) and non-graded zones, which were generally characterized by synanthropic bird species (yellow font). The ellipses are the bivariate confidence interval assuming a student's t -distribution and indicate the potential composition of the avian community within a HOLC-graded or non-graded zone. The dotted lines represented vectors of environmental variables that were significantly associated with the ordination scores. The four-letter codes are the plotted Bray-Curtis dissimilarity of 21 avian species and one family group (see Supplementary Table 2) that were significantly correlated with axes one or two scores. Their placement from the center node indicates the strength of association with a given axis. Vector abbreviations are as follows: ft^2 = Square footage, B&B = Bedrooms & bathrooms, Dom = Street-tree relative dominance, Den = Street-tree relative density, IV = Street-tree importance value.

with the other zones, indicating that CD zones, in particular, harbor a higher abundance of synanthropic species at higher land values (Figure 6B). Other notable patterns included the interacting slopes between AB, CD, and non-graded zones for the year a parcel was built and forest and synanthropic bird abundance (Figure 6C and D). For forest, shrub, natural lands, migratory and resident birds, data from non-graded zones showed consistent positive slopes that trended toward significant interactions compared with negative or flat slopes for AB or CD zones—with the opposite pattern for synanthropic birds (Figure 6C and D). These findings suggest that newer developments, which were all low-income in our analysis, were constructed in a way that supported a higher abundance of forest birds, and a lower abundance of synanthropic birds compared with CD zones.

Overall, both the among and within-group differences among predictor variables (residential housing and habitat variables), bird-group richness response variables, and HOLC categories were generally similar, though weaker than the abundance results (Supplementary Material Table 5). Of note, street-tree importance was the strongest predictor of the

richness of shrub, natural lands, migratory, and resident birds either among or within HOLC categories (Supplementary Material Appendix 1 and Table 5).

Objective No. 3: Predictions of Bird Abundance throughout Greater Los Angeles

There were substantial differences in tree canopy cover, parcel land values, and the predicted forest- and synanthropic-bird abundances throughout L.A. (Figure 7A–D). The spatial patterns of avifaunal abundance were opposite, similar to patterns from the objective 2 analyses.

There was a significant trend from high to low predicted forest-bird abundance among A, B, C, and D zones, with the opposite patterns uncovered for synanthropic birds (Figure 8A and C). In non-graded zones of the city, there was a general alignment where high-income areas of L.A. had a significantly higher abundance of forest birds than low-income areas, with the opposite pattern for synanthropic birds (Figure 8B and D). The differences in the means between predicted forest bird abundance in A and D zones were 36.47 birds per 200 m radius (from the prediction data) and between high- and low-income areas of L.A. that were non-graded was 32.83 (10% difference). The differences in the means for synanthropic birds were similar. However, the effect sizes were stronger between A and D zones (Cohen's $d = 0.27$) than in high and low-income areas (Cohen's $d = 0.09$) (Figure 8A and B). We note that the differences in sample sizes likely influenced the effect-size calculations, and thus, we stress focusing on the differences in the means among groups. The differences in the means appear to be driven by the A zones, which harbor more forest birds than other zones of the city with a mean predicted abundance of 94 compared with 77 in high-income non-graded zones (18% difference). On the other hand, low-income, non-graded zones appear to have the lowest predicted forest bird abundance (mean of 44 compared with 58 in redlined zones, 24% difference). The mean predicted synanthropic-bird abundance in A and D zones (110 and 145, respectively, 24% difference), was similar to the difference in the means between high- and low-income areas in the non-graded zones (125 and 161, respectively, 22% difference; Figure 8C and D).

Objective No. 4: Patterns of Race and Ethnicity in HOLC Grades

The distribution of race and ethnicity throughout L.A. was highly variable, yet also generally spatially segregated (Figure 9). The highest percentage of the Asian population was in the San Gabriel Valley, and east L.A. County, with pockets along the southeastern border with Orange County and the Palos Verdes Peninsula (Figure 9A). The highest percentage of the Black population was along a corridor that extended from the interior of west L.A. southeast into South L.A. (Figure 9B). The highest percentage of the Hispanic population was throughout downtown and South L.A., East L.A., the eastern San Gabriel, and Pomona Valleys, and the central and northeastern portion of the San Fernando Valley (Figure 9C). The highest percentage of the White population ranged from the Palos Verdes Peninsula, north along the Pacific Coast and into the Santa Monica Mountains, the border of Orange County, and the foothills of the San Gabriel Mountains (Figure 9D).

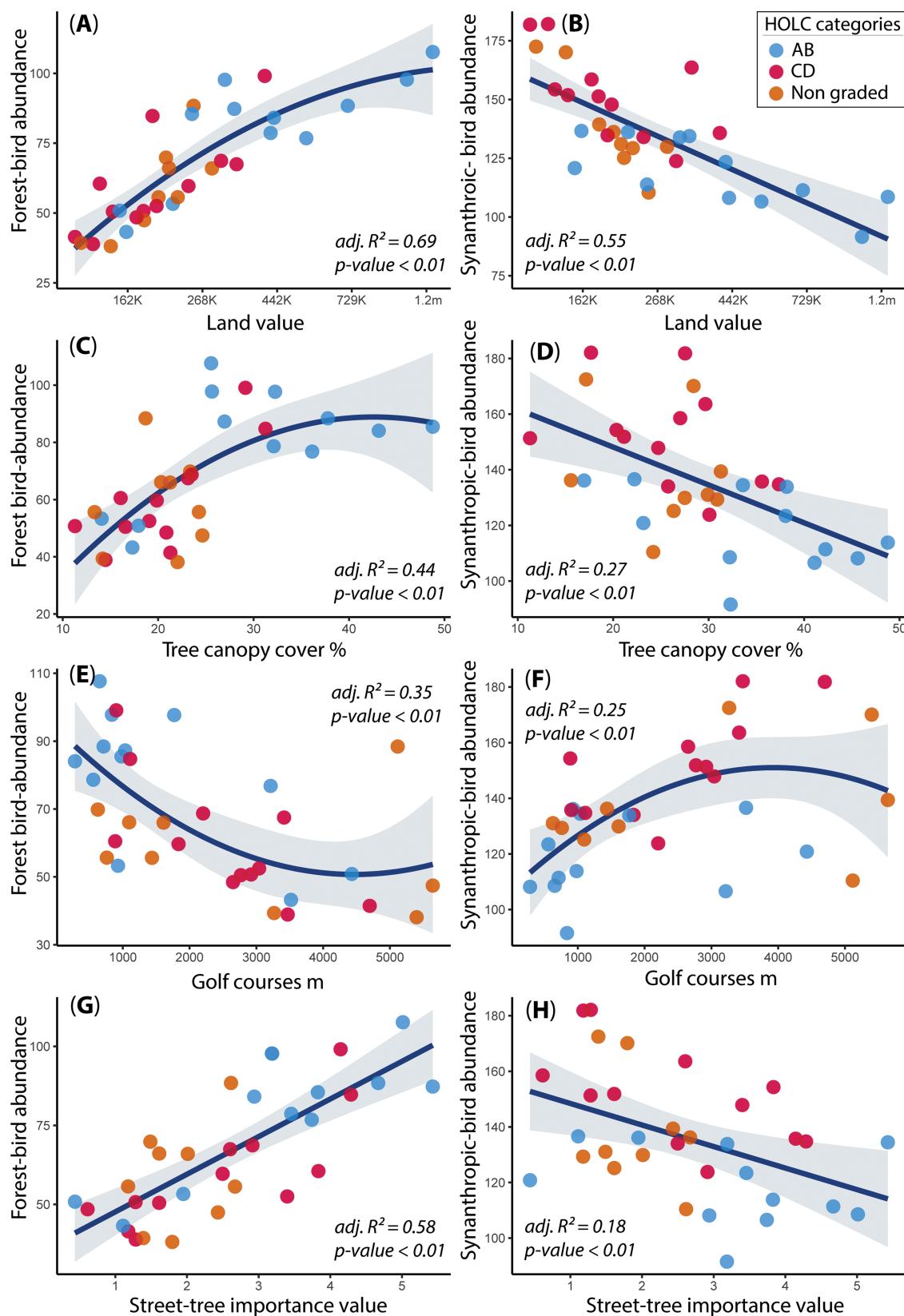


FIGURE 4. Scatterplots characterizing the positive relationship between (A) forest-bird abundance and the negative relationship for (B) synanthropic-bird abundance with parcel land values and the variable relationships between (C–H) habitat variables with bird response variables among HOLC-graded zones (AB = best and still desirable; CD = definitely declining and hazardous) and non-graded areas. The negative slope for (E) forest birds with distance to golf courses indicates a higher abundance of forest birds the closer to a golf course, with opposite patterns for (F) synanthropic species. The associated adjusted R^2 and p -values for each relationship were based on a least-squares regression analysis.

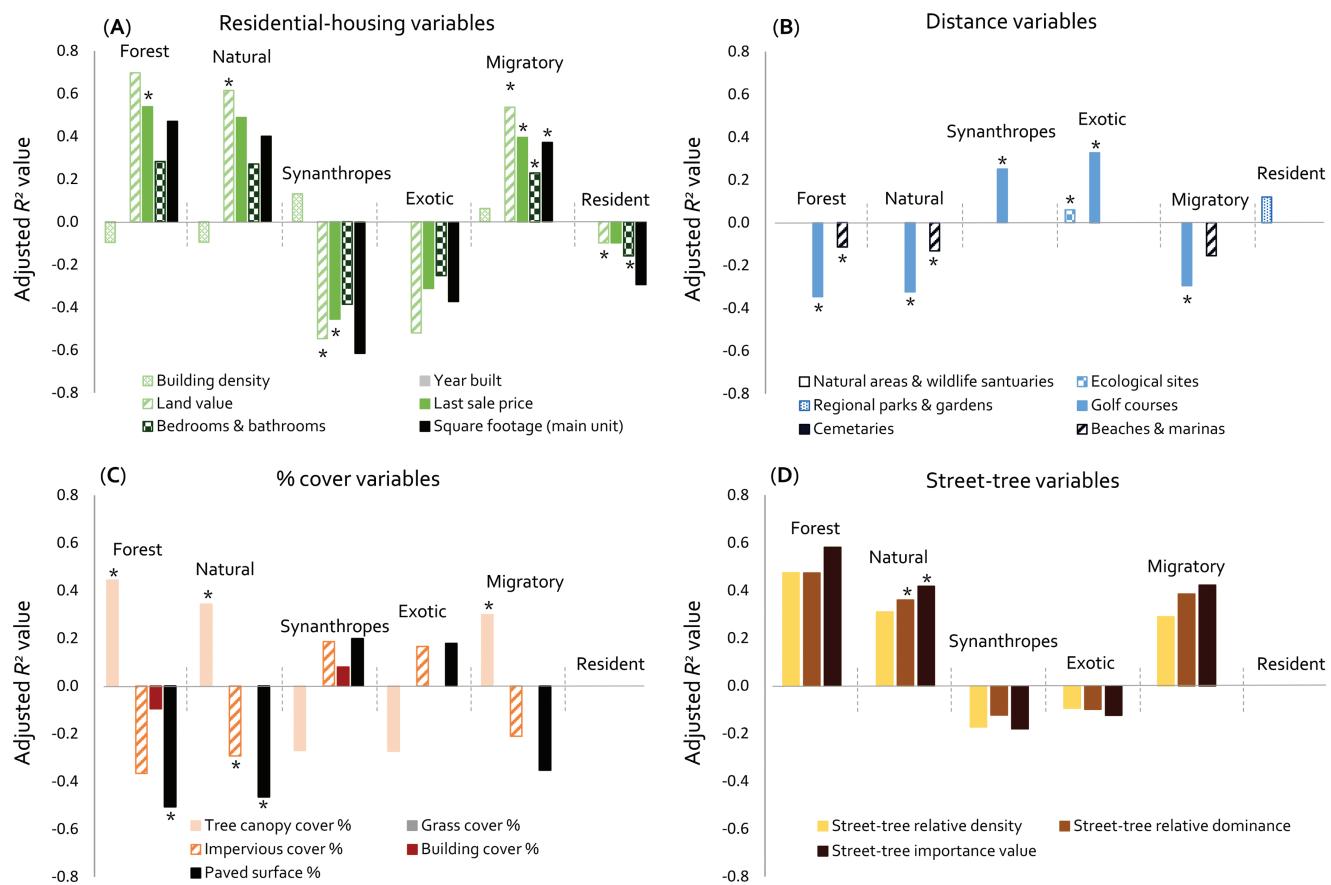


FIGURE 5. Forest, natural lands (natural), and migratory birds were generally positively related (bars above zero line) with (A) parcel land values and larger parcels, (B) distance to golf courses and beaches and marinas (negative relationships, which equates to a closer distance), (C) tree canopy cover, and a well-developed (D) street tree canopy. The relationships were opposite for synanthropes and exotic bird species, with resident bird species responding less to the residential housing, distance, cover, and street-tree variables. The bars were derived from the adjusted R^2 values from least-squares regression models. Bars are displayed in either a positive or negative direction depending on the coefficient estimate from the model. Asterisks (*) indicate models are fitted with a quadratic function in which we only display the initial direction of the quadratic shape. If a bird group does not contain bars for a particular variable, models were not significant.

The race and ethnicity patterns of L.A. have shifted markedly from 1940 to 2020 (Figure 10A-E, Supplementary Material Appendix 2). The White share of the population has declined precipitously throughout our L.A. study area from composing 94% of the population in 1940 to 25% of the population in 2020. The Black share of the population generally increased from 1940 to 1990, from 1% to 10% of the population but declined to 7% in 2020. The Hispanic population has had the most dramatic increase in the region from composing 2% of the population in 1940 to 45% in 2000 but has since declined to 35% of the total in our study area in 2020 (Figure 10). Patterns were generally similar among HOLC and non-graded zones, with the most muted shifts in A zones (Figure 10A).

Percentages of the Asian and Black populations were generally similar across A, B, C, D, and non-graded zones (Figure 11A and B). A notable deviation was for the Black population between A (median of 2.1% of the population was Black) and D (3.3%) zones, which trended towards a significant difference ($P = 0.02$). The Hispanic population was greater in C (36.3%) and D (58.7%) zones compared with A (6.8%), B (17.8%), and non-graded zones (25.2%) (Figure 11C). Of note, there was nearly 9 times the Hispanic population in D than in A zones (Figure 11C). All other comparisons for the Hispanic population among HOLC and non-graded

categories were strongly and significantly different ($P < 0.01$). The White population was more likely to live in A-graded zones (48.8%) than in B (14.3%), C (7.6%), D (4.1%), or non-graded zones (14.6%) (Figure 11D). The percentage of the White population was 12 times greater in A- than in D-graded zones, and all pairwise comparisons for the White population among zones were strongly significantly different ($P < 0.01$).

Objective No. 5: Relationships Between Race and Ethnicity and Urban Avifauna

We detected substantial differences in the patterns of parcel land values, tree canopy cover, and predicted forest- and synanthropic-bird abundances among racial and ethnic groups (Figure 12A-D). Census tracts that were majority White were associated with the most expensive land values, greater tree canopy cover, the highest abundance of predicted forest birds, and the lowest predicted synanthropic-bird abundance (Figure 12A-D). The patterns for predictor variables were similar for the Asian population—although they were more muted and significantly lower from patterns in the majority White census tracts—ranging from a low of 26% in difference (tree-canopy cover) to 60% in difference (back-transformed scale) for land value. Patterns for census tracts

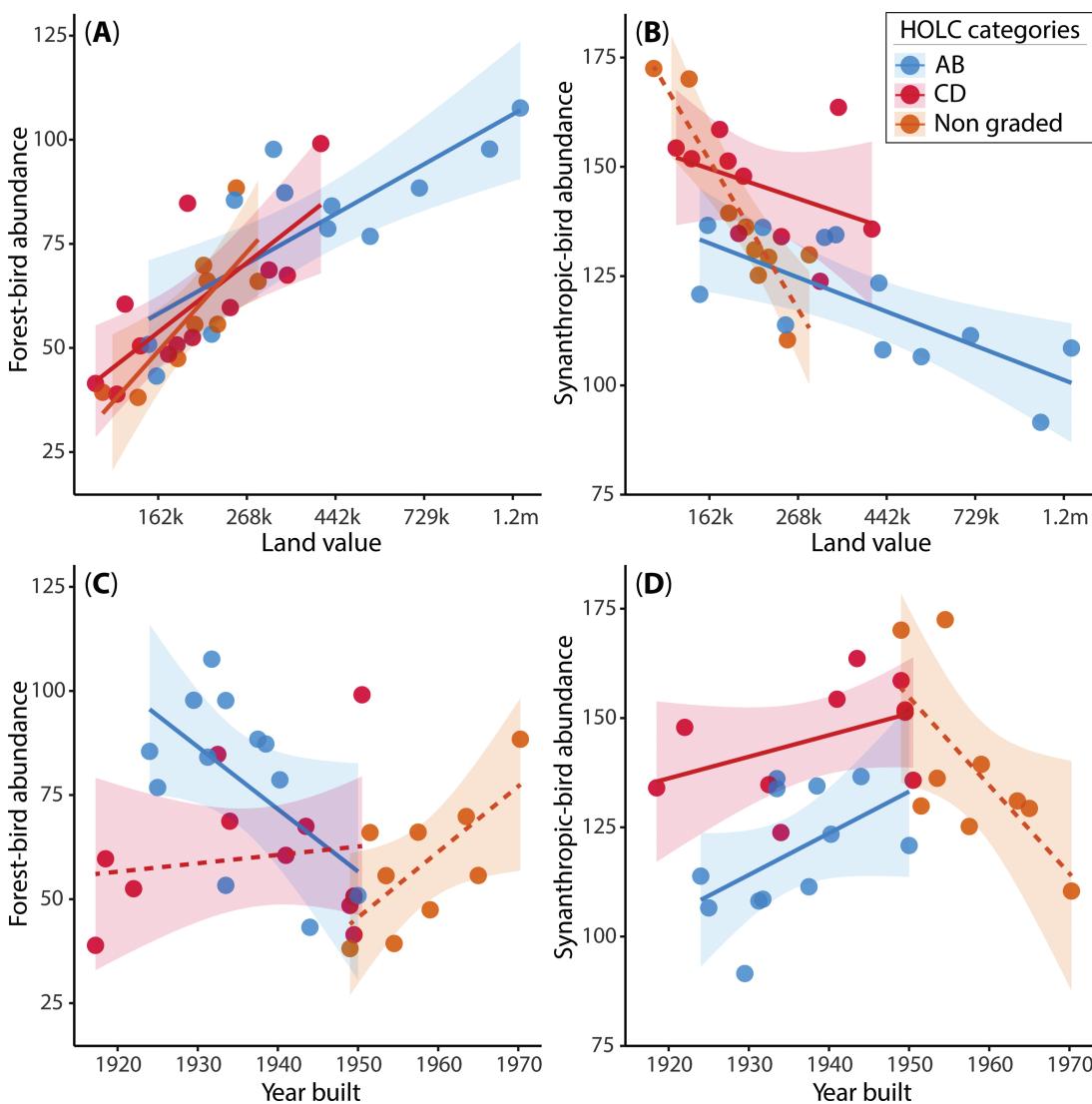


FIGURE 6. Relationships between (A) forest-bird abundance and parcel land values were consistent within HOLC-graded zones (AB = best and still desirable; CD = definitely declining and hazardous) and non-graded zones. (B) Synanthropic-bird abundance dropped considerably in non-graded zones in relation to parcel land values in comparison with AB and CD zones. (C) Forest-bird abundance was highest in AB zones with parcels developed in the 1920s and 1930s and dropped considerably based on housing age—with opposing patterns for forest birds in CD and non-graded zones. The response of (D) synanthropic bird species was generally opposite to the patterns for forest-bird abundance. The fitted lines were computed based on a least-square regression analysis. Dotted lines within a scatterplot indicated a significant interaction with a variable with a solid line(s).

where most residents were either Black or Hispanic were strongly different than majority White census tracts (Figure 12A–D). Census tracts where the majority of residents were Black had the lowest tree canopy coverage, the lowest parcel land values, the lowest abundance of forest birds, and the highest abundance of synanthropic bird species (Figure 12A–D). The Cohen's d value for tree canopy cover between majority Black and majority White census tracts was 0.16, which was the greatest effect size of all comparisons. Census tracts that were majority Hispanic also had relatively low land values, lower levels of forest-bird abundance, and higher levels of synanthropic-bird abundance (Figure 12A–D). Notably, data within census tracts that were majority Hispanic had a larger variance than majority Black census tracts for each assessed metric indicating a more substantial range between poor and rich majority-Hispanic communities including the amenities that are typically affiliated with income gradients

in cities (e.g., tree canopy cover, Figure 12A–D). Outside of tree canopy cover, the effect sizes between majority Black and Hispanic census tracts compared with majority White census tracts for parcel land values, and forest- and synanthropic-bird abundance were generally similar with Cohen's d values ranging from 0.10 to 0.11.

For the among-HOLC category regressions concerning race and ethnicity and birds, there were weak associations between the Asian and Black populations with patterns of predicted forest bird and synanthropic-bird abundance (Figure 13A–D; for a colorblind-friendly version of Figure 13, please view Supplementary Material Figure 4). The Hispanic population was negatively related to predicted forest-bird abundance ($R^2_{kl} = 0.38, P < 0.01$), and positively to synanthropic-bird abundance ($R^2_{kl} = 0.33, P < 0.01$) (Figure 13E and F). The White population had opposite patterns to the Hispanic population with a positive relationship with forest bird abundance

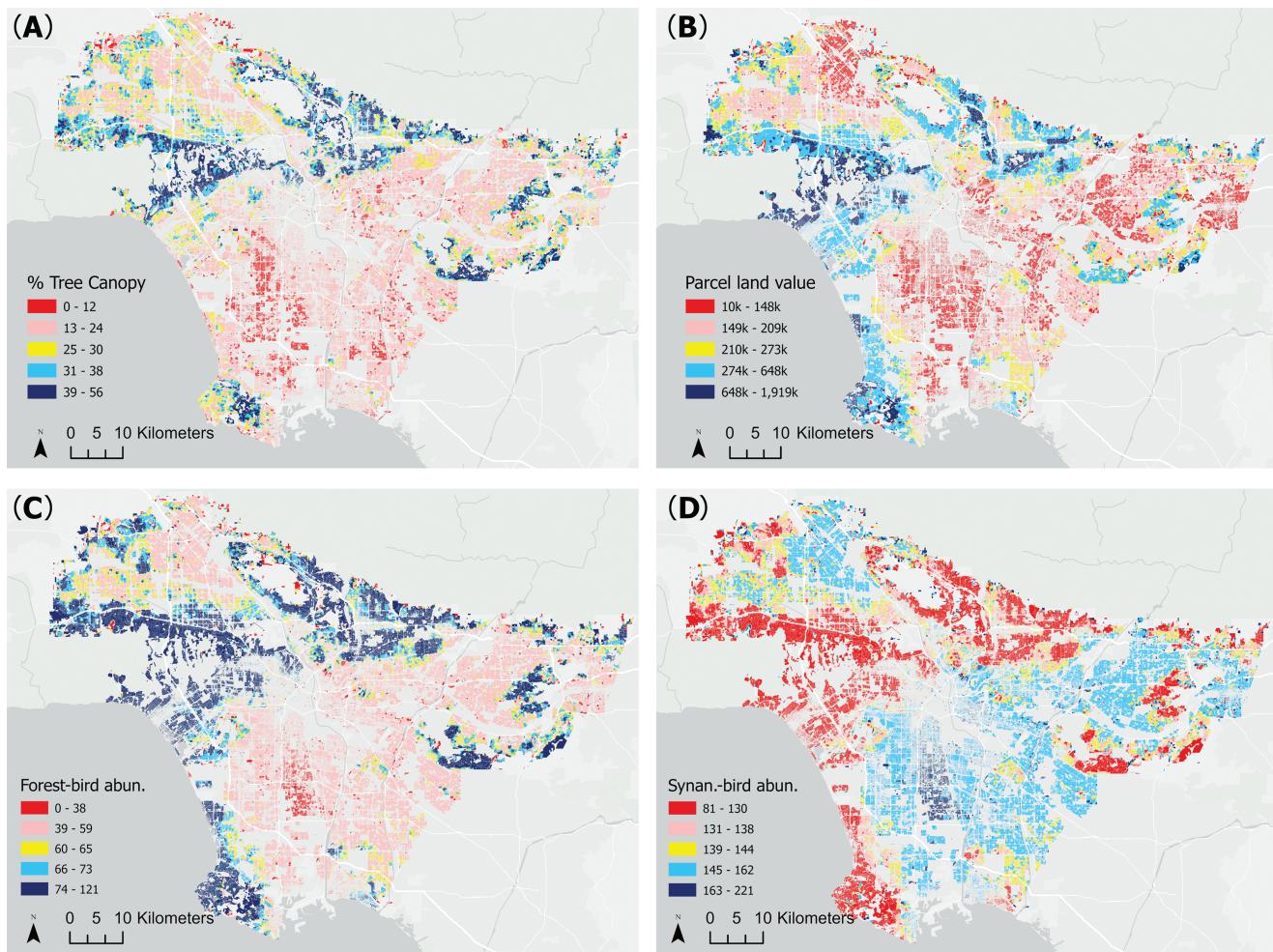


FIGURE 7. Maps characterizing the strong spatial variability in (A) percent tree canopy cover, (B) parcel land values, and predicted (C) forest- and (D) synanthropic-bird abundance across our L.A. study area. The predicted forest- and synanthropic-bird abundance maps were derived from the coefficients of a multiple linear regression model, that included both (A) and (B).

($R^2_{kl} = 0.41$, $P < 0.01$) and a negative relationship with synanthropic bird abundance ($R^2_{kl} = 0.37$, $P < 0.01$; Figure 13G and H).

Interestingly, the within-HOLC category regressions concerning race and ethnicity and birds generally showed nearly the same relationships as the among-group results (Supplementary Material Appendix 3). Regardless of whether in an A- or D-graded zone, the percentage of the White population generally had a positive relationship with forest birds and a negative relationship with synanthropic birds, with the opposite patterns for Hispanic residents.

DISCUSSION

Our analysis provided substantial evidence that redlining is negatively associated with urban avifauna, their habitat, and the people who may experience them in L.A. Further, and expectedly, our results suggested that other zones of L.A. that were not part of the HOLC grading process but fall on the low end of the spectrum of land-value lack an avian community associated with “natural features” (e.g., trees, compared with affluent zones). Overall, our results strongly supported the luxury-effect hypothesis stating that affluent areas of cities experience unique components of biodiversity presumably

because residents and municipalities have the means to afford amenities, such as greenery, that support wildlife (Leong et al. 2018). Moreover, and more importantly, our findings also provided considerable support for the legacy-effect hypothesis, layered on top of the patterns of luxury, where disparate patterns of urban avifauna and the potential human experience of birds were often stronger between redlined zones than in non-graded low-income areas of the city. Taken together, our results illuminate patterns of income inequality, both past and present, that carry over to influence urban biodiversity.

Disinvestment, and more accurately, reduced lending, was historically driven by racism throughout the nation (Hillier 2003, Aaronson et al. 2018, Mitchell and Franco 2018). In cities everywhere, and very much so in L.A., the legacy effects due to the HOLC grading criteria appear to remain a considerable hurdle for urban greening (Locke et al. 2021, Nardone et al. 2021, Nowak et al. 2022, Burghardt et al. 2022), which influences the composition of birds throughout the city. It is abundantly clear, based on our findings, that the Black and Hispanic population in L.A. experience far less urban greening and biodiversity than the affluent White population. Many studies of urban systems have focused on the adverse effects of income inequality on urban function (Schell et al. 2020). Our study supports those and strongly indicates that

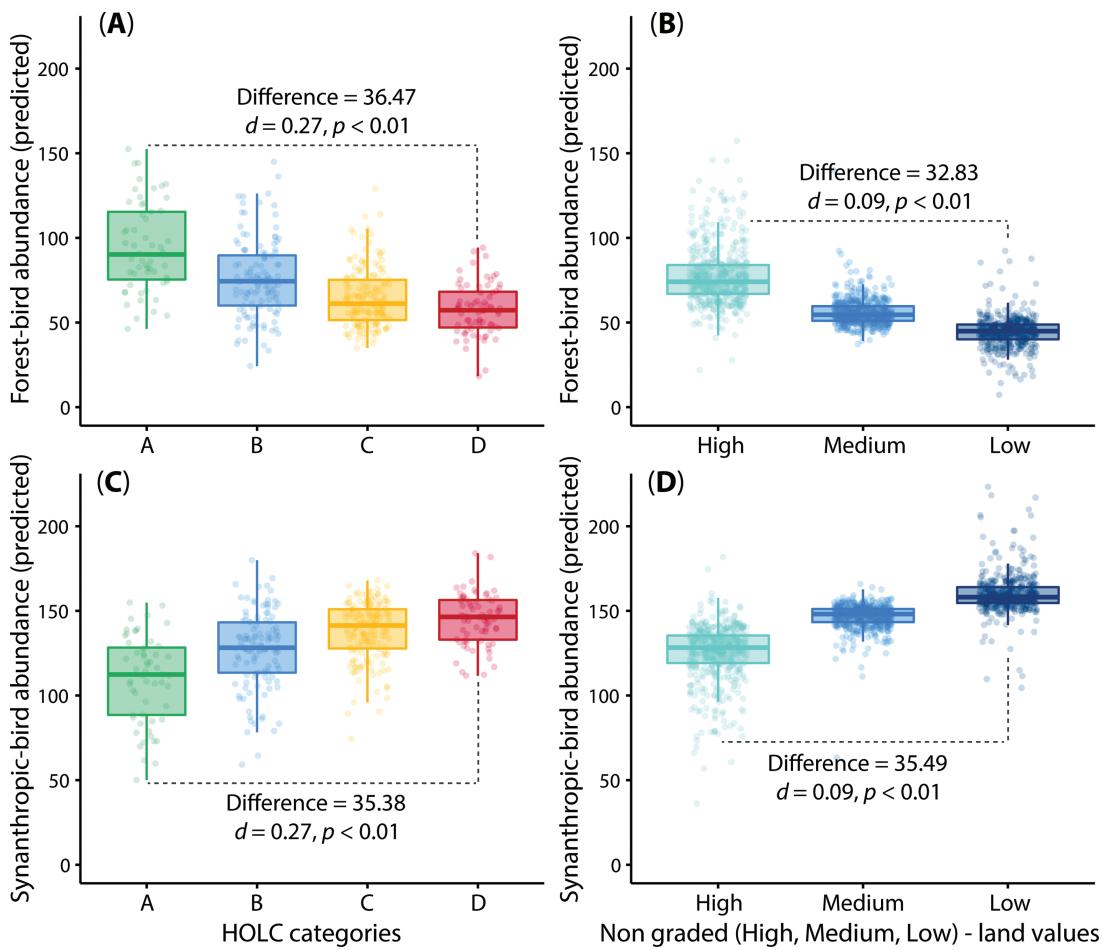


FIGURE 8. Box plots highlighting the increase in **(A, B)** predicted forest-bird abundance based on a categorized affluence gradient with the opposite patterns for **(C, D)** predicted synanthropic-bird abundance. The categorized gradient in **(A)** and **(C)** is based on the historical HOLC grading practice [green ("best," HOLC grade = A), blue ("still desirable" HOLC grade = B), yellow ("definitely declining," HOLC grade = C), and red, (HOLC grade = D)]. The gradient in **(B)** and **(D)** characterizes a contemporary high-to-low-income gradient as it is focused on data from locations of L.A. that were not graded by the HOLC. The d scores are Cohen's d values and are a measure of effect size. Values further from zero indicate an increasing effect. "Differences" refers to differences in the means of relationships highlighted by the dotted lines. The P -values were computed based on a Tukey's post hoc test following a significant one-way analysis of variance test.

failure to act will continue to negatively influence avifauna by the uneven filtering of bird species across L.A. and likely other cities throughout the world.

Bird and Habitat Patterns

Globally, urban biodiversity is primarily for the affluent (Matthew McConnachie and Shackleton 2010, Kaoma and Shackleton 2014, Richards et al. 2017, Gerrish and Watkins 2018, Chamberlain et al. 2019, Kuras et al. 2020, Schell et al. 2020, Venter et al. 2020). This is clear in L.A., where, nearly across the board, habitat features that support birds are far greater in the wealthiest portions of the metropolis. Whether it is for public resources (e.g., street trees; Wood and Esaian 2020) or private amenities (e.g., yard plant diversity; Clarke et al. 2013), our findings move beyond the simple, yet persistent explanation of the luxury-effect hypothesis (Leong et al. 2018) and build on the narrative of a city struggling to cope with its past segregationist history affecting its contemporary character. Los Angeles is not alone in this venture, as cities across the U.S. continue to display inequities in urban habitat features that carry over to affect biodiversity (Schwarz et al. 2015). This is especially true considering the

redlining practice, as numerous cities have lower tree-canopy cover in redlined areas (HOLC grade = D) than in best zones (HOLC grade = A) (Locke et al. 2021, Nardone et al. 2021, Nowak et al. 2022, Burghardt et al. 2022). The disparity in green amenities is amplified when considering the cascading effects on wildlife because most animals in cities that are not strictly synanthropic require habitat features that superficially resemble the ecosystems they are adapted to. Indeed, forest, shrub, and natural-lands birds were far more abundant in the wealthiest portions of L.A., whereas the opposite patterns were apparent for synanthropes, supporting patterns from other cities across the U.S. (Chamberlain et al. 2020) and the world (Dubovský et al. 2020)—although patterns may differ for other taxonomic groups (Longcore and Rich 2008).

Socioeconomic variables associated with wealth, such as income level, are commonly a strong predictor of plant and wildlife diversity in other cities throughout the world (Leong et al. 2018, Avolio et al. 2020, Schell et al. 2020, Blanchette et al. 2021). However, what remains a question is why the residential housing variables (e.g., parcel land values) were overwhelmingly the strongest explanatory variables in our study. While it is of course not money the birds respond to,

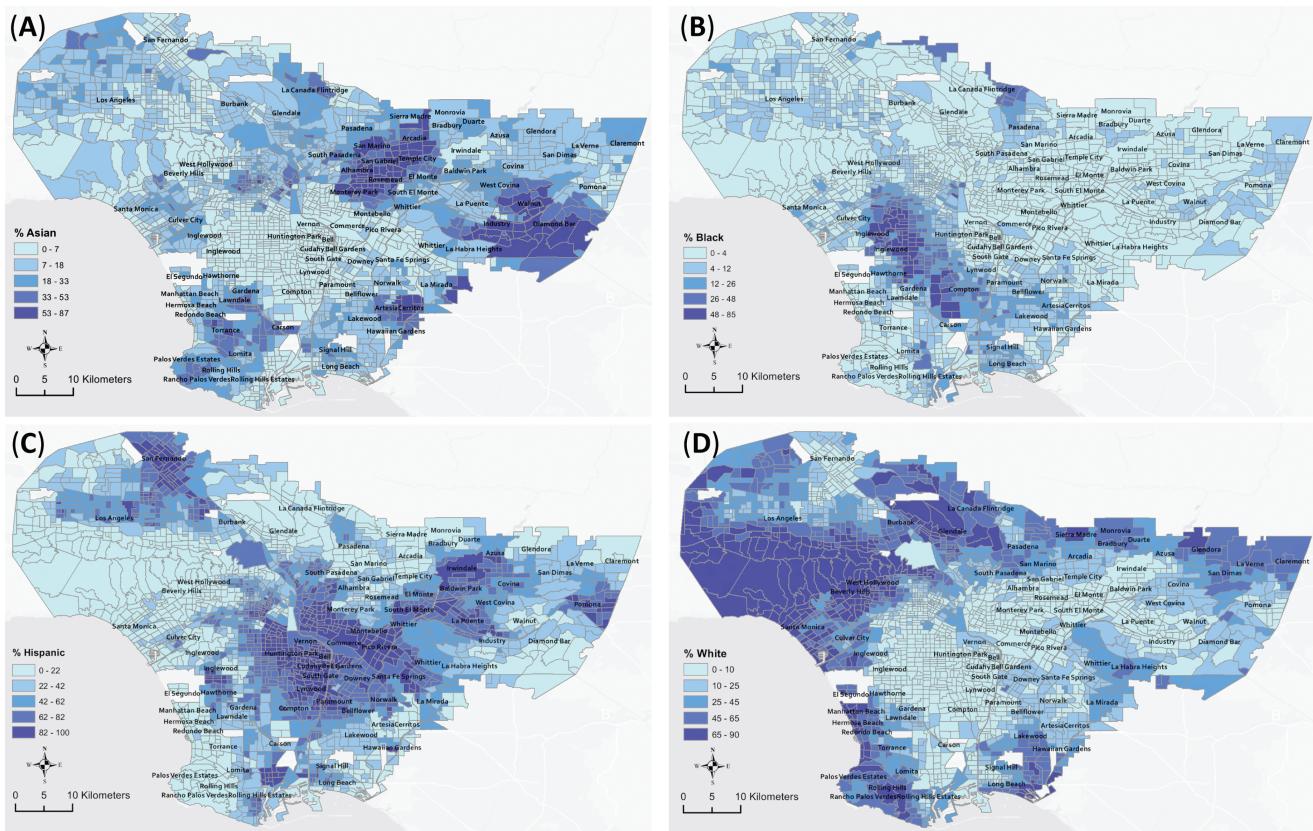


FIGURE 9. Maps characterizing the spatial variability in the (A) Asian, (B) Black, (C) Hispanic, and (D) White populations within census tracts based on census projections from 2015 to 2019 across the L.A. study area.

we suggest that the land value and parcel size variables were a surrogate for numerous amenities that our residential housing and habitat variables did not capture (Lee et al. 2010). These could include manicured vegetation in yards (Lerman and Warren 2011, Smallwood and Wood 2023), landscaping practices (Polsky et al. 2014) or preferences (Hope et al. 2003), irrigation and mesic vegetation (Neel et al. 2014, Chamberlain et al. 2020), supplemental water or food (Greig et al. 2017, Lerman et al. 2021), or larger yard spaces (Belaire et al. 2014)—all related to and requiring money—that likely attract distinct avian communities affiliated with green amenities (e.g., a well-developed tree canopy). Interestingly, the percent cover, distance, and street tree variables were generally weaker predictors, which was surprising given their important roles in describing bird distribution patterns in other urban systems (Donnelly and Marzluff 2004, Lerman and Warren 2011, Wood and Esaian 2020).

Another residential-housing variable that we did not measure, but which could be an important variable in describing patterns of urban wildlife is homeownership. Homeownership may result in converging landscaping practices to the norms of one's neighbors (Locke et al. 2018), or where broader urban greening initiatives are typically targeted (Perkins et al. 2004). In the Los Angeles region, homeownership is associated with greater tree cover (Lee et al. 2010). Further, with homeownership comes control, where a homeowner can simply do as they prefer with their property. Control is often not possible if renting, thus highlighting another avenue where wealthier neighborhoods, with high rates of homeownership, may have more distinct and possibly diverse and abundant

landscaping, that may carry over to attract a diversity of wildlife. While land values, or income levels, continue to be important for describing urban wildlife, we suggest that the field of urban ecology needs to continue quantifying additional predictor variables that may play an important and interwoven role in better explaining wildlife assemblages and associated characteristics (e.g., diversity or abundance). This is especially critical when considering urban management actions—especially at the scale of the householder or the community.

Birds, Humans, and Redlining

One of the most glaring findings from our work was the disparity in the potential of the human population in L.A. to experience distinct avifaunal communities. Our findings suggest, overwhelmingly, that the White population is in a position to experience the highest abundance of forest birds and other species that require features in the cityscape that resemble natural conditions (e.g., trees and shrubs). This is the opposite pattern for the Black and Hispanic populations which are in a position to experience high abundances of synanthropic birds that are affiliated with dense, urban conditions. Our findings strongly point to a carry-over effect of inequities. In addition to the inequities in services (Mays et al. 2011), food insecurity (Algert et al. 2006), and quality of life (Centers for Disease Control and Prevention 2001) in the Black and Hispanic communities of L.A., our results strongly suggest and support that a large proportion of the Black and Hispanic populations likely also experiences inequities in urban biodiversity and greening and their potential ability to experience them in

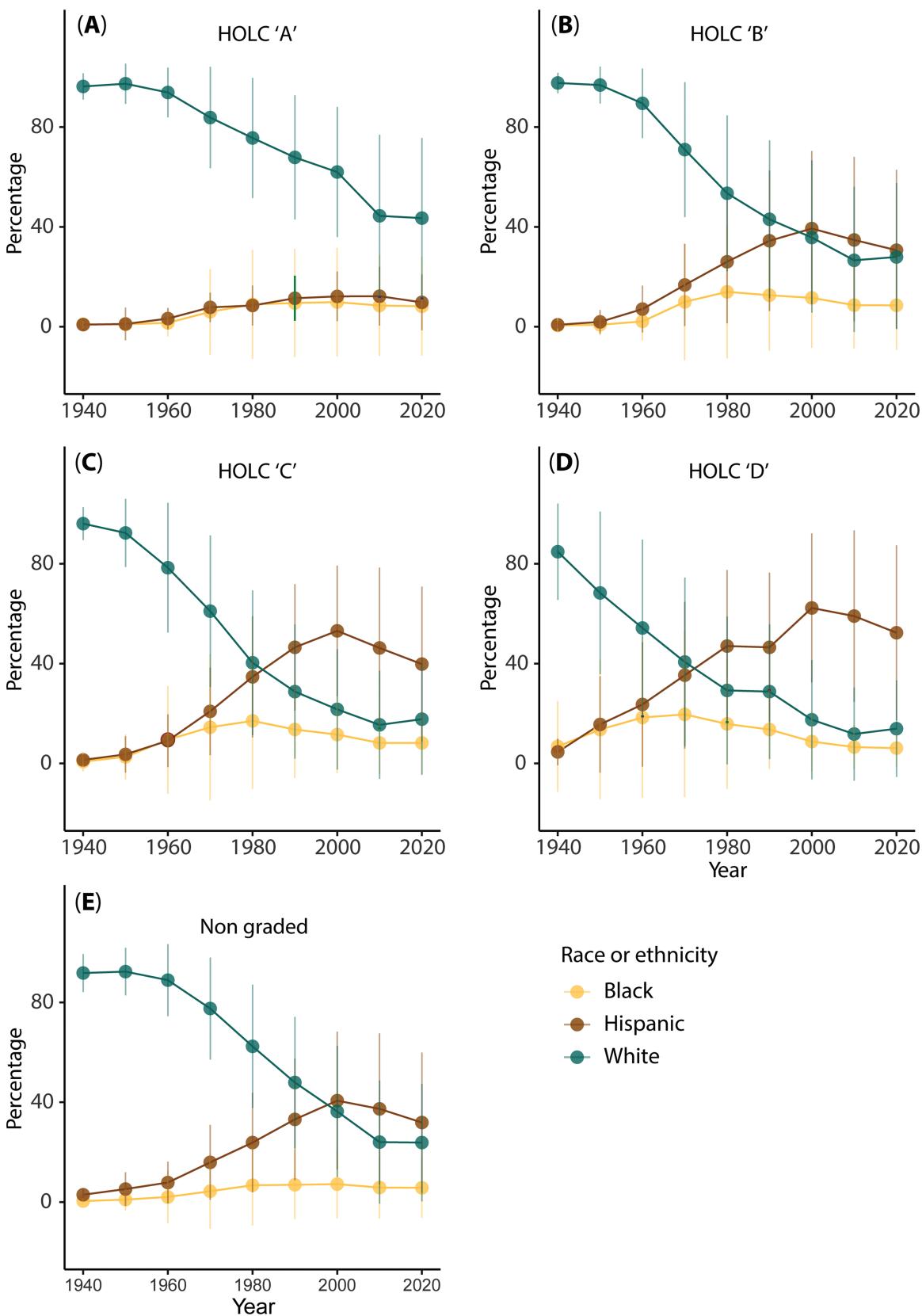


FIGURE 10. Line plots depicting the decrease in the White population, the increase in the Hispanic population, and the relative similarity in the Black population among all HOLC zones in L.A. from 1940 to 2020 (**A–E**). Dots represent the mean of the percentage data and the whiskers on either side of a dot are the standard deviation.

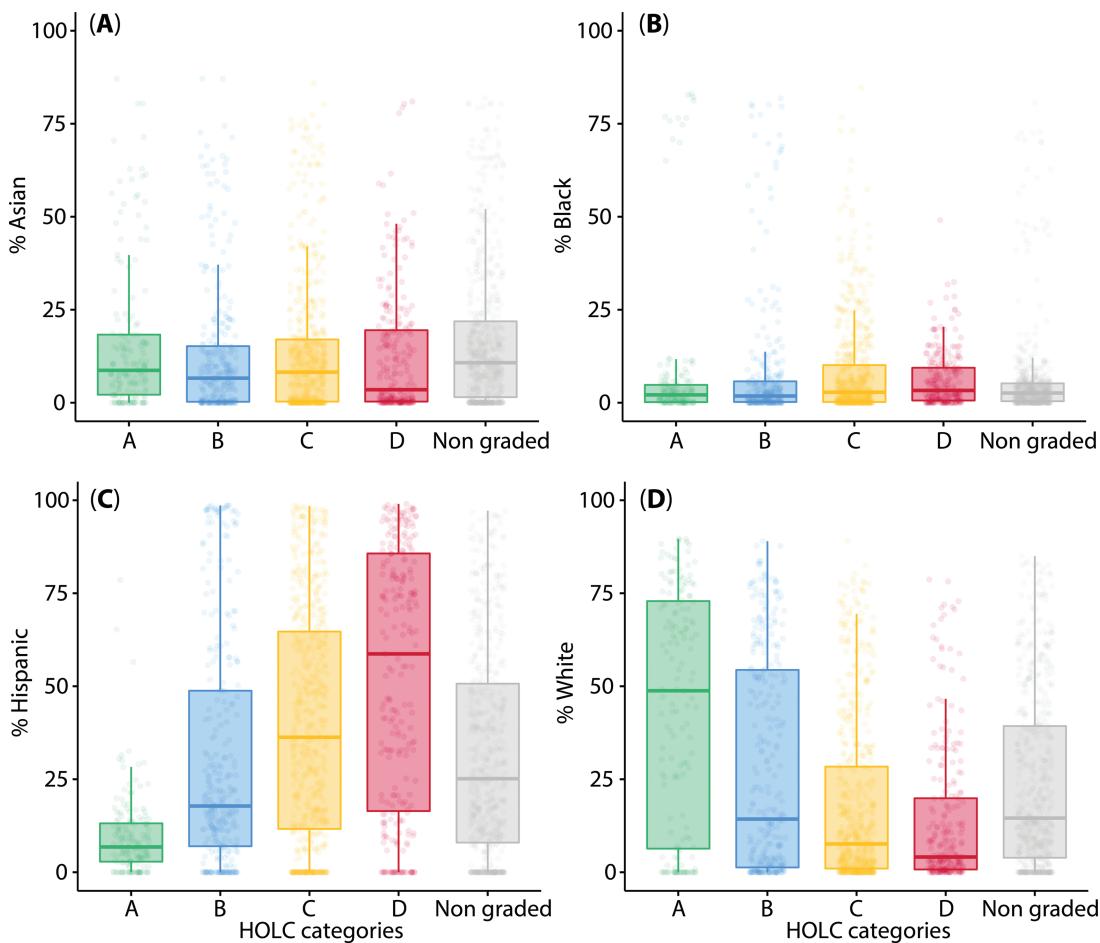


FIGURE 11. Box plots characterizing the relative similarity in the (A) Asian population among HOLC categories, the slightly higher proportion of the (B) Black population in C and D zones compared with other zones, the substantially higher proportion of the (C) Hispanic population in C and D zones compared with A zones, and the considerably higher proportion of the (D) White population in A, B, and non-graded zones relative to the C and D zones. The HOLC groups are categorized as, green (“best,” HOLC grade = A), blue (“still desirable” HOLC grade = B), yellow (“definitely declining,” HOLC grade = C), and red, (HOLC grade = D). The boxes were drawn based on census projections from 2015 to 2019 in HOLC-graded zones and zones that were non-graded.

their community of residence (Wolch et al. 2013). Our findings echo those from Milwaukee, Wisconsin, Tampa, Florida, and Phoenix, which found Hispanic (Tampa and Phoenix) and Black communities (Milwaukee and Tampa) repeatedly were associated with less urban biodiversity (e.g., birds and trees; Kinzig et al. 2005, Heynen et al. 2006, Landry and Chakraborty 2009, Lerman and Warren 2011). Similar findings where the Black and Hispanic populations experience less urban greenness than the White population were also uncovered in both a spatial and meta-analysis of urban forest cover, income, and race and ethnicity in cities across the U.S. (Gerrish and Watkins 2018, Nesbitt et al. 2019).

Our results paint a clear picture of division, not unlike that which is found in other countries in the world that have experienced deep racism and classism. One of the clearest examples illustrating this pattern is South Africa, where the country’s race-based history under the apartheid system has led to patterns in which green amenities in cities and towns across the country are overwhelmingly found in affluent White communities (Matthew McConnachie and Shackleton 2010, Venter et al. 2020). Further inequities in urban biodiversity across socioeconomic classes are found in numerous cities across the world including Vancouver, Canada (Melles 2005), Brisbane,

Australia (Shanahan et al. 2014), Paris, France (Cohen et al. 2012), and cities in Latin America (e.g., Rio de Janeiro, Brazil, Pedlowski et al. 2002). In the Vancouver study, aboriginal communities were segregated from wealthy White and Asian communities and generally experienced a bird community with species that would fall in our synanthropic-birds group (Melles 2005). The studies in Brisbane, Paris, and Rio de Janeiro effectively illustrate the luxury effect and do not explicitly link patterns of race and ethnicity with socioeconomic class (Pedlowski et al. 2002, Cohen et al. 2012, Shanahan et al. 2014). However, given that there is a strong link between these two factors throughout the world (Dumont 1980, Williams 1996, Nesbitt et al. 2019), it is not a stretch to assume inequities exist in cities across the globe in which race and ethnic groups (or class) may experience urban biodiversity like what we observed in L.A.

Inequities in the experience of nature in urban centers are a cause for concern when considering public health outcomes in low-income communities in cities across the U.S. (Williams 1996, Corburn 2016, Nardone et al. 2020a, c) and poorer countries throughout the world (Popkin and Doak 1998, Prentice 2006). Numerous lines of research have linked experiencing nature with increases in human health (Brown and

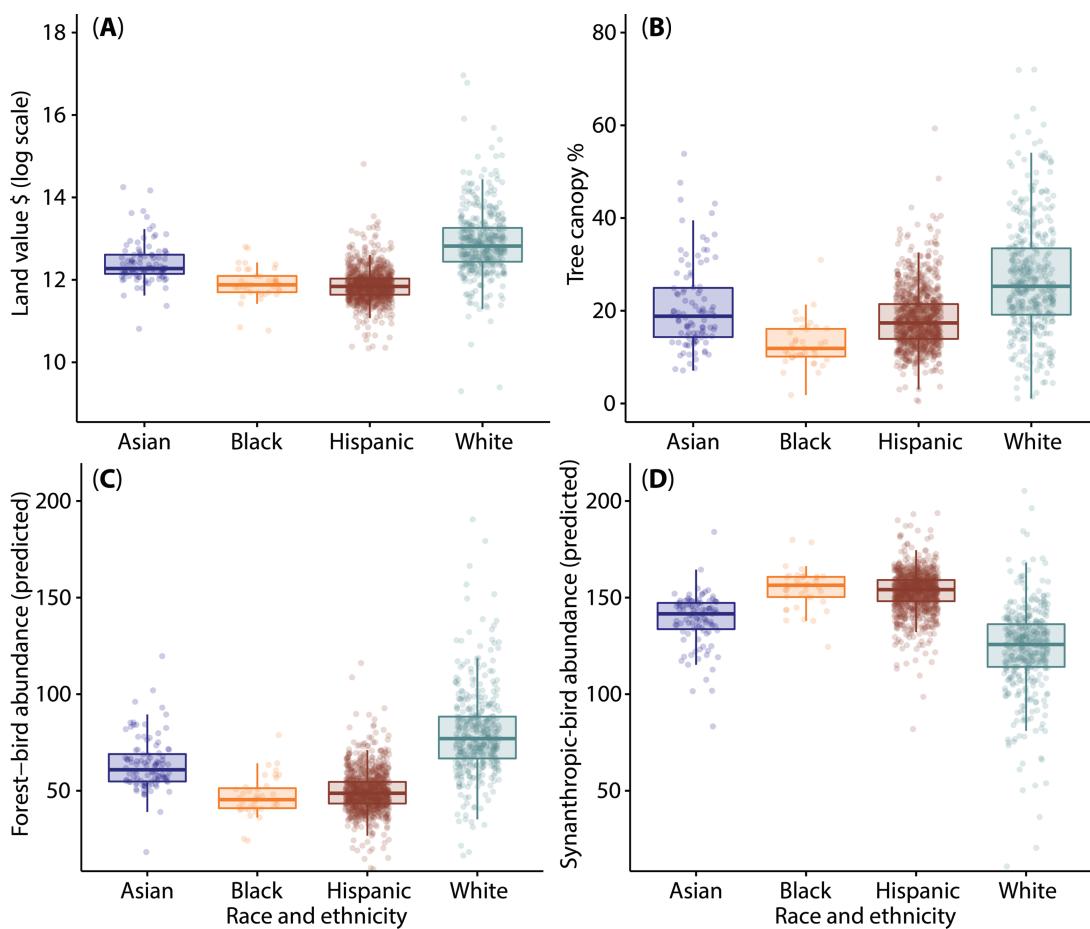


FIGURE 12. Box plots detailing how census tracts dominated by the White population had higher (A) parcel land values, (B) tree canopy cover, and (C) predicted forest-bird abundance, with similar, yet more muted patterns for census tracts dominated by the Asian population. Census tracts dominated by the Black and Hispanic populations had the lowest (A) parcel land values and (B) tree canopy cover, and the highest predicted abundance of (D) synanthropic-bird species. The census data are based on projections from 2015 to 2019 and are meant to capture the demographic composition of L.A. in 2020. The land value and tree canopy cover data were derived from a LiDAR-remote sensing product capturing conditions in 2016, from which the bird predictions were computed.

Grant 2005, Fuller et al. 2007, Bratman et al. 2012, Russell et al. 2013). This may be especially true in urban ecosystems as experiencing nature has many positive effects on residents' lived experience in cities, ranging from psychological benefits to a commitment to community-based conservation actions (Fuller et al. 2007, Hartig and Kahn 2016, Prévôt et al. 2018, Colding et al. 2020). Nevertheless, one confounding question from our work is whether it matters from a public health perspective if humans are experiencing forest versus synanthropic birds. Humans have distinct preferences for which birds they prefer, from larger, more colorful, or rarer birds to those that are charismatic, or that sing beautiful songs (Yang and Kang 2007, Garnett et al. 2018, Andrade et al. 2022, Stoudt et al. 2022). In each of our bird groups, there are colorful birds such as the Townsend's Warbler (*Setophaga townsendi*) in the forest and natural lands group and the House Finch (*Haemorhous mexicanus*) in the synanthropic-birds group. Further, some birds sing complex and beautiful songs during the spring before their departure to the breeding grounds, including the forest-breeding Yellow-rumped Warbler (*Setophaga coronata*), or during the breeding season in the city, such as the Northern Mockingbird (*Mimus polyglottos*), a common urban-dwelling species in L.A. Therefore, from a public health perspective, our results suggest there should

be birds available for each resident of the city to enjoy if an individual can find space outside where the birds in their neighborhood occur. Yet, we suggest this assumption is too simplistic as there is a chasm of difference between the low- and high-income neighborhoods of L.A., especially between many A and D zones, and the conditions available to residents (e.g., green cover, access to green amenities; Trust for Public Land 2021, Vasquez and Wood 2022).

Building on the differences in access to nature, there are safety concerns (Cohen et al. 2016, Han et al. 2018) and other urban unpleasantries such as pollution that are more prevalent in low-income communities (Rigolon et al. 2017) that likely negatively affect the experience of nature (Kelly et al. 2022). Thus, when attempting to link experiencing nature and public health in cities and considering the question of whether it matters if human residents are experiencing different aspects of the avian community, we suggest a more holistic approach. This may include addressing the differences in access to nature (Trust for Public Land 2021), considering the potential lack of ecosystem services or an increase in dis-services delivered by birds (Bolund and Hunhammar 1999), or simply the disparity in urban green amenities (Schwarz et al. 2015) that may positively influence the lived experience of people living far from natural areas.

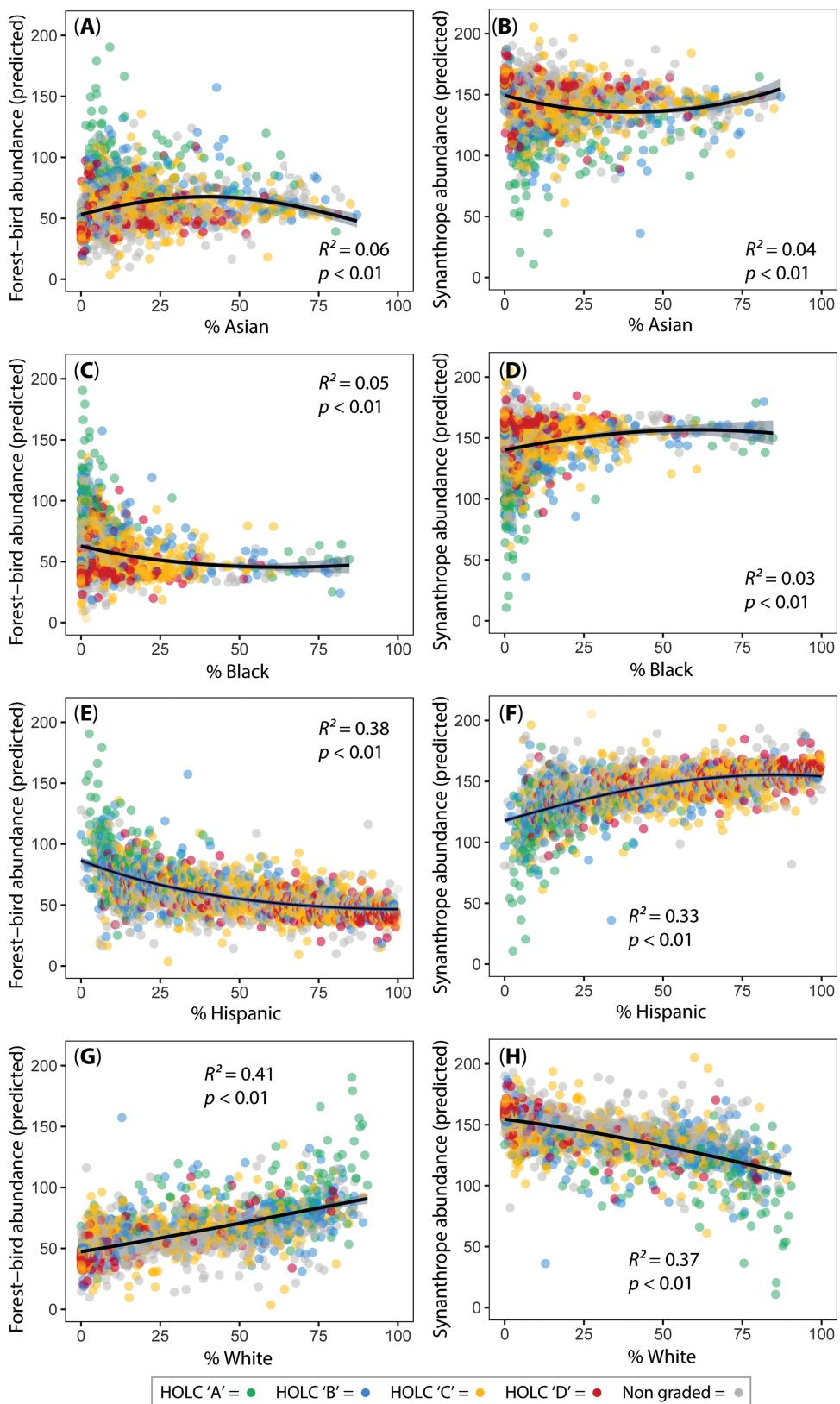


FIGURE 13. Percentage of the (A, B) Asian and (C, D) Black population within census tracts was generally weakly related to the predicted abundance of forest- and synanthropic birds. The percentage of the Hispanic population in census tracts was negatively related to (E) forest-bird abundance and positively to (F) synanthropic-bird abundance, with opposite patterns for (G, H) the White population. The fitted lines and confidence intervals were derived from negative binomial generalized linear models. The R^2 values are Kullback–Leibler-divergence-based R_{kl}^2 values were generated by calculating the likelihood ratio index of a fitted model.

One other alternative explanation for differences in green amenities across urban centers, as well as our within-HOLC category regression and race and ethnicity analysis, could involve preferences and values of natural amenities among racial and ethnic groups (Kaplan and Talbot 1988, Jay et al. 2012, Ordóñez-Barona 2017). “Biocultural diversity” focuses on the interrelationships between nature and culture and has been suggested as a framework for recognizing the inherent cultural differences and preferences among urban dwellers to avoid a one-size-fits-all approach to managing city amenities (Buizer et al. 2016). While our work did not focus on biocultural diversity per se, our findings (e.g., the differences in tree canopy cover among race and ethnic groups) potentially point towards differences in people’s preferences for components of urban biodiversity.

Cultural preferences and values are important when considering urban greening projects. For example, in Chicago, Illinois, in the 1990s the Chicago Park District studied user preferences for park attributes for the master planning effort for Lincoln Park, the largest park in the city and one developed for use by all its residents. While across the board, Black, Hispanic, Asian, and White respondents all appreciated the park and its natural settings, there were key differences including a higher preference for trees among White respondents (18.7% of 898 respondents), compared with Hispanic (11.1%), Asian (7.1%), and Black (3.7%) (Gobster 2002). In Southern California, wealthy residents, which correlate generally with being White, and to a lesser extent Asian, preferred trees on their property compared with lower-income residents (Avolio et al. 2015), which generally correlated with the Black or Hispanic populations in our study. Additionally, based on a questionnaire study of urban park preferences in Atlanta, Georgia, and Philadelphia, Pennsylvania, Ho et al. (2005) found that Hispanic and White respondents more strongly preferred wildlife than Black and Asian respondents. There are numerous correlative examples of race and ethnicity with urban green amenities (Schwarz et al. 2015), and each can help provide clues to how cities can reach shared goals (e.g., urban greening for heat mitigation). Our study cannot offer any evidence of cultural or race and ethnicity preferences for wildlife or urban green amenities as it is merely correlational without the inclusion of focus groups or experimental approaches. Nonetheless, given the evidence from other cities, and the patterns we observed, considering cultural preferences for city planning and management of its green amenities are likely critical to promoting community-centered approaches towards urban stewardship.

The Luxury Effect, the Legacy of Redlining, Urban Avifauna, Habitat, and People

We designed our study to weave a thread through the complicated story of redlining, avifauna, people, and the combination of each across L.A. Further, we used the conceptual frameworks of the luxury- and legacy-effect hypotheses, to test whether historical investment patterns structured by redlining have led to stronger effects on L.A.’s avifauna and their habitat compared with more modern patterns of income inequality throughout the city. We expected to find strong support for the luxury-effect hypothesis—regardless of whether parcels were in HOLC-graded or non-graded zones—where wealthier communities have greater green amenities that attract a higher abundance of birds affiliated with natural

ecosystems. Indeed, our work strongly supports our expectation that the luxury effect is an overarching theme regarding avifauna and their habitat in L.A. (Wood and Esaian 2020, Table 2, Figure 14). Notable patterns we uncovered included the general alignment of the bird community with an affluence gradient, a strong positive relationship for forest birds and a strong negative relationship for synanthropic birds in relation to parcel land values, and non-graded zones having 23% less forest-bird abundance than redlined zones (HOLC D zones) (Table 2, Figure 14). Further, the response of the abundance and richness of some bird groups (e.g., see bird richness patterns), parcel land values, and some habitat variables (e.g., tree canopy cover, street-tree density) were similar between non-graded and CD zones and distinct from AB zones (Table 2). These findings suggest that newer housing developments on the low end of the economic spectrum provide similar conditions for birds as historically redlined areas (Table 2, Figure 14). Our results highlight that the income gradient, prevalent throughout much of L.A., generally structures the avian community and their habitat, which is similar to a related investigation focused on the importance of street trees to feeding migratory birds in the city (Wood and Esaian 2020).

Interestingly, we also uncovered numerous lines of evidence supporting the legacy-effect hypothesis, framed in our case, through the lens of redlining (Table 2, Figure 14). While it was clear that the avifauna of L.A. is structured along an affluence gradient, avian community dissimilarity was greatest between AB and CD zones indicating a wide gap in avifauna between sections of the city that experienced greenlining and redlining (Table 2). Additionally, based on our field surveys, synanthropic birds were more abundant in CD than in AB zones, indicating CD zones of the city have the highest abundance of species affiliated with dense urban conditions (Table 2, Figure 14). Further, synanthropic birds decreased in their abundance much more starkly in low-income non-graded areas of L.A. than in CD zones in relation to parcel land values, suggesting CD zones support a higher number of synanthropic species throughout the city, even at relatively higher levels of parcel land values (Table 2, Figure 14). Our L.A.-wide predictions indicated forest-bird abundance was substantially greater in greenlined (HOLC-A) zones than high-income non-graded zones, possibly due to the historical patterns of investment in large lots, leafy streets, and quiet neighborhoods—conditions that are similar in historically greenlined zones today (Table 2, Figure 14). Regarding the human population, changes in race and ethnicity patterns were less drastic across time (1940-2020) in A-graded zones than in B-, C-, and D-graded zones as well as non-graded areas. This result indicates a strong “island effect” that the historical investment patterns had on buffering change within communities (A-graded zones) in relation to other sections of the city (Table 2). Lastly, our results suggest a strong and potentially different experience for residents of A-graded zones (generally White) and D-graded zones (generally Hispanic) with forest and synanthropic birds (Table 2). The support we uncovered suggests that roughly 80 years following the application of the HOLC security maps in L.A. in 1939, the investment and disinvestment practices appear to continue driving a wedge between A- and D-graded zones in L.A., including the avifauna, their habitat, and the people that are associated with either.

TABLE 2. Lines of support for the luxury- and legacy-effect hypotheses.

Objective	Support	Description
Luxury-effect hypothesis support		
Objective no. 1 (NMDS)	Figure 2	Bird composition and habitat features were generally aligned with an affluence gradient.
Objective no. 1 (ANOVA)	Figure 3C, E, F	Bird abundance and richness for some groups, along with land values, tree canopy, and impervious cover of parcels were similar in CD and non-graded zones but distinct from AB zones, suggesting a general low-to-high-income gradient for variables regardless of redlining designation.
Objective no. 2 (Regression)	Figures 4A, B and 5, 6A, B	The land value of parcels was the strongest predictor in the among- and within-group regression analyses.
Objective no. 3 (Predictive maps)	Figures 7C, D and 8B	Spatial patterns of avifaunal distributions were strongly correlated with parcel-land values, and thus the luxury effect. Low-income non-graded communities had the lowest levels of forest-bird abundance—23% less than redlined zones—highlighting the low-end of luxury-effect patterns in the more recently developed, low-income portions of L.A.
Legacy-effect hypothesis support		
Objective no. 1 (ANOSIM)	ANOSIM	Avian community dissimilarity was strongest between AB and CD zones. Avifaunal communities were similar in AB and non-graded zones.
Objective no. 1 (ANOVA)	Figure 3B, D and Table 2	There were greater differences between AB and CD zones for the abundance of synanthropic- and exotic birds, and natural-lands bird richness when compared with non-graded zones. Also, there were notably smaller parcels in CD zones than in non-graded zones.
Objective no. 2 (Regression)	Figure 6B–D	The opposing slopes for synanthropic-bird abundance in the non-graded group concerning land value, when compared with AB and CD zones, suggested a strong drop-off in the abundance of synanthropes in more expensive non-graded parcels—potentially due to the more expensive properties being developed in a way that attracted more forest birds (e.g., trees). Note that most parcels in our non-graded group from our field data had relatively low parcel land values. Synanthropes in the AB and CD zones concerning parcel land values had similar and more muted slopes suggesting potentially less change in bird-habitat conditions from baseline levels in the HOLC zones.
Objective no. 3 (ANOVA)	Figure 8A, B	The opposing slopes for forest and synanthropic birds related to the year parcels were built within AB or CD zones compared with non-graded newer homes suggested that newer developments were constructed in a way that potentially attracted distinct avifauna. Parcels in AB or CD zones had opposite or similar patterns for forest- and synanthropic birds regardless of when built suggesting potentially different habitat conditions among HOLC zones based on when parcels were constructed compared with non-graded zones.
Objective no. 4 (LMM)	Figure 10A–E	Forest birds were more abundant in HOLC-graded A zones than in high-income zones of the city that were not graded by the HOLC. The mean value within an A-graded neighborhood was 94, and 77.2 in high-income non-graded neighborhoods—a 17.8% difference.
Objective no. 5 (GLM)	Figure 13E–H	Changes in race and ethnicity patterns were less drastic across time (1940–2020) in A-graded zones than in B-, C- and D-graded zones as well as non-graded areas.

Notes: The HOLC categories referenced in the table are as follows: the AB group is a combination of “best,” HOLC grade = A, and “still desirable” HOLC grade = B zones. The CD group is a combination of “definitely declining,” HOLC grade = C, and red, HOLC grade = D zones. The non-graded zones are sections of L.A. that were not subjected to the HOLC grading system.

Recommendations and Conclusion

We recommend that researchers in urban settings interested in income inequality, racial injustice, and biodiversity focus first on luxury-effect patterns (e.g., income levels

across a city), as differences in wealth strongly characterize urban biodiversity and race and ethnicity patterns in L.A. and likely many cities across the country—both large and small. If luxury-effect patterns are well understood, our

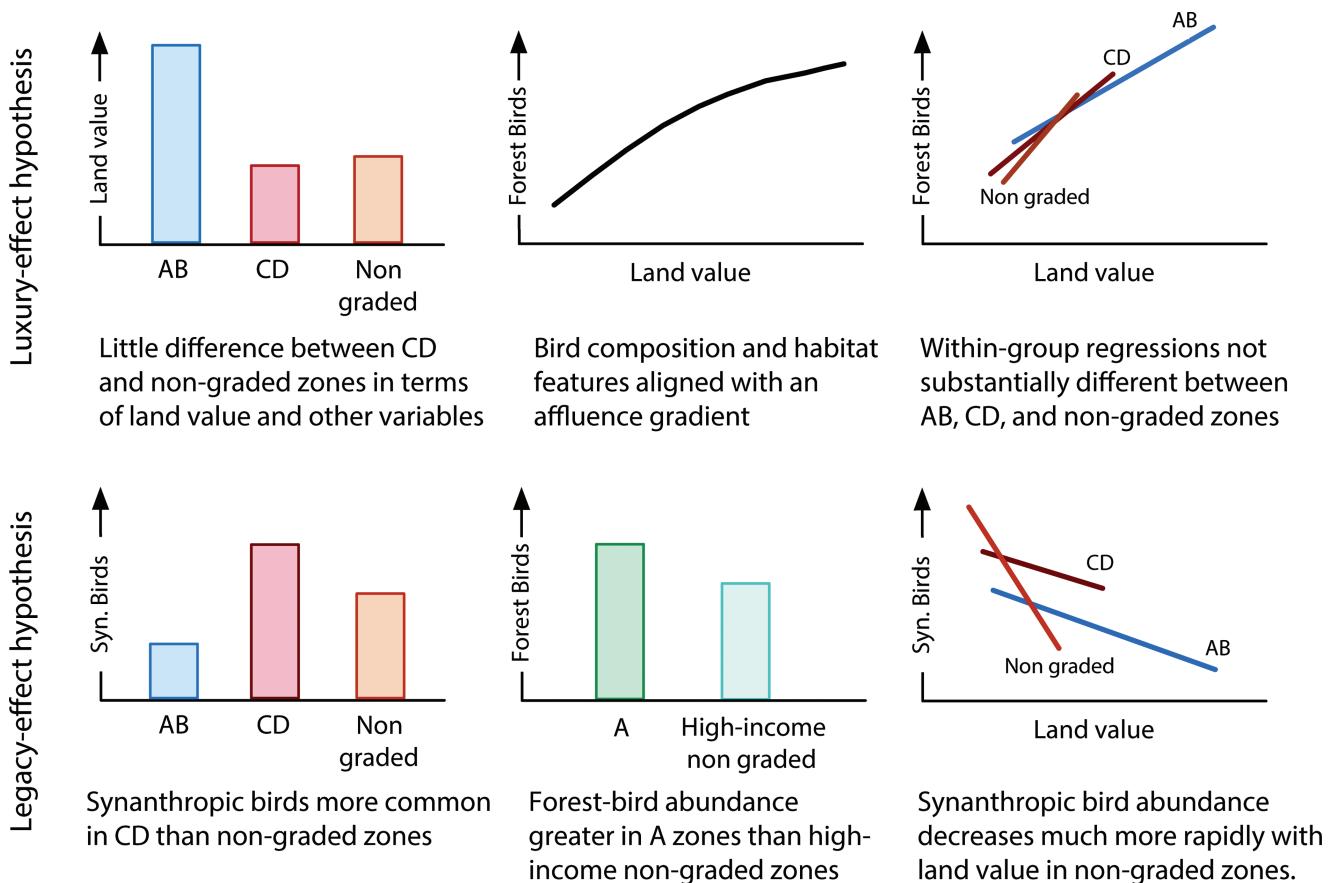


FIGURE 14. Lines of support for the luxury- and legacy-effect hypotheses (Table 2). For a full summary of supporting evidence for either the luxury- or legacy-effect hypotheses. Please see Table 2.

results indicate there are likely numerous avenues for further investigating the potentially lasting effects of redlining on urban biota. Redlining was one of many institutionalized forms of racism in the U.S. that continues to affect urban centers. Thus, moving beyond redlining and understanding other forms of oppressive development (e.g., freeways), or actions (e.g., “slum clearance”), which were often targeted in redlined zones because of the people living there, could be important for better understanding current urban function and equitable development practices.

If promoting biodiversity is a goal, cities across the U.S. and the world must work to understand their racist and segregationist histories (e.g., redlining, blockbusting, single-family zoning, racial housing covenants; [Sadler and Lafreniere 2017](#), [Schell et al. 2020](#), [Menendian et al. 2022](#)), which is a necessary step towards creating conditions that support urban wildlife along with a more equitable experience of wildlife for a city’s inhabitants. Otherwise, urban wildlife—in our case, birds—will likely continue to be as segregated as a city’s population, which calls into question the entire notion of cities as homogenous zones for wildlife ([McKinney and Lockwood 1999](#)) or hotspots for regional biodiversity ([Spotswood et al. 2021](#)). Currently, in the case of L.A., our results suggest it is neither throughout the entirety of its boundaries. Without strong, yet careful intervention (e.g., [Agyeman et al. 2003](#), [Wolch et al. 2014](#), [Rigolon and Németh 2020](#)), residential urban biodiversity will continue to be primarily for the affluent in the City of Angels.

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement

No animals were handled during this research. Further, no human subjects were included in this work. This research was conducted in compliance with the Guidelines to the Use of Wild Birds in Research.

Conflict of interest statement

There are no conflicts of interest with our work.

Author contributions

E.M.W conceived the research; E.M.W and S.E designed the study; S.E, C.B, L.Y.P, P.J.E, and E.M.W conducted fieldwork and data development; E.M.W and L.Y.P analyzed data and produced figures; all authors contributed to writing and editing the manuscript.

Data availability

Data, including markdown files, which are on Zenodo, can be found in [Wood et al. \(2023\)](#).

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