Historical redlining impacts wildlife biodiversity across California

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Author's Contributions: COE and CJS designed the project, with support from CEW and RMF. COE acquired the data. COE led the analysis with support from MF and CJS. COE made the figures. COE was responsible for leading the writing of the manuscript. CEW, MF, RMF, and CJS contributed to writing and editing the manuscript.

Competing Interest Statement: Authors declare no competing interests.

Data Availability: Data and code used in this manuscript will be available upon acceptance of this manuscript.

Abstract

Legacy effects describe the persistent, long-term impacts on an ecosystem following the removal of an abiotic or biotic feature. Redlining, a policy that codified racial segregation and disinvestment in minoritized neighborhoods, has produced legacy effects with profound impacts on urban ecosystem structure and health. These legacies have detrimentally impacted public health outcomes, socioeconomic stability, and environmental health. However, the collateral impacts of redlining on nonhuman species are uncertain. Here, we investigated whether faunal biodiversity was associated with redlining. We used home-owner loan corporation (HOLC) maps [grades A (i.e., “best” and “greenlined”), B, C, and D (i.e., “hazardous” and “redlined”)] across four cities in California and participatory science data (iNaturalist) to estimate alpha and beta diversity across six clades (mammals, birds, insects, arachnids, reptiles, and amphibians) as a function of HOLC grade. We found that greenlined neighborhoods were able to detect unique species with less sampling effort, with redlined neighborhoods needing over 8,000 observations to detect the same number of unique species. Historically redlined neighborhoods had lower native and nonnative species richness compared to greenlined neighborhoods across each city, with disparities remaining at the clade level. Further, community composition (i.e., beta diversity) consistently differed among HOLC grades for all cities, including large differences in species assemblage observed between green and redlined neighborhoods. Our work spotlights the lasting effects of social injustices on the community ecology of cities, additionally emphasizing that urban conservation and management efforts must incorporate an anti-racist, justice-informed lens to improve biodiversity in urban environments.

Keywords: redlining, iNaturalist, environmental justice, legacy effects, species richness

Significance Statement

The legacy of redlining has had dramatic consequences on human and environmental health. Yet our knowledge on the ecological consequences of redlining on wildlife remain nascent. Using participatory science data, we show that biodiversity is greatly diminished across six taxonomic clades in redlined neighborhoods, including mammals, birds, and insects. We also provide evidence suggesting that unique species are detected with less effort in greenlined than redlined neighborhoods. Thus, policies designed to address biodiversity conservation will greatly benefit from considering land-use legacies and the accompanying societal inequities that impact species resilience, ultimately affecting urban resilience, function, and human health. Our work bolsters the case for integrating social and environmental justice as critical lens in creating more equitable and biodiverse cities.

Introduction

Urban biodiversity is quintessential for ecosystem functioning, services, and resilience (1–3), ultimately influencing human and environmental well-being. For instance, bottom-up processes are strengthened by high plant diversity providing more ecological niches to support a greater diversity of fauna relative to more species depauperate areas. Greater plant diversity also mitigates climate-induced challenges by maintaining biogeochemical processes and regulating ecosystem dynamics that support ecological resilience with increasing environmental stochasticity (2, 4). Animal biodiversity can similarly undergird ecosystem function and processing via pollination services and regulating populations which have myriad positive feedbacks on global food systems and maintaining dynamic species relationships that support more biodiversity (4–6). However, the spatial distribution of urban biodiversity, as well as the environmental components necessary to support urban species, is markedly unequal. Thus, determining the factors that generate an unequal distribution of species is essential to the goal of strengthening ecosystem resilience.

Cities are structured by societal inequity, prominently marked by socioeconomic disparities (7, 8). Resource inequity can undergird ecological components, wherein wealthier neighborhoods have greater biodiversity (i.e., the luxury effect (9)). This phenomenon is widespread, having been noted across taxa, including avian and mammalian biodiversity (10–12). Additionally, vegetation and canopy cover – which buffer against air pollutants and reduce urban heat island effects – can vary with socioeconomics(13, 14) . Thus, societal inequity fundamentally biases resource distributions, shaping differences in environmental quality across cities. To understand the ecology of cities, it is imperative to unpack how the social dimensions of cities influence environmental quality and biodiversity (15, 16).

Redlining – a policy in the United States established by the Home Owner's Loan Corporation (HOLC) following the Great Depression – has been shown to influence the environmental quality of urban neighborhoods (17–20). Starting in the 1930s, appraisers ranked neighborhood quality, from favorable (i.e., Grade A, or "greenlined" areas) to the most hazardous areas (i.e., Grade D, or "redlined" areas) (21). These grades led to high disinvestment in redlined neighborhoods, which were Black and/or minoritized populations, compared to greenlined neighborhoods, which were composed of mostly wealthy and white populations. Redlining has subsequently led to poor environmental quality, with redlined neighborhoods having more environmental hazards such as higher pollution burdens and heat-risk than other HOLC grades (22). As a result, redlining has been linked to adverse human health effects such as preterm births, cancer, and asthma (22, 23). This unequal distribution of environmental hazards may be equally salient for nonhuman organisms inhabiting cities. Yet, ecologists are just beginning to grasp the potential ecological effects of redlining on wildlife (24).

Given the long-lasting impacts of redlining on contemporary environmental quality, it is likely that urban biodiversity may be similarly affected in the United States(24). Indeed, recent work has shown that redlining is associated with the distribution of urban bird biodiversity in Los Angeles(25), as well as biodiversity sampling densities across the US (26). However, the impact of redlining on other taxa remains uncertain, and the association between redlining and faunal biodiversity may vary by clade. For example, the life-histories and ecologies of insects and amphibians (e.g., limited movement, smaller home ranges, etc.) may increase these species' relative exposures to harsh environmental conditions associated with redlining. As a consequence, we may observe greater species reductions in certain clades relative to others, such as birds and mammals. Moreover, the effect of redlining may vary across cities due to differences in city size and climate – as seen in relation to societal wealth(10). Yet, there is no empirical support that articulates how redlining legacies are differentially experienced across clades and cities.

Examining the association between redlining across multiple clades and cities requires incredibly fine-scale data and large geographic coverage. Participatory science data – where data is collected voluntarily by individuals – can alleviate this due the vast spatial coverage and low-cost the data (27, 28). Despite biases within these data (29–31), participatory data sources are incredibly powerful for answering large-scale questions concerning biodiversity. One of the more prominent participatory platforms – iNaturalist – has proven essential for assessing urban biodiversity due to its vast taxonomic coverage (32). Over 40% of the recorded observations in the Global Biodiversity Information Facility (GBIF), the largest global repository of biodiversity data, come solely from iNaturalist, and over 50% of the unique species catalogued in GBIF were derived from iNaturalist (33). Indeed, such participatory data provide extraordinary resolution to understand local to global patterns in species diversity (34), evaluate how urbanization affects biodiversity hotspots (35), and assess species' responses to climate change (36). Participatory data therefore provide an ideal data source to examine the relationship between historical redlining and urban biodiversity across various cities.

Here, we merged HOLC maps with participatory science data (iNaturalist) to determine whether redlining was associated with differences in faunal biodiversity in Californian cities. We focused on California, the most biodiverse and populous state in the US, with some of the largest cities co-located with biodiversity hotspots. In addition, our previous work has demonstrated that previously redlined neighborhoods in California have higher pollution burdens, less vegetation, elevated temperatures, and more noise (37) – habitat conditions that likely structure neighborhood biodiversity via bottom-up processes (24). First, we predicted that greenlined neighborhoods would detect more unique species with less sampling effort compared to redlined neighborhoods due to differences in green space and vegetation as well as potential skews in participation (26, 38). Next, we examined species richness (i.e., alpha diversity) within each HOLC grade, and predicted that after controlling for the effect of urbanization (i.e., urban intensity), neighborhood area, and uneven sampling, that redlined neighborhoods would have reduced species richness and native biodiversity relative to greenlined neighborhoods due to reductions in environmental quality (24). We also predicted that greenlined neighborhoods would reach their maximum number of observed species in fewer observations compared to redlined neighborhoods due to differences in green space and vegetation as well as potential skews in participation (26, 38). Lastly, we examined differences in species communities (i.e., beta diversity) by comparing species assemblages among HOLC grades. We predicted that greenlined neighborhoods would be more dissimilar to redlined neighborhoods due to strong differences in environmental quality (22, 24). We expected that HOLC grades that were closely ranked (i.e., A vs B or C vs D) would not differ in species assemblages.

Results

Accumulated Species Richness

We calculated accumulated species richness, i.e., cumulative *observed* species richness, by correlating the observed number of unique species with the number of total observations across all species per HOLC grade. We extracted accumulated species richness in greenlined neighborhoods, and the observations needed to reach this total. We then used this value to calculate the differences in observations needed for redlined neighborhoods to reach an equivalent accumulated species richness in greenlined neighborhoods. Accumulated species richness deals with biases in biodiversity sampling, which can contribute to differences in observed biodiversity based on observations within a HOLC grade and is crucial for equitable conservation.

We found that Grade C had the highest accumulated species richness (1,281 species), followed by B (1,124 species), D (1,039 species), and A (964 species) (Figure 1). In grade A, it took 17,095 observations to reach the grade's maximum observed species richness (964). To reach an observed species richness of 964 in grade D, it took 25,445 observations (Δ = 8,350), while in grades B and C, it took 27,519 (Δ = 10,424) and 29,730 (Δ = 12,635) observations, respectively (Figure 1). We observed this trend between grades A and D for all cities except for San Diego, where grade D reached the maximum species richness observed in grade A with fewer observations (Figure S1). We also observed this trend in accumulation curves for native and nonnative species, though the delta values between grades A and D were smaller (native Δ = 621; nonnative Δ = 691) (Figure S2).

Alpha diversity: Species Richness

We analyzed species richness across six clades: birds, mammals, insects, arachnids, reptiles, and amphibians. We used a Bayesian approach to parameterize our model with HOLC grade and percentage of impervious surface as fixed effects. The model intercept and HOLC grade were also allowed to vary by city (i.e., random intercept and slope terms) to quantify associations between HOLC grades and species richness across cities. We included area and the number of observations as a log-offset term to control for differences in neighborhood size and observation intensity (see Methods). We used this model to predict species richness for each neighborhood rather than raw data to control for uneven sampling (Figure 1). We then disaggregated our data into native and nonnative species to ascertain potential drivers of overall species richness. For overall, native, and nonnative species richness, we found significant differences among HOLC grades (Table 1).

After controlling for urban intensity, neighborhood area, and the number of observations in a HOLC neighborhood, we found that redlined neighborhoods had the lowest species richness (Figure 2; Table 1), including at the clade-level (Table S2). On average, across all cities, grade A had the highest species richness (median = 20.41, CI: 3.18, 65.15), followed by grades B (14.61, CI: 1.59, 92.33), C (11.82, CI: 1.43, 62.72), and D (5.59, CI: 0.71, 28.88), with significant differences between grades A and D (median: 23.95, CI: 0.80, 47.11) (Table 1). Similar trends were observed for native species richness, with redlined neighborhoods having the lowest native species richness (3.39, CI: 0.46, 16.99) and significant differences between grades A and D (15.07, CI: 0.61, 29.53) (Table 1). We found no significant differences among HOLC grades for nonnative species richness.

We found significant differences between each HOLC grade per city. However, cities varied in how HOLC grades were associated with species richness with redlined neighborhoods holding the lowest species richness in three of the four cities examined (Figure 2; Table 1). San Diego and San Francisco had the largest disparities in average species richness between greenlined and redlined neighborhoods, at Δ = 44 and Δ = 29, respectively, compared to Los Angeles (Δ = 6) and Oakland (Δ = 5). Species richness trends did not always follow the ranked HOLC grading at the city level (Figure 2). While San Diego followed the ordered trend, San

Francisco, Los Angeles, and Oakland had different patterns. In San Francisco, greenlined neighborhoods had the highest species richness and were followed by grades C, D, and B. In Los Angeles, B-grade neighborhoods had the highest species richness, followed by grades A, C, and D, and similarly, in Oakland, B-grade neighborhoods had the highest species richness but was followed by grades C, A, and D (Table 1). Similar trends were observed for native and nonnative richness (Figure S3-4; Table 1). We found significant differences at the city level between most HOLC grades for native and nonnative species richness except native richness in Los Angeles between grades A and C (0.34, CI: -0.10, 0.78) and nonnative richness in San Francisco between grades C and D (0.23, CI: -0.12, 0.57).

We found similar differences in species richness across all six clades, with grades A and B having the highest species richness and grade D having the lowest across clades (Figure 3; Tables S1-7), except for bird and insect richness in San Francisco, which was slightly lower in grade B. We found significant differences at the clade level between green and redlined neighborhoods across all clades within each city, except for mammals, reptiles, and arachnids in Oakland (Figure 3; Tables S1-7). We found consistent disparities between green and redlined neighborhoods for native and nonnative richness across clades, though there was some variation (Tables S1-7).

Beta diversity

We calculated beta diversity (i.e., differences in types of species) using Jaccard's index and tested for differences in species assemblage among HOLC grades using PERMANOVAs. We found a significant effect of city ($R^2 = 0.0606$, $F = 15.1827$, $p < 0.0001$) and HOLC grade ($R^2 = 0.0091$, $F = 2.2888$, $p < 0.0001$) on beta diversity (Figures 4, S5-9). We found similar results when we solely examined native (city: $R^2 = 0.0651$, $F = 16.3574$, $p < 0.0001$; HOLC grade: $R^2 = 0.0090$, $F = 2.2969$, $p < 0.0001$), and nonnative species (city: $R^2 = 0.05581$, $F = 13.6553$, $p < 0.0001$; HOLC grade: $R^2 = 0.00939$, $F = 2.2694$, $p < 0.0001$).

Across each city, we found that HOLC grades were associated with beta diversity (Figure 4; Table S8). For Los Angeles, we found significant differences in beta diversity between all HOLC grades (Table S8), with grades A and C, A and D and B and D showing the strongest differences in species assemblages ($p < 0.001$). In San Francisco, we found significant differences between grades A and C ($p < 0.01$), A and D ($p < 0.001$), B and D ($p < 0.001$), as well as B and C ($p < 0.01$). In Oakland, we found significant differences between grades A and D, B and C, and B and D ($p < 0.05$). In San Diego, we found significant difference between grades A and C as well as A and D ($p < 0.05$). For native and nonnative species, we found nearly identical patterns in significant differences between HOLC grades for each city (Figures S; Table S8), except for native species in San Diego, where no significant differences in beta diversity were found ($p = 0.1955$).

Discussion

By analyzing 708 previously HOLC-graded neighborhoods in four California cities, we found three main linkages between redlining and biodiversity. First, we found that greenlined neighborhoods detected species in significantly fewer observations than other HOLC grades. Second, redlining was uniformly associated with decreased alpha diversity across all cities and observed in each clade. Third, we found that species assemblages varied in each HOLC grade, with green and redlined neighborhoods having significantly different species assemblages in each city examined. The evidence presented here supports previous theoretical linkages between redlining and faunal biodiversity introduced in Schell et al. (2020) across major taxonomic clades, highlighting the connections among systemic racism and urban ecosystems. Disentangling the relationship between redlining and biodiversity provides a critical first-step in evaluating how inequitable policies have downstream consequences for the community ecology of cities.

In support of our hypotheses, the number of unique species potentially present in a community pool was more effectively estimated in fewer observations for greenlined neighborhoods relative to other grades. These results align with recent work by Ellis-Soto and colleagues (2023), showing that bird biodiversity sampling is typically more even and higher in greenlined neighborhoods compared to redlined neighborhoods. However, for iNaturalist data, this disparity is not due to differences in observation efforts, as in California. Our results indicated that non-greenlined neighborhoods (i.e., B, C, and D) had higher observations than greenlined neighborhoods. Rather, our results suggest that an individual is more likely to encounter a greater diversity of species with less search effort in California's greenlined neighborhoods than in non-greenlined neighborhoods. This may potentially be explained by greenlined neighborhoods customarily having increased environmental quality (i.e., higher vegetation cover and reduced ecological disturbances (19, 22, 37, 39, 40)), which in turn improves the likelihood of unique species occupying the given area. This holds broad implications for human well-being in urban spaces, as equity in nature access and quality, as well as promoting positive human-environment relationships (which are more likely with increased access to biodiverse spaces) are increasingly being considered as central issues of environmental justice (41, 42).

After controlling for differences in observations, as well as neighborhood area and urban intensity, we found that redlined neighborhoods had less species richness than greenlined neighborhoods. Conversely, there was slight variation in which grade had the highest richness, with greenlined neighborhoods in San Diego and San Francisco and B-grade neighborhoods in LA and Oakland having the highest species richness. Both A and B-graded neighborhoods in California have relatively improved environmental quality (37), suggesting there may be more viable wildlife habitat compared to C and D-graded neighborhoods. We found consistent disparities on the clade level, with redlined neighborhoods frequently exhibiting the lowest species richness. Taken together, our results suggest that redlining has pronounced legacy effects on species richness, in spite of apparent social and ecological variation among cities. Further, despite differences in mobility and tolerances to environmental hazards associated with redlining, our evidence suggests wildlife across all clades are detrimentally impacted by the legacy effects of redlining. The legacy effect of redlining is particularly pronounced in San Diego and San Francisco, with large differences in species richness between green and redlined neighborhoods across most taxonomic groups. This may be due in part to the relative area covered by HOLC maps in these cities. Urban greenspaces often serve as *de facto* biogeographic "islands", with smaller and more distant patches showing reduced species richness and colonization (43). It is possible that the combination of reduced geographic space (e.g., HOLC maps for San Diego and San Francisco cover 59 and 109km^2 relative to Oakland and LA at 123 and 846km^2, respectively) and smaller HOLC neighborhoods concentrate disturbances in redlined areas, resulting in more pronounced reductions in species richness for previously C and D-graded neighborhoods.

Contrary to our predictions, we failed to detect higher nonnative species richness in redlined areas. Rather, we found that greenlined neighborhoods had higher nonnative species than non-greenlined neighborhoods. Greenlined neighborhoods may have higher nonnative species richness for several reasons. While urban areas generally have high levels of nonnative species (44), they are not uniformly distributed. Wealthy urban neighborhoods tend to have higher abundances of nonnative trees and plants (45, 46), which have the potential to dampen native richness by selecting against species that may rely on native plants (47, 48). A reduction of native species can free up space within an ecosystem, potentially allowing for nonnative species to spread and establish within an environment (49). Moreover, the intentional selection of nonnative plant species with aesthetic characteristics (e.g., flowering, ornamentation, and color) deemed desirable can bolster their abundances in greenlined neighborhoods (50). Nonnative plants considered aesthetically pleasing are often expensive, and residents that live in greenlined areas often have more economic mobility to purchase these plants. Thus, although nonnative species tend to do better in more disturbed habitat (51, 52), such as redlined neighborhoods, our results suggest that varying social-ecological drivers of plant communities across neighborhoods may dilute or offset any potential differences in nonnative species richness across red and greenlined areas.

We found that beta diversity differed between HOLC grades across cities, with green and redlined neighborhoods having consistently different species assemblages. This result held true when we examined native and nonnative species for each city, except for San Diego, where native species assemblage did not differ across HOLC grades. These results may be explained city-level attributes that exacerbate the influence of redlining on species assemblages across the observed cities. For instance, San Francisco is the most densely populated city in California (7,194 people/km^2) with extensive impervious surface cover on a peninsula with a large highway on the southern border. Thus, San Francisco may function as an urban island with limited immigration pathways for terrestrial organisms to colonize the city. In addition, the geographic space is further partitioned by highways I-280 and I-101 in the east, creating multiple urban islands on the peninsula. These biogeographic factors, combined with uneven vegetation, may amplify differences in species pools between greenlined neighborhoods in the west and redlined neighborhoods in the east. Thus, species in San Francisco's redlined neighborhoods may consist of a few generalist species (e.g., raccoons, pigeons, brown rats, etc.) that can cope with myriad human-driven ecological disturbances. Differences in vegetation and built environment, which determine habitat availability and connectivity, hold implications for species assemblages and the related ecosystem services, such as pollination of small-scale gardens, which is critical for food justice.

Cities have historically been excluded from biodiversity conservation efforts, due to this broad assumption that cities represent "biological deserts" devoid of unique species and assemblages (53–55). As the world continues to urbanize, this archaic worldview is becoming less common (56–59). Recent efforts to conserve global biodiversity, such as 30x30 and the United Nations' Goal 15 (60, 61), are now acknowledging cities important conservation hubs, especially given the fact that more than 400 cities globally are situated in biodiversity hotspots (62, 63). Reimagining cities as biodiversity centers subsequently shifts the focus to assessing the social-ecological drivers that facilitate or hinder species persistence. Our results highlight that societally driven disparities in housing have profound impacts on urban faunal biodiversity in California cities, with redlined neighborhoods having orders of magnitude less faunal biodiversity than greenlined neighborhoods. In cities, societal injustices that contribute to disparities in environmental and human well-being are often highly concentrated in marginalized communities (64); thus, urban areas may serve as ideal test cases for understanding the broader impacts of inequities on wildlife via metrics such as biodiversity. Our results demonstrating the association between redlining and faunal biodiversity within and across cities provide a novel set of metrics to bolster ongoing efforts to rectify harmful legacy effects (e.g., City of Oakland's Race and Equity Department), especially as redlined neighborhoods in California are predominantly composed of marginalized populations along both race and class lines (65). Recognizing and prioritizing social justice will be key for accomplishing equitable conservation and achieving lasting outcomes that safeguard our urban ecosystems for generations.

Materials and Methods

Study region

Our study takes place throughout the state of California within the United States of America. Within California, eight cities have digitized HOLC maps via the University of Richmond's Mapping Inequality project (66): Fresno, Los Angeles, Oakland, Sacramento, San Diego, San Francisco, San Jose, and Stockton. In our analysis, we only included cities with at least five observations in each HOLC grade per clade. Thus, our analysis was restricted to Los Angeles, Oakland, San Diego, and San Francisco. Note: the Oakland HOLC map includes Oakland, Berkeley, San Leandro, Piedmont, Emeryville, and Albany and the Los Angeles HOLC map includes the greater Los Angeles area (66).

Datasets and Geospatial Processing

We used three data sources: (1) HOLC grade maps via the Mapping Inequality project (66), (2) iNaturalist data, and (3) the National Land Cover Database's (NLCD) 2019 impervious surface layer.

We downloaded the digitized HOLC maps of California from the Mapping Inequality database and all iNaturalist research-grade observations of mammals, birds, reptiles, amphibians, insects, and arachnids from the past five years (January 1, 2017 - January 1, 2022) within HOLC polygons for each city. We selected the these years to coincide with the rise in the use of iNaturalist (67), which resulted in 123,235 total observations. Although we selected research-grade observations, some rows lacked species information (<50). These rows were filtered out, yielding 123,191 observations. We then selected for the four cities in our analysis, yielding 114,711 observations for biodiversity analysis (1800 unique species). Because we were interested in differences between native and nonnative species among grades, we then redownloaded native species data from iNaturalist and filtered for native species (via selecting 'no' on introduced species and 'yes' on native species). We used this data to extract the number of native and nonnative species in our original dataframe. To control for differences in observations within our dataset (Figure S9), we log-offset the number of observations per neighborhood (see details below). Lastly, we obtained the mean percentage of impervious surfaces from the NLCD for each HOLC neighborhood using NLCD layer via Zonal Statistics in ArcGIS Pro.

Data analysis

We investigated the influence of HOLC grade on biodiversity. All statistical analyses were completed in R v.4.1.0 (68) and all plots were made using the *ggplot2* package (69)).

For biodiversity data, we calculated alpha and beta diversity. For alpha diversity, we calculated the accumulated observed species richness, i.e., the number of unique species in relation to observations within a HOLC grade, and species richness, i.e., the number of unique species, and. To calculate accumulated observed species richness, we manipulated our data to track the number of observations of species in a HOLC grade as well as the absence of observations (i.e., a value of 0). Hence, a value of 0 does not contribute to species richness but contributes to the observation count, and a value of 1 or higher contributes to species richness and observation count. We used this to visualize how species richness accumulates as observations increase until maximum observed richness is reached in a grade. We calculated beta diversity by using a presence-absence (Jaccard's) metric in the *adonis* function via the *vegan* package (70), which generates values between 0, representing complete dissimilar species assemblages, and 1, representing completely similar assemblages. To examine significant differences in beta diversity among HOLC grades, we used a PERMANOVA with 10000 permutations and a Benjamin-Hochberg correction.

We used a Bayesian framework to understand the influence of HOLC grade on species richness, using a Poisson mixed-effects model via the *nimble* package in R (71). Our response variable was the number of species observed in each HOLC neighborhood. We included HOLC grade as a fixed effect, though the model intercept and HOLC grades were allowed to vary by city (i.e., a random intercept, random slope model). To account for variation in sampling and neighborhood size, we logged and summed neighborhood area and number of observations per neighborhood, which we then included as an offset term in the model. Before log-offsetting observations, we ensured that each neighborhood had at least one observation (72). Finally, we included impervious surface in our model to control for the negative influence impervious surface has on species richness (10, 73). Fixed effects were given Normal (0, 2) priors, while standard deviation terms associated to city-level random effects were given Gamma (1,1) priors. Following a 110,000-step burn-in, we sampled the posterior for 40,000 iterations across 4 chains. To check for model convergence, we ensured that Gelman-Rubin diagnostics were < 1.10 (74). To examine if there were significant differences between HOLC grades, we conducted hypothesis testing in a Bayesian framework. After fitting our model, we calculated contrasts between each HOLC grade, representing differences in species richness between grades. We then calculated the credible intervals of these differences and examined if they overlapped zero. For significant differences, we report the median and confidence intervals.

Acknowledgements

We would like to thank Annie Taylor for advice and guidance in ArcGIS, Andy Lee and Sam Larkin for helping troubleshoot R-code, and Diego Ellis-Soto for suggestions that improved this paper. C.O.E. was supported by the University of California, Berkeley's Chancellor Fellowship and the National Science Foundation Graduate Research Fellowship under Grant No. DGE-2146752. C.E.W. was supported by Schmidt Science Fellows, in partnership with the Rhodes Trust. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation.

Figures and Tables

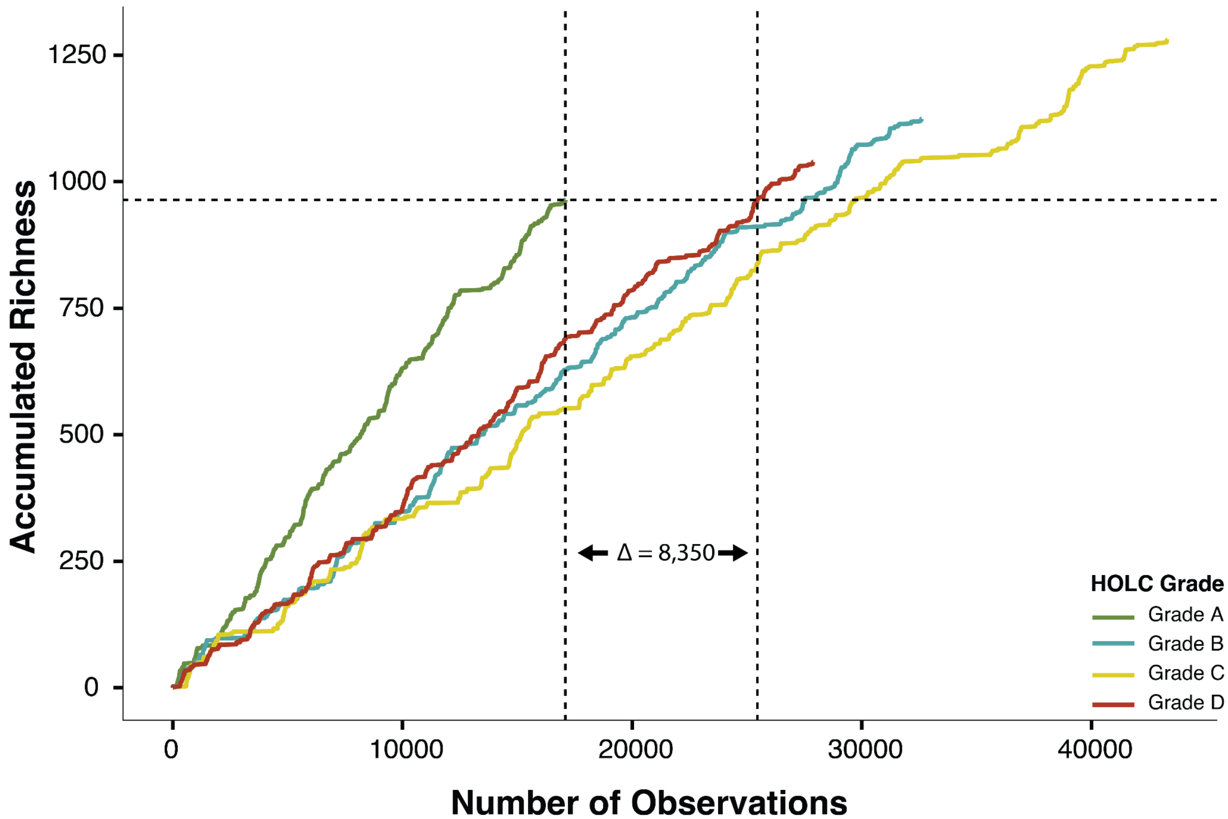

Figure 1. Greenlined neighborhoods detect more unique species with less sampling effort. Species accumulation curves for each HOLC grade across six clades. The x-axis shows the number of observations within each HOLC grade. The y-axis shows accumulated species richness. The dashed horizontal line* shows the maximum accumulated richness for Grade A. The vertical lines** show the number of observations to reach Grade A's maximum accumulated richness in Grade A (left vertical line) and in Grade D (right vertical line). The difference in observations between redlined (i.e., grade D) and greenlined (i.e., grade A) and neighborhoods is shown as a delta value.

*Horizontal line: y = 964

**Vertical lines (grade A, grade D): x = 17,095; 25,445

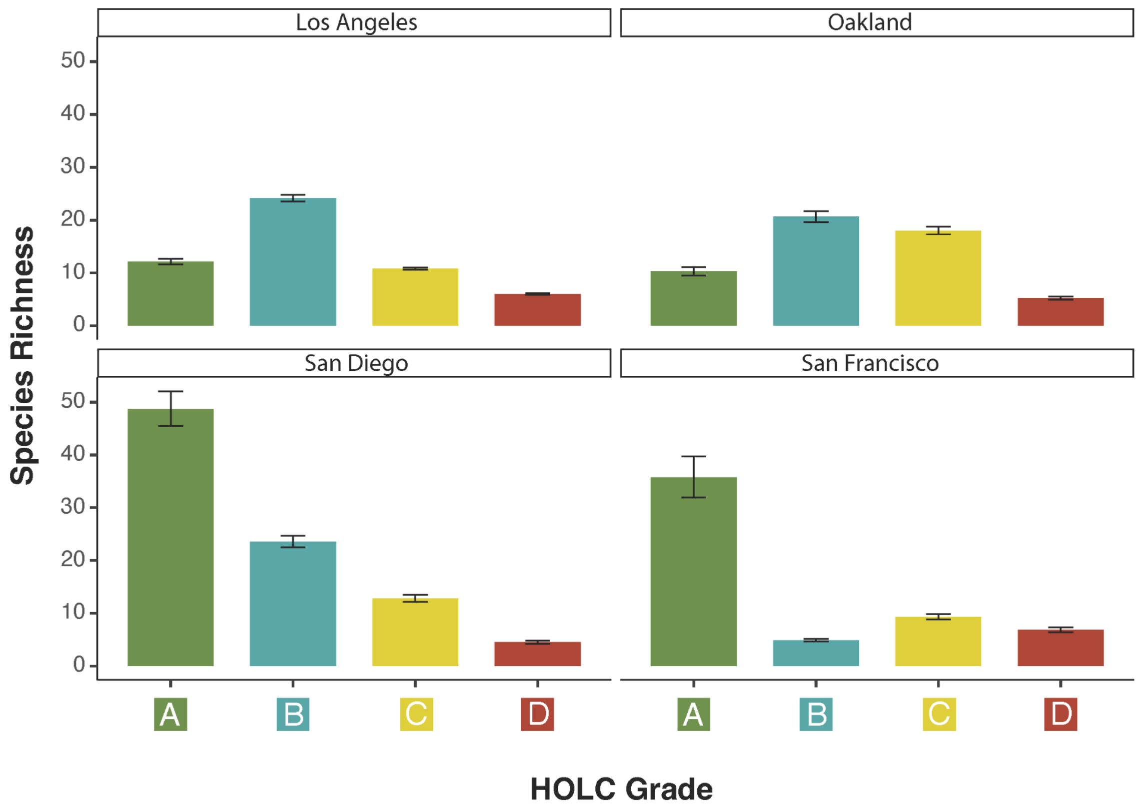

Figure 2. Redlined neighborhoods across California have lower species richness. Species richness for all species across six clades among HOLC grades for Los Angeles (top left), Oakland (top right), (C) San Diego (bottom left), and San Francisco (bottom right). Bars represent the mean, and whiskers represent 95% credible intervals. All pairwise comparisons are significant.

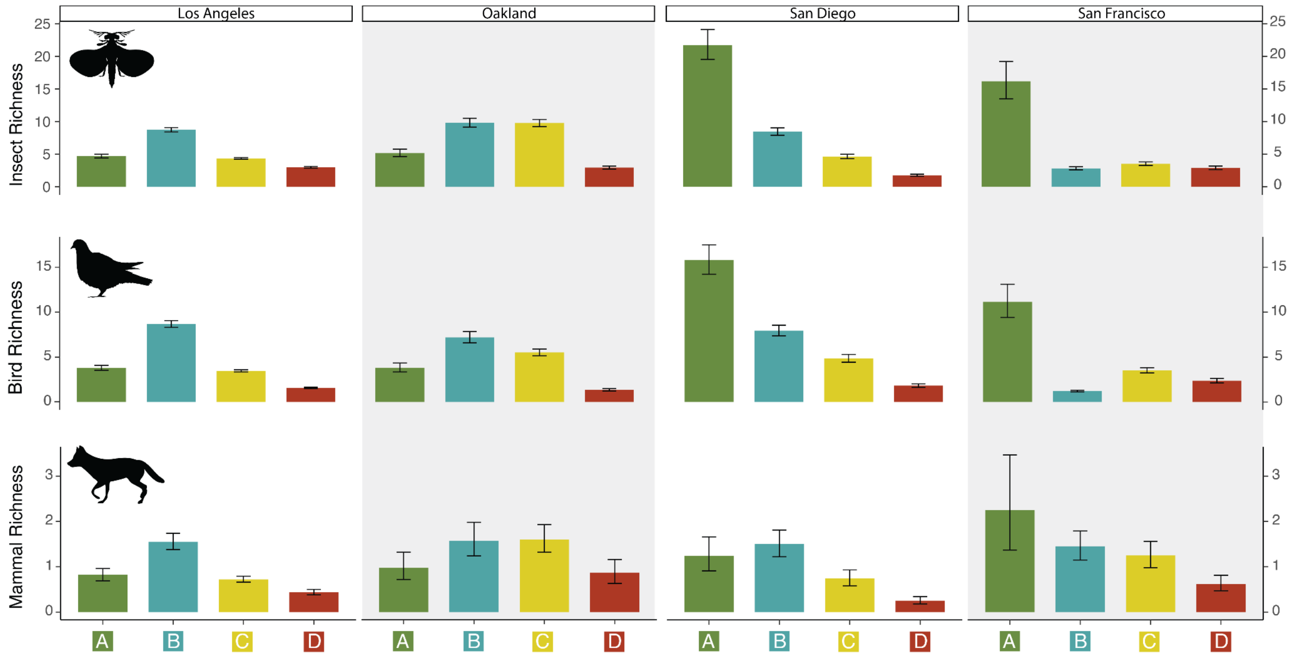

Figure 3. Clade richness is consistently lower in redlined neighborhoods. Species richness for insects (top row), birds (middle row), and mammals (bottom row) shown among HOLC grades for each Californian city (columns). Los Angeles is on the far left, Oakland is on the middle left, San Diego is on the middle right, and San Francisco is on the far right. Bars represent the mean, and whiskers represent 95% credible intervals. All pairwise comparisons are significant. All comparisons between green- (i.e., grade A) and redlined (i.e., grade D) neighborhoods are significant. *Note*: for each clade, the y-axis (species richness) is subject to change.

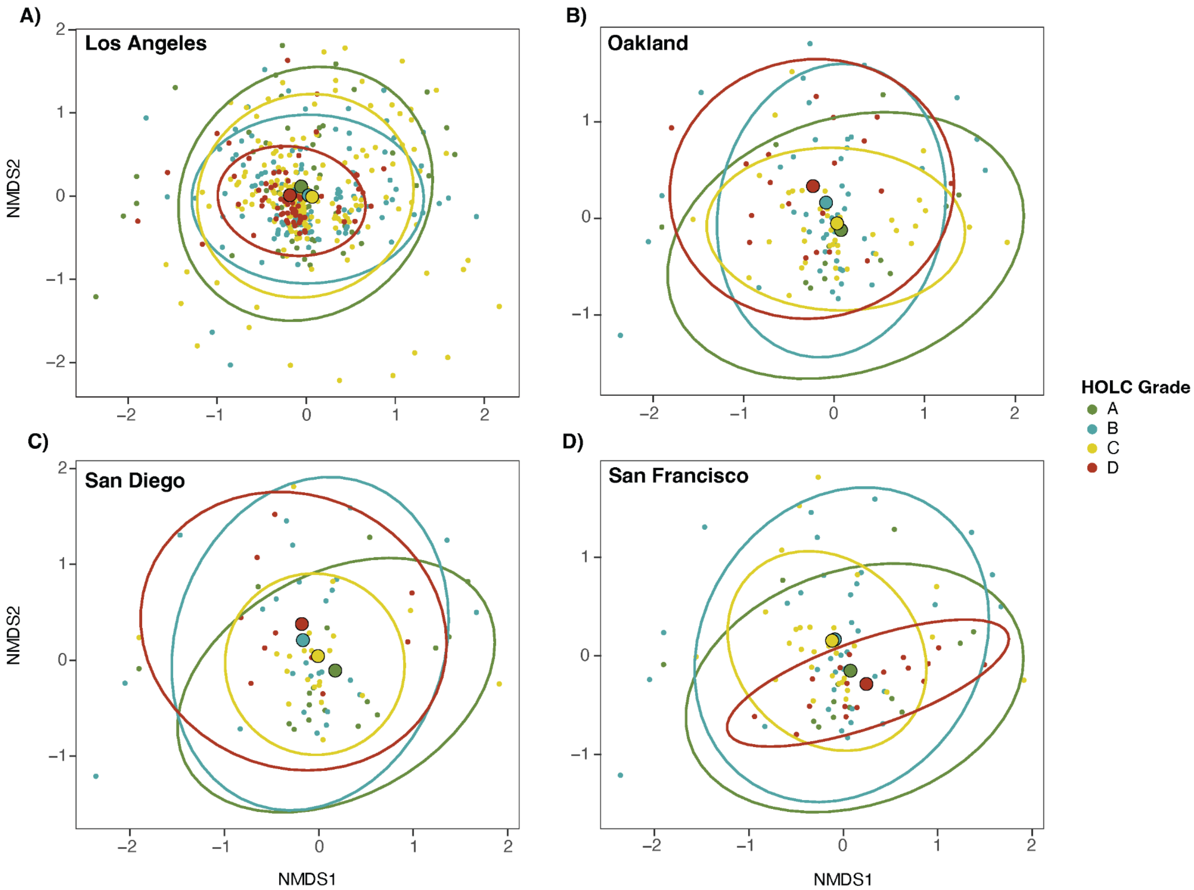

Figure 4. Redlined neighborhoods differ in their species assemblage. Non-metric multidimensional scaling (NMDS) for β-diversity (Jaccard's metric) among HOLC grades in (A) Los Angeles, (B) Oakland, (C) San Diego, and (D) San Francisco. Each dot represents a neighborhood and ellipses encompass 95% data points. No overlap between ellipses suggests that HOLC grades have distinct beta diversity patterns and strong dissimilarity in species assemblage. Substantial overlap in ellipses suggests that beta diversity between HOLC grades is more similar to each other and there is strong similarity in species assemblage.

City	HOLC Grade	Mean Richness	Mean Native Richness	Mean Nonnative Richness
ALL	A	20.4 (3.25, 65.29)	12.72 (2.06, 40.82)	7.47 (1.10, 24.73)
ALL	B	14.65 (1.60, 92.26)	8.9 (0.98, 56.53)	5.81 (0.60, 36.69)
ALL	C	11.74 (1.45, 62.93)	7.5 (0.95, 39.07)	4.20 (0.47, 24.22)
ALL	D	5.57 (0.72, 28.32)	3.39 (0.46, 16.99)	2.17 (0.25, 12.33)
Los Angeles	A	12.15 (11.65, 12.65)	7.16 (6.79, 7.55)	5.2 (4.85, 5.58)
Los Angeles	B	24.17 (23.55, 24.8)	14.71 (14.23, 15.21)	9.69 (9.29, 10.1)
Los Angeles	C	10.78 (10.57, 10.98)	6.83 (6.66, 7)	4.09 (3.97, 4.22)
Los Angeles	D	5.99 (5.81, 6.17)	3.57 (3.43, 3.71)	2.53 (2.41, 2.65)
Oakland	A	10.3 (9.56, 11.10)	6.71 (6.11, 7.34)	3.25 (2.83, 3.71)
Oakland	B	20.66 (19.65, 21.70)	12.29 (11.54, 13.07)	8.24 (7.56, 8.95)
Oakland	C	18.02 (17.31, 18.75)	10.89 (10.36, 11.44)	6.77 (6.32, 7.25)
Oakland	D	5.23 (4.94, 5.53)	3.06 (2.85, 3.27)	2.11 (1.92, 2.31)
San Diego	A	48.73 (45.43, 51.98)	32.56 (29.98, 35.23)	16.33 (14.36, 18.47)
San Diego	B	23.55 (22.50, 24.64)	15.81 (14.95, 16.7)	7.49 (6.91, 8.1)
San Diego	C	12.81 (12.16, 13.49)	8.95 (8.38, 9.54)	3.73 (3.42, 4.06)
San Diego	D	4.49 (4.21, 4.79)	3.2 (2.95, 9.54)	1.24 (1.11, 1.38)
San Francisco	A	35.84 (32.02, 39.97)	20.77 (18.19, 23.49)	10.4 (8.28, 12.87)
San Francisco	B	4.9 (4.64, 5.16)	2.63 (2.46, 2.8)	1.83 (1.66, 2.01)
San Francisco	C	9.3 (8.83, 9.79)	5.63 (5.28, 6)	2.57 (2.35, 2.8)
San Francisco	D	6.86 (6.42, 7.31)	3.77 (3.48, 4.07)	2.34 (2.08, 2.61)

Table 1. Species Richness across HOLC grades. Species richness across all clades is shown for all cities (first four rows) and each city per HOLC grade (grades A = "best" and "greenlined", B, C, and D = "hazardous" and "redlined"). We show overall species richness, native species richness, and nonnative species richness with mean and 95% credible intervals.

References

1. S. Diaz, D. Wardle, A. Hector, “Incorporating biodiversity in climate change mitigation initiatives” in *Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective*, (OUP Oxford, 2009), pp. 149–166.
2. G. G. Mittelbach, B. J. McGill, *Community Ecology* (Oxford University Press, 2019).
3. A. Truchy, D. G. Angeler, R. A. Sponseller, R. K. Johnson, B. G. McKie, “Chapter Two - Linking Biodiversity, Ecosystem Functioning and Services, and Ecological Resilience: Towards an Integrative Framework for Improved Management” in *Advances in Ecological Research*, Ecosystem Services., G. Woodward, D. A. Bohan, Eds. (Academic Press, 2015), pp. 55–96.
4. N. Schwarz, *et al.*, Understanding biodiversity-ecosystem service relationships in urban areas: A comprehensive literature review. *Ecosystem services* **27**, 161–171 (2017).
5. G. M. Mace, K. Norris, A. H. Fitter, Biodiversity and ecosystem services: a multilayered relationship. *Trends in ecology & evolution* **27**, 19–26 (2012).
6. P. Harrison, *et al.*, Linkages between biodiversity attributes and ecosystem services: A systematic review. *Ecosystem services* **9**, 191–203 (2014).
7. L. Cushing, R. Morello-Frosch, M. Wander, M. Pastor, The Haves, the Have-Nots, and the Health of Everyone: The Relationship Between Social Inequality and Environmental Quality. *Annual Review of Public Health* **36**, 193–209 (2015).
8. M. Kuhn, M. Schularick, U. I. Steins, “Income and Wealth Inequality in America, 1949-2013” (CESifo Working Paper, 2017).
9. D. Hope, *et al.*, Socioeconomics drive urban plant diversity. *Proceedings of the national academy of sciences* **100**, 8788–8792 (2003).
10. S. B. Magle, *et al.*, Wealth and urbanization shape medium and large terrestrial mammal communities. *Glob. Chang. Biol.* **27**, 5446–5459 (2021).
11. D. E. Chamberlain, D. A. W. Henry, C. Reynolds, E. Caprio, A. Amar, The relationship between wealth and biodiversity: A test of the Luxury Effect on bird species richness in the developing world. *Global Change Biology* **25**, 3045–3055 (2019).
12. M. Leong, R. R. Dunn, M. D. Trautwein, Biodiversity and socioeconomics in the city: a review of the luxury effect. *Biology Letters* **14**, 20180082 (2018).
13. K. Schwarz, *et al.*, Trees Grow on Money: Urban Tree Canopy Cover and Environmental Justice. *PLOS ONE* **10**, e0122051 (2015).
14. C. B. Riley, M. M. Gardiner, Examining the distributional equity of urban tree canopy cover and ecosystem services across United States cities. *PLoS One* **15**, e0228499 (2020).
15. S. T. A. Pickett, M. L. Cadenasso, D. L. Childers, M. J. Mcdonnell, W. Zhou, Evolution and future of urban ecological science: ecology in, of, and for the city. *Ecosystem Health and Sustainability* **2**, e01229 (2016).
16. S. Des Roches, *et al.*, Socio-eco-evolutionary dynamics in cities. *Evol. Appl.* **14**, 248–267 (2021).
17. D. J. X. Gonzalez, A. Nardone, A. V. Nguyen, R. Morello-Frosch, J. A. Casey, Historic redlining and the siting of oil and gas wells in the United States. *J. Expo. Sci. Environ. Epidemiol.* (2022).
18. H. M. Lane, R. Morello-Frosch, J. D. Marshall, J. S. Apte, Historical Redlining Is Associated with Present-Day Air Pollution Disparities in U.S. Cities. *Environ Sci Technol Lett* **9**, 345–350 (2022).
19. D. H. Locke, *et al.*, Residential housing segregation and urban tree canopy in 37 US Cities. *npj Urban Sustain* **1**, 1–9 (2021).

20. L. J. Cushing, S. Li, B. B. Steiger, J. A. Casey, Historical red-lining is associated with fossil fuel power plant siting and present-day inequalities in air pollutant emissions. *Nat Energy* **8**, 52–61 (2023).
21. A. E. Hillier, Redlining and the Home Owners' Loan Corporation. *J. Urban Hist.* **29**, 394–420 (2003).
22. C. B. Swope, D. Hernández, L. J. Cushing, The Relationship of Historical Redlining with Present-Day Neighborhood Environmental and Health Outcomes: A Scoping Review and Conceptual Model. *J Urban Health* **99**, 959–983 (2022).
23. E. K. Lee, *et al.*, Health outcomes in redlined versus non-redlined neighborhoods: A systematic review and meta-analysis. *Social Science & Medicine* **294**, 114696 (2022).
24. C. J. Schell, *et al.*, The ecological and evolutionary consequences of systemic racism in urban environments. *Science*, eaay4497 (2020).
25. E. M. Wood, *et al.*, Historical racial redlining and contemporary patterns of income inequality negatively affect birds, their habitat, and people in Los Angeles, California. *Ornithological Applications*, duad044 (2023).
26. D. Ellis-Soto, M. Chapman, D. H. Locke, Historical redlining is associated with increasing geographical disparities in bird biodiversity sampling in the United States. *Nat Hum Behav*, 1–9 (2023).
27. J. L. Dickinson, B. Zuckerberg, D. N. Bonter, Citizen Science as an Ecological Research Tool: Challenges and Benefits (2010).
28. L. B. Sousa, *et al.*, Citizen science and smartphone e-entomology enables low-cost upscaling of mosquito surveillance. *Science of the Total Environment* **704**, 135349 (2020).
29. E. J. Carlen, *et al.*, A framework for contextualizing social-ecological biases in contributory science data. *People and Nature (In Press)* (2024).
30. M. Rocha-Ortega, P. Rodriguez, A. Córdoba-Aguilar, Geographical, temporal and taxonomic biases in insect GBIF data on biodiversity and extinction. *Ecological Entomology* **46**, 718–728 (2021).
31. E. García-Roselló, J. González-Dacosta, J. M. Lobo, The biased distribution of existing information on biodiversity hinders its use in conservation, and we need an integrative approach to act urgently. *Biological Conservation* **283**, 110118 (2023).
32. J. Beninde, T. W. Delaney, G. Gonzalez, H. B. Shaffer, Harnessing iNaturalist to quantify hotspots of urban biodiversity: the Los Angeles case study. *Frontiers in Ecology and Evolution* **11**, 983371 (2023).
33. S. Loarie, Thank you for helping generate most GBIF records for most species since 2020. *iNaturalist* (15:04:12 UTC) (November 6, 2023).
34. A. C. Hughes, M. C. Orr, Q. Yang, H. Qiao, Effectively and accurately mapping global biodiversity patterns for different regions and taxa. *Global Ecology and Biogeography* **30**, 1375–1388 (2021).
35. B. Sun, *et al.*, Urbanization affects spatial variation and species similarity of bird diversity distribution. *Science Advances* **8**, eade3061 (2022).
36. A. Lajeunesse, Y. Fourcade, Temporal analysis of GBIF data reveals the restructuring of communities following climate change. *Journal of Animal Ecology* **92**, 391–402 (2023).
37. C. O. Estien, C. E. Wilkinson, R. Morello-Frosch, C. J. Schell, Historical redlining is associated with disparities in environmental quality in California. *In Review at Environmental Science and Technology Letters*.
38. A. Nardone, K. E. Rudolph, -Frosch Rachel Morello, J. A. Casey, Redlines and Greenspace: The Relationship between Historical Redlining and 2010 Greenspace across the United States. *Environmental Health Perspectives* **129**, 017006 (2021).
39. T. Gallo, et al., Legacy effects of redlining on the distribution of greenspaces in US cities. *In Review*.

40. J. R. Nelson-Olivieri, *et al.*, Inequalities in noise will affect urban wildlife. *Nature Ecology & Evolution*, 1–12 (2023).
41. E. C. Betley, *et al.*, Assessing human well-being constructs with environmental and equity aspects: A review of the landscape. *People and Nature* (2021).
42. A. McInturff, C. E. B. Cannon, P. S. Alagona, D. N. Pellow, Meeting at the crossroads. *Elementa (Wash., DC)* **9** (2021).
43. R. R. Dunn, *et al.*, A theory of city biogeography and the origin of urban species. *Frontiers in Conservation Science* **3**, 761449 (2022).
44. M. A. Schlaepfer, Do non-native species contribute to biodiversity? *PLoS biology* **16**, e2005568 (2018).
45. Á. Bayón, O. Godoy, N. Maurel, M. van Kleunen, M. Vilà, Proportion of non-native plants in urban parks correlates with climate, socioeconomic factors and plant traits. *Urban Forestry & Urban Greening* **63**, 127215 (2021).
46. E. R. Kuras, *et al.*, Urban socioeconomic inequality and biodiversity often converge, but not always: A global meta-analysis. *Landscape and Urban Planning* **198**, 103799 (2020).
47. A. R. Litt, D. E. Pearson, Non-native plants and wildlife in the Intermountain West. *Wildlife Society Bulletin* **37**, 517–526 (2013).
48. K. T. Burghardt, D. W. Tallamy, C. Philips, K. J. Shropshire, Non-native plants reduce abundance, richness, and host specialization in lepidopteran communities. *Ecosphere* **1**, 1–22 (2010).
49. T. M. Blackburn, *et al.*, A proposed unified framework for biological invasions. *Trends Ecol. Evol.* **26**, 333–339 (2011).
50. M. L. Avolio, D. E. Pataki, T. L. Trammell, J. Endter-Wada, Biodiverse cities: the nursery industry, homeowners, and neighborhood differences drive urban tree composition. *Ecological Monographs* **88**, 259–276 (2018).
51. B. Gallardo, A. Zieritz, D. C. Aldridge, The Importance of the Human Footprint in Shaping the Global Distribution of Terrestrial, Freshwater and Marine Invaders. *PLOS ONE* **10**, e0125801 (2015).
52. M. W. Cadotte, S. L. E. Yasui, S. Livingstone, J. S. MacIvor, Are urban systems beneficial, detrimental, or indifferent for biological invasion? *Biol Invasions* **19**, 3489–3503 (2017).
53. E. N. Spotswood, *et al.*, The biological deserts fallacy: cities in their landscapes contribute more than we think to regional biodiversity. *Bioscience* **71**, 148–160 (2021).
54. M. Lambert, C. Schell, *Urban Biodiversity and Equity: Justice-Centered Conservation in Cities* (Oxford University Press, 2023).
55. C. Oke, *et al.*, Cities should respond to the biodiversity extinction crisis. *npj Urban Sustainability* **1**, 11 (2021).
56. J. Beninde, M. Veith, A. Hochkirch, Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. *Ecology letters* **18**, 581–592 (2015).
57. A. Kantsa, T. Tscheulin, R. R. Junker, T. Petanidou, S. Kokkini, Urban biodiversity hotspots wait to get discovered: The example of the city of Ioannina, NW Greece. *Landscape and urban planning* **120**, 129–137 (2013).
58. R. I. McDonald, Global urbanization: can ecologists identify a sustainable way forward? *Frontiers in Ecology and the Environment* **6**, 99–104 (2008).
59. W. Solecki, K. C. Seto, P. J. Marcotullio, It's time for an urbanization science. *Environment: science and policy for sustainable development* **55**, 12–17 (2013).
60. G. G. Gurney, V. M. Adams, J. G. Álvarez-Romero, J. Claudet, Area-based conservation: Taking stock and looking ahead. *One Earth* **6**, 98–104 (2023).
61. United Nations, Sustainable Development Goal 15: Life on Land (2021).
62. C. D. Ives, *et al.*, Cities are hotspots for threatened species. *Global Ecology and biogeography* **25**, 117–126 (2016).

63. M. McDonnell, Cities as refuges for species on the brink? *ECOS* (2013) https:/doi.org/10.1071/EC13288.
64. M. H. Murray, *et al.*, One Health for All: Advancing Human and Ecosystem Health in Cities by Integrating an Environmental Justice Lens. *Annu. Rev. Ecol. Evol. Syst.* (2022).
65. A. Nardone, *et al.*, Associations between historical residential redlining and current age-adjusted rates of emergency department visits due to asthma across eight cities in California: an ecological study. *The Lancet Planetary Health* **4**, e24–e31 (2020).
66. R. K. Nelson, L. Winling, R. Marciano, N. Connolly, E. L. Ayers, Mapping inequality: Redlining in new deal America. *American Panorama: An Atlas of United States History. University of Richmond: Digital Scholarship Lab* **17**, 19 (2020).
67. Loarie, 25,000,000 Observations! (November 6, 2023).
68. R. C. Team, R: A language and environment for statistical computing. Published online 2020. *Supplemental Information References S* **1**, 371–78 (2021).
69. H. Wickham, W. Chang, M. H. Wickham, Package 'ggplot2.' *Create elegant data visualisations using the grammar of graphics. Version* **2**, 1–189 (2016).
70. J. Oksanen, *et al.*, The vegan package. *Community ecology package* **10**, 719 (2007).
71. P. de Valpine, *et al.*, Programming with models: writing statistical algorithms for general model structures with NIMBLE. *Journal of Computational and Graphical Statistics* **26**, 403–413 (2017).
72. R. O'Hara, J. Kotze, Do not log-transform count data. *Nature Precedings*, 1–1 (2010).
73. M. L. McKinney, Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosyst* **11**, 161–176 (2008).
74. A. Gelman, J. Carlin, H. Stern, D. Rubin, Bayesian data analysis crc press. *New York* (2004).

SUPPLEMENTAL MATERIALS

Historical redlining impacts wildlife biodiversity across California

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Contents:

Supplemental Materials 1: Results

SM 1: Clade-level species richness across HOLC grades

Statewide

Across clades, we found variation in species richness across HOLC grades for all, native, and nonnative species (Table S2-7). For insects, we found that greenlined neighborhoods had the highest species richness on average but found no significant differences between grades. We found the same trends for native and nonnative insect richness. For arachnids, we found that B-graded neighborhoods had the highest species richness on average but found no significant differences between grades. We found the same trends for native and nonnative arachnid richness. For birds, we found that greenlined neighborhoods had the highest species richness on average and found significant differences between green and redlined neighborhoods (8.10, CI: 0.63, 15.57). We found similar trends in native bird richness, but not nonnative bird richness between green and redlined neighborhoods (1.13, CI: -0.39, 3.07). For mammals, we found that B-grade neighborhoods had the highest species richness on average but found no significant differences between grades. We found similar trends in native and nonnative mammalian richness but found significant differences between grades B and D (1.77, CI: 0.07, 3.47). For reptiles, we found that B-grade neighborhoods had the highest species richness on average but found no significant differences between grades. We found similar trends for native and nonnative richness but found significant differences in nonnative reptiles between grades B and D (1.74, CI: 0.03, 3.45). For amphibians, we found that B-grade neighborhoods had the highest species richness on average, and we found significant differences between grades A and C (0.48, CI: 0.04, 0.92), A and D (0.73, CI: 0.23, 1.23), and B and D (1.21, CI: 0.05, 2.37). We found similar trends for native richness, except no significant differences between A and C were found (0.43, CI: -0.07, 0.94). We found no significant differences in nonnative amphibian richness between HOLC grades.

City-level

For insects, we found significant differences in richness between green and redlined neighborhoods in every city (Figure 3), and this remained true for native and nonnative insects. For arachnids, we found significant differences in richness between green and redlined neighborhoods in each city except Oakland (-0.11, CI: -0.38, 0.15). For native arachnid richness, we found significant differences between green and redlined neighborhoods in San Diego (2.35, CI: 1.11, 3.59) and San Francisco (1.44, CI: 0.34, 2.53), but not Los Angeles (0.11, CI: -0.04, 0.25) and Oakland -0.09, CI: -0.21, 0.04). For nonnative arachnid richness, we found significant differences between green and redlined neighborhoods in San Diego (3.11, CI: 1.71, 4.51) and Los Angeles (0.93, CI: 0.62, 1.23), but not San Francisco (median = 1.14, CI: -0.19, 2.47) and Oakland (0.08, CI: -0.22, 0.38). For birds, we found significant differences in richness between green and redlined neighborhoods in each city (Figure 3), and this remained true for native and nonnative birds, except for nonnative birds in Oakland (0.13, CI: -0.11, 0.59). For mammals, we found significant differences between green and redlined neighborhoods in each city except for Oakland (0.12, CI: -0.29, 0.54) (Figure 3). These patterns remained true for native and non–native mammals, except for in nonnative mammalian richness in San Francisco (0.66, CI: -0.15, 1.47). For reptiles, we found significant differences between green and redlined neighborhoods in each city except for Oakland (0.12, CI: -0.23, 0.11), and these trends remained true for native reptiles. For nonnative reptiles, we only found a significant difference between green and redlined neighborhoods in Los Angeles (0.27, CI: 0.03, 0.51) and San Diego (0.47, CI: 0.01, 0.93), but not Oakland (.11, CI: -0.22, 0.44) or San Francisco (0.27, CI: -0.65, 1.18). For amphibians, we found significant differences between green and redlined neighborhoods in each city, and these trends remained true for native and nonnative amphibian richness, except for nonnative amphibians in Oakland (1.51, CI: -2.31, 5.33) and San Francisco (0.22, CI: -0.08, 0.53).

Supplemental Materials 2: Figures

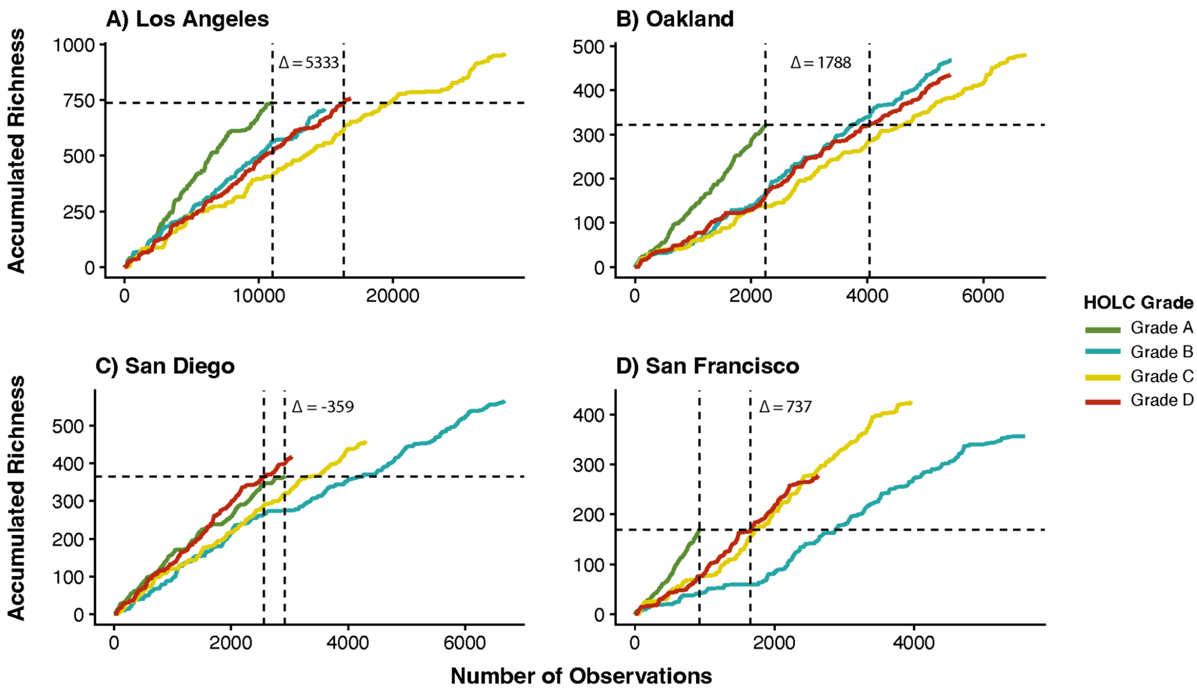

Figure S1. City-level species accumulation curve per HOLC grade. Species accumulation curves for each HOLC grade across six clades for all species in (A) Los Angeles, (B) Oakland, (C) Oakland, and San Francisco. The x-axis shows the number of observations within each HOLC grade. The y-axis shows accumulated species richness. The dashed horizontal line* shows the maximum accumulated richness for Grade A. The vertical lines** show the number of observations to reach Grade A's maximum accumulated richness in Grade A (left vertical line) and in Grade D (right vertical line). The difference in observations between redlined (i.e., grade D) and greenlined (i.e., grade A) and neighborhoods is shown as a delta value.

*Horizontal line (y): Los Angeles: 738; Oakland: 322; San Diego: 365; San Francisco: 169

**Vertical lines (x; grade A, grade D): Los Angeles: 11005, 16338; Oakland: 2247, 4035; San Diego: 2917, 2558; San Francisco: 921, 1658

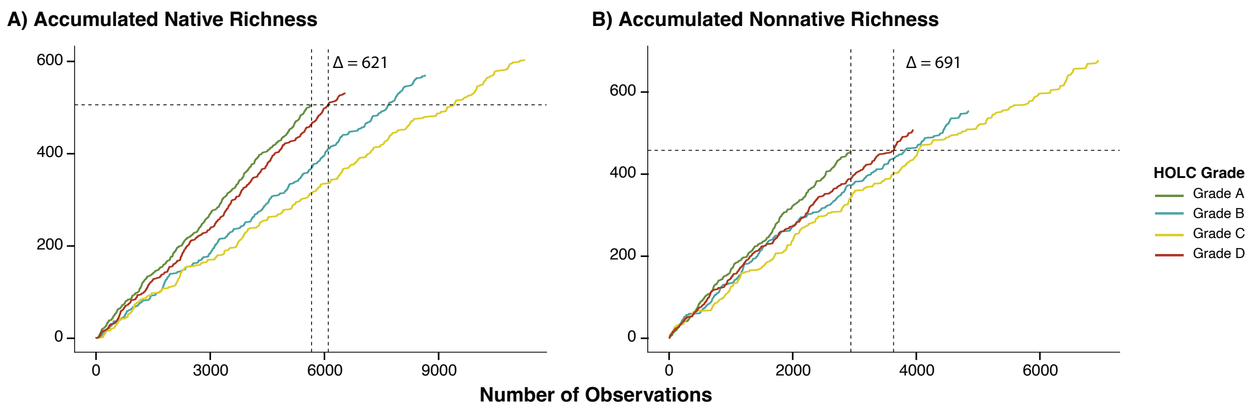

Figure S2. Native and nonnative species accumulation curve per HOLC grade. Species accumulation curves for each HOLC grade across six clades for (A) native species and (B) nonnative species. The x-axis shows the number of observations within each HOLC grade. The y-axis shows accumulated species richness. The dashed horizontal line* shows the maximum accumulated richness for Grade A. The vertical lines** show the number of observations to reach Grade A's maximum accumulated richness in Grade A (left vertical line) and in Grade D (right vertical line). The difference in observations between redlined (i.e., grade D) and greenlined (i.e., grade A) and neighborhoods is shown as a delta value.

*Horizontal lines (y): native = 506; nonnative = 458

**Vertical lines (x; grade A, grade D): native = 4607, 5228, nonnative = 2941, 3632

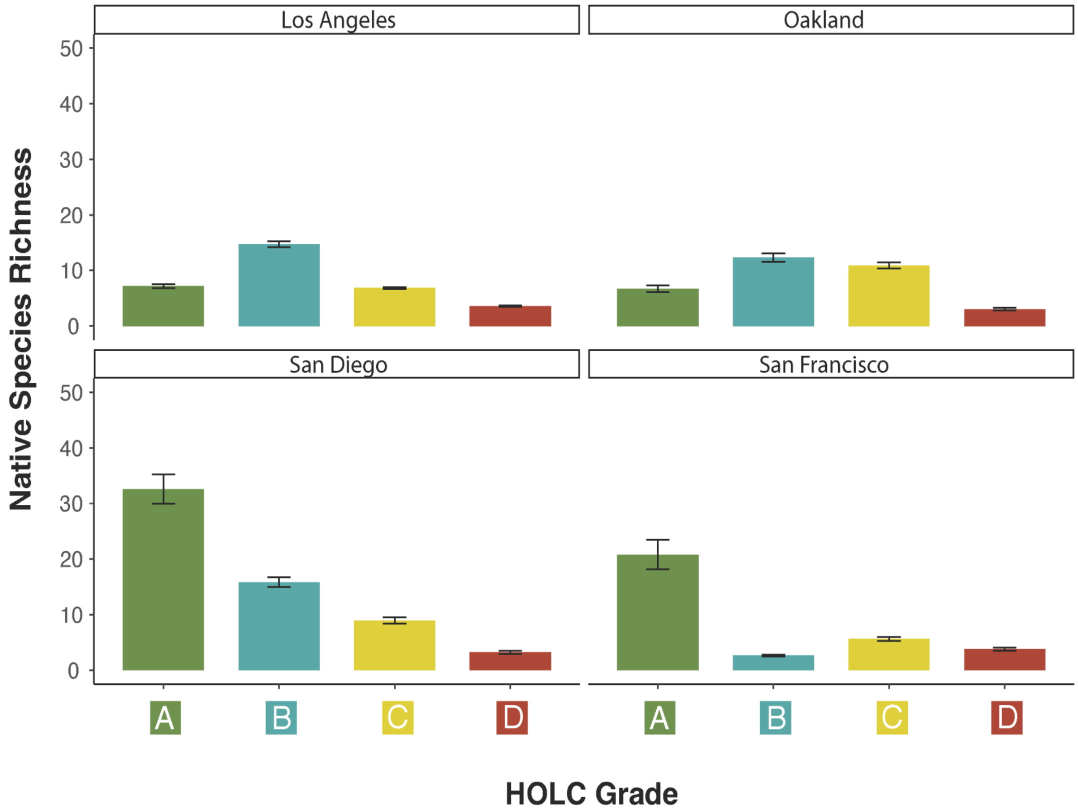

Figure S3. City-level differences in native species richness across HOLC grades. The relationship between HOLC grade and native species richness for Los Angeles (top left), Oakland (top right), (C) San Diego (bottom left), and San Francisco (bottom right). Bars represent the mean, and whiskers represent 2.5 and 97.5% confidence intervals. All pair-wise comparisons are significant except grades A and C in Los Angeles.

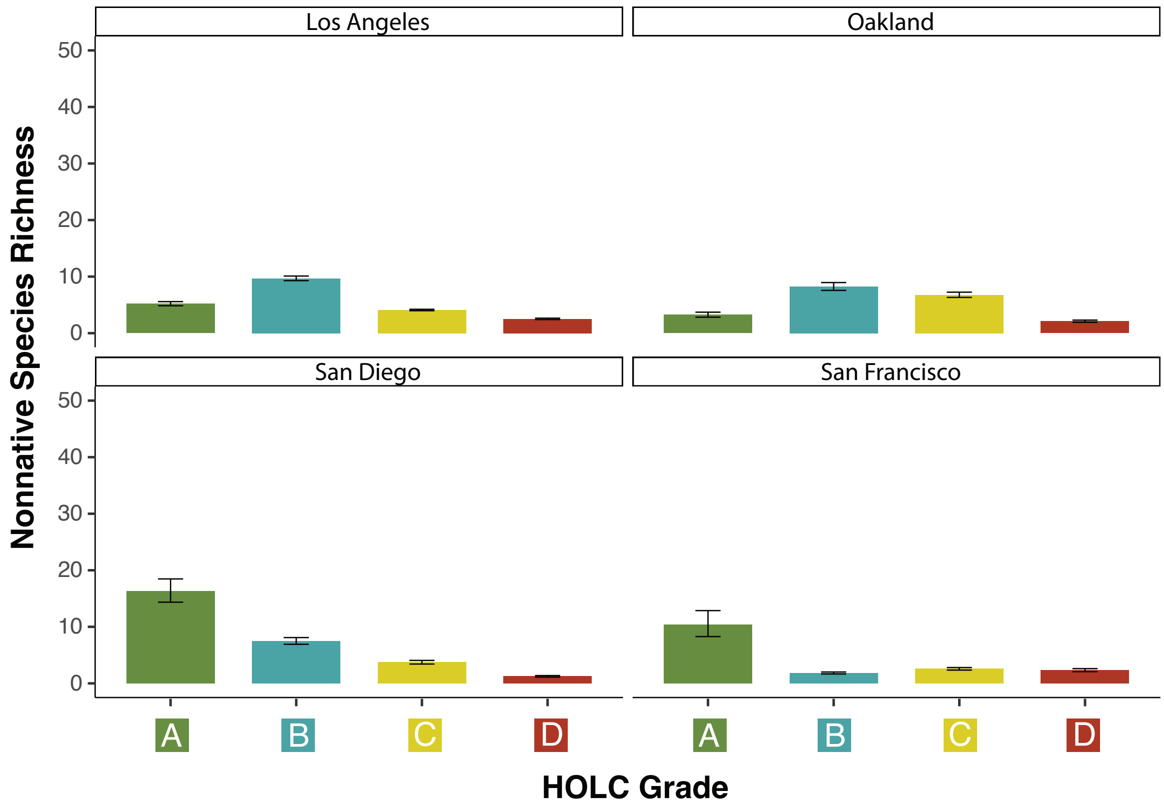

Figure S4. City-level differences in nonnative species richness. The relationship between HOLC grade and nonnative species richness for Los Angeles (top left), Oakland (top right), (C) San Diego (bottom left), and San Francisco (bottom right). Bars represent the mean, and whiskers represent 2.5 and 97.5% confidence intervals. All pair-wise comparisons are significant except grades C and D in San Francisco.

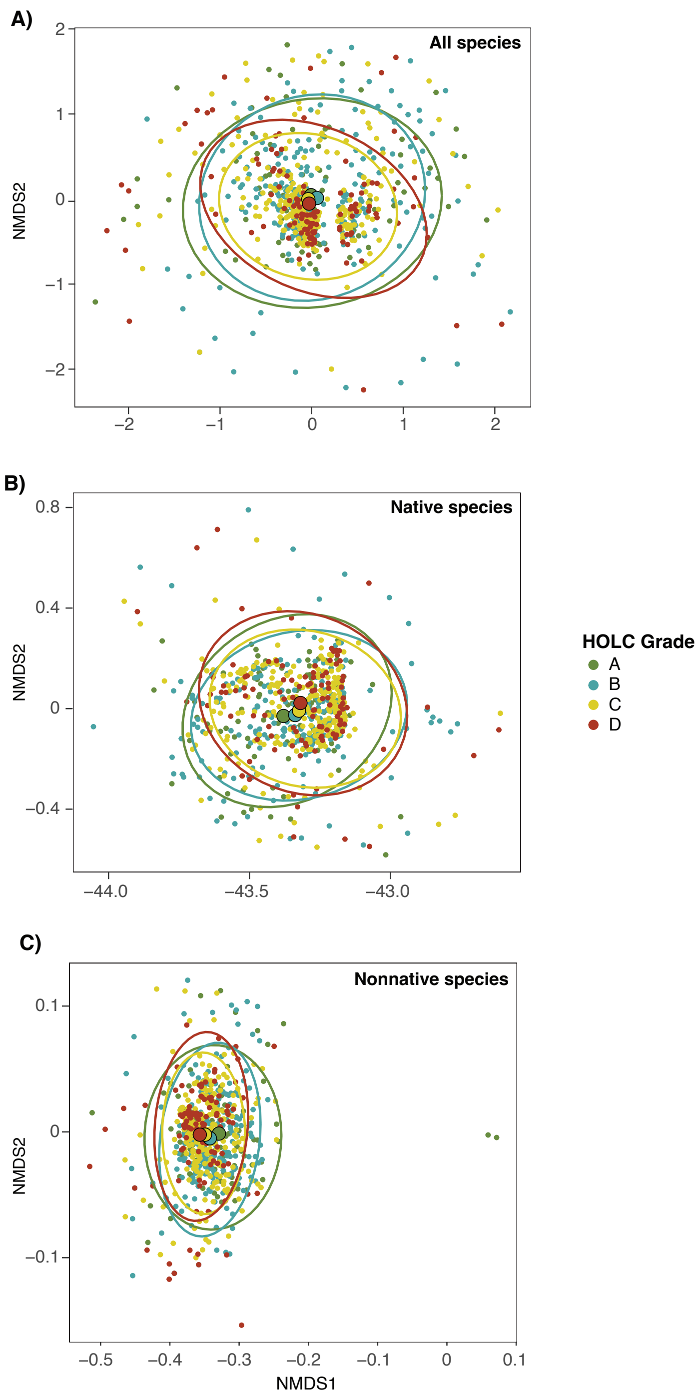

Figure S5. HOLC grade beta diversity**.** Non-metric multidimensional scaling (NMDS) for β-diversity (Jaccard's metric) among HOLC grades for (A) all species, (B) native species, and (C) nonnative species. Each dot represents a neighborhood within a city and ellipses encompass 95% data points. No overlap between ellipses suggests that HOLC grades have distinct beta diversity patterns and strong dissimilarity in species assemblage. Substantial overlap in ellipses suggests that beta diversity between HOLC grades is more similar to each other and there is strong similarity in species assemblage.

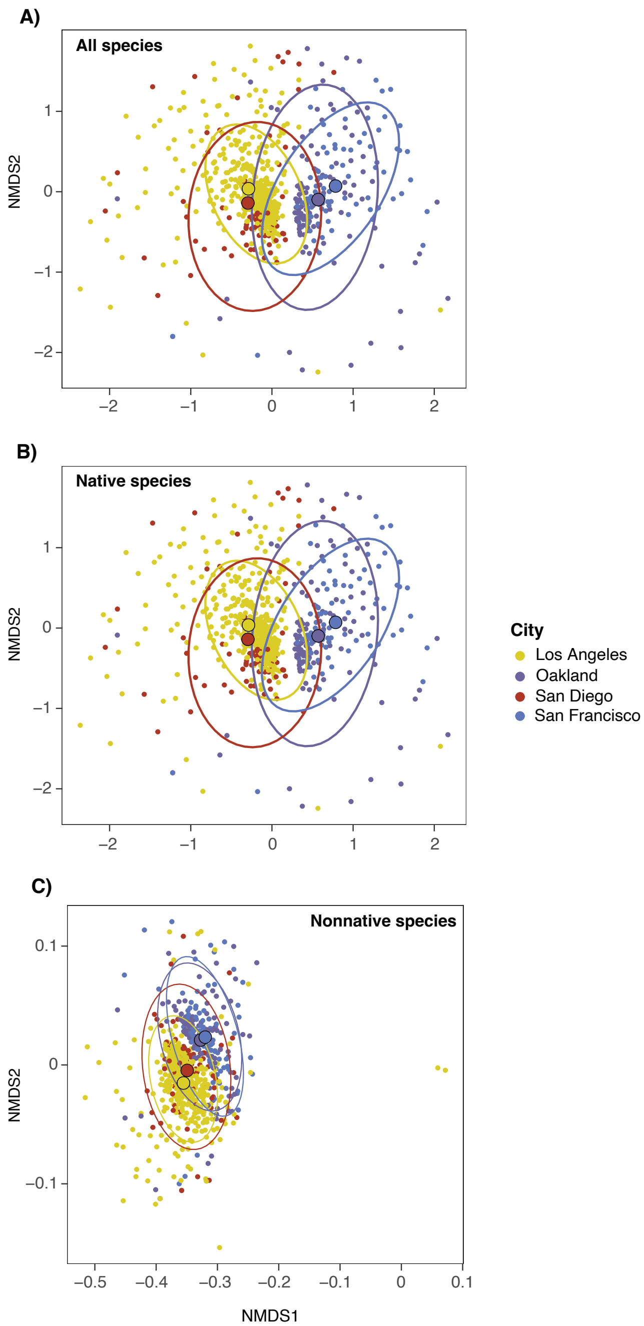

Figure S6. Beta diversity per city. Non-metric multidimensional scaling (NMDS) for β-diversity (Jaccard's metric) among cities for (A) all species, (B) native species, and (C) nonnative species. Each dot represents a neighborhood within a city and ellipses encompass 95% data points. No overlap between ellipses suggests that HOLC grades have distinct beta diversity patterns and strong dissimilarity in species assemblage. Substantial overlap in ellipses suggests that beta diversity between HOLC grades is more similar to each other and there is strong similarity in species assemblage. *Note: Outlier points removed for native (2 points) and nonnative species (2 points) in Los Angeles as well as nonnative species (1 point) in Oakland to assist in visualization.*

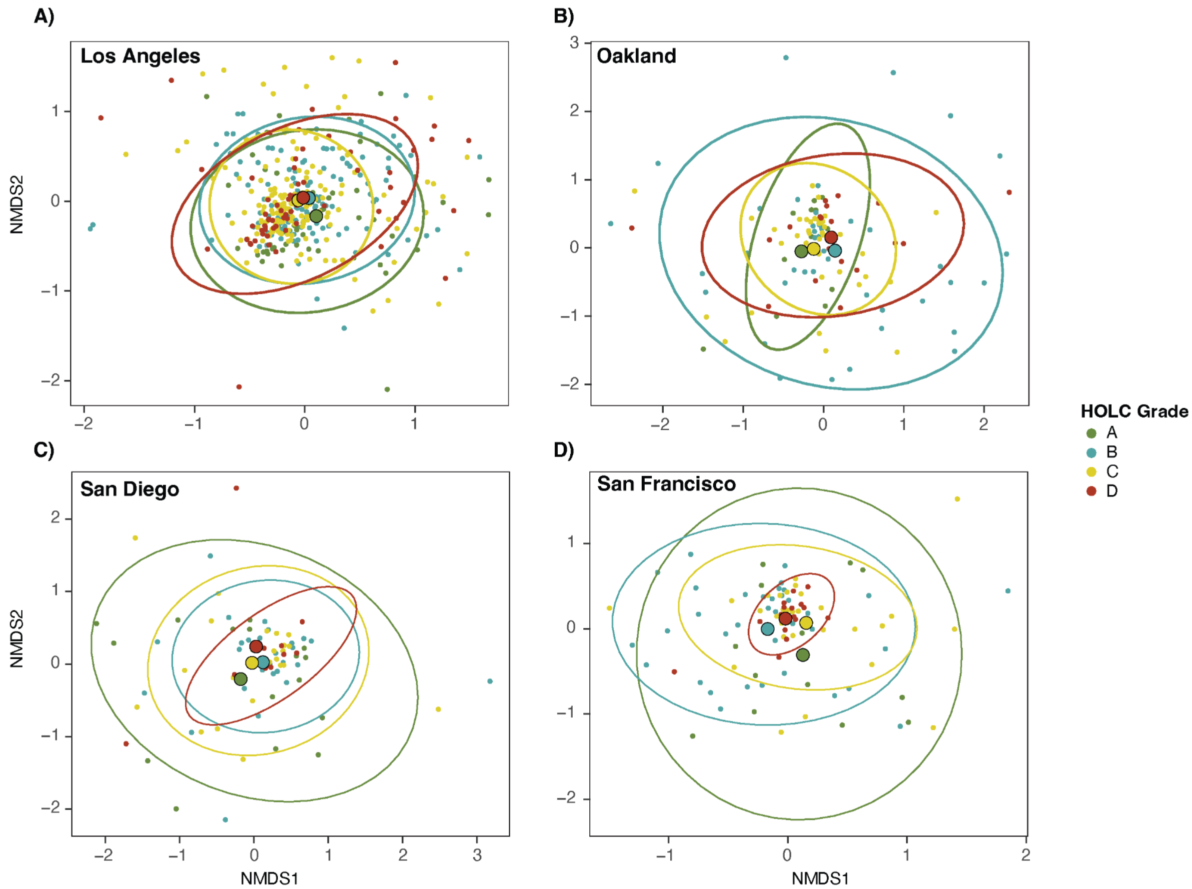

Figure S7. HOLC grade native beta diversity by city. Non-metric multidimensional scaling (NMDS) for native β-diversity (Jaccard's metric) among HOLC grades in (A) Los Angeles, (B) Oakland, (C) San Diego, and (D) San Francisco. Each dot represents a neighborhood within a city and ellipses encompass 95% data points. No overlap between ellipses suggests that HOLC grades have distinct beta diversity patterns and strong dissimilarity in native species assemblage. Substantial overlap in ellipses suggests that beta diversity between HOLC grades is more similar to each other and there is strong similarity in native species assemblage. *Note: Outlier points removed for Los Angeles to assist in visualization (2 points in grade D).*

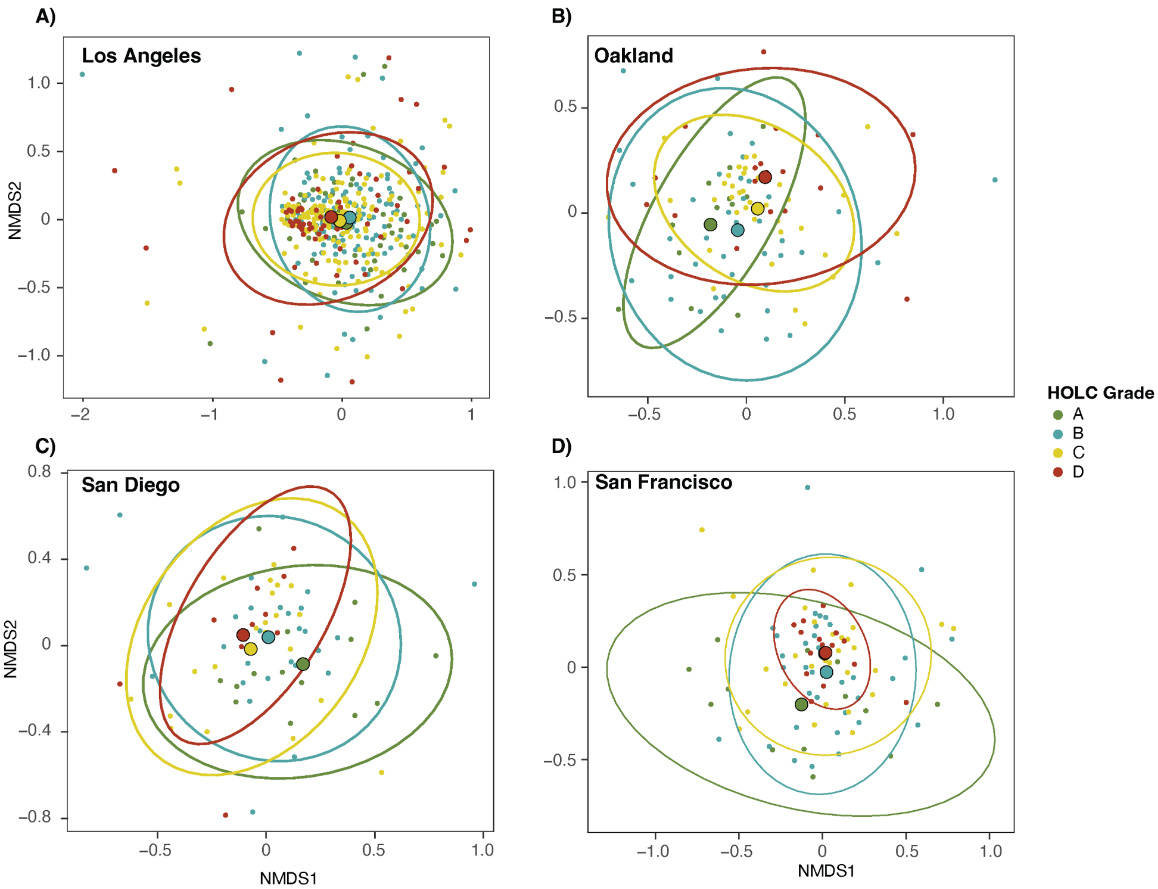

Figure S8. HOLC grade nonnative beta diversity by city. Non-metric multidimensional scaling (NMDS) for nonnative β-diversity (Jaccard's metric) among HOLC grades in (A) Los Angeles, (B) Oakland, (C) San Diego, and (D) San Francisco. Each dot represents a neighborhood within a city and ellipses encompass 95% data points. No overlap between ellipses suggests that HOLC grades have distinct beta diversity patterns and strong dissimilarity in nonnative species assemblage. Substantial overlap in ellipses suggests that beta diversity between HOLC grades is more similar to each other and there is strong similarity in nonnative species assemblage. *Note: Outlier points removed for Los Angeles (2 points in grade D) and Oakland (1 point in grade C) to assist in visualization.*

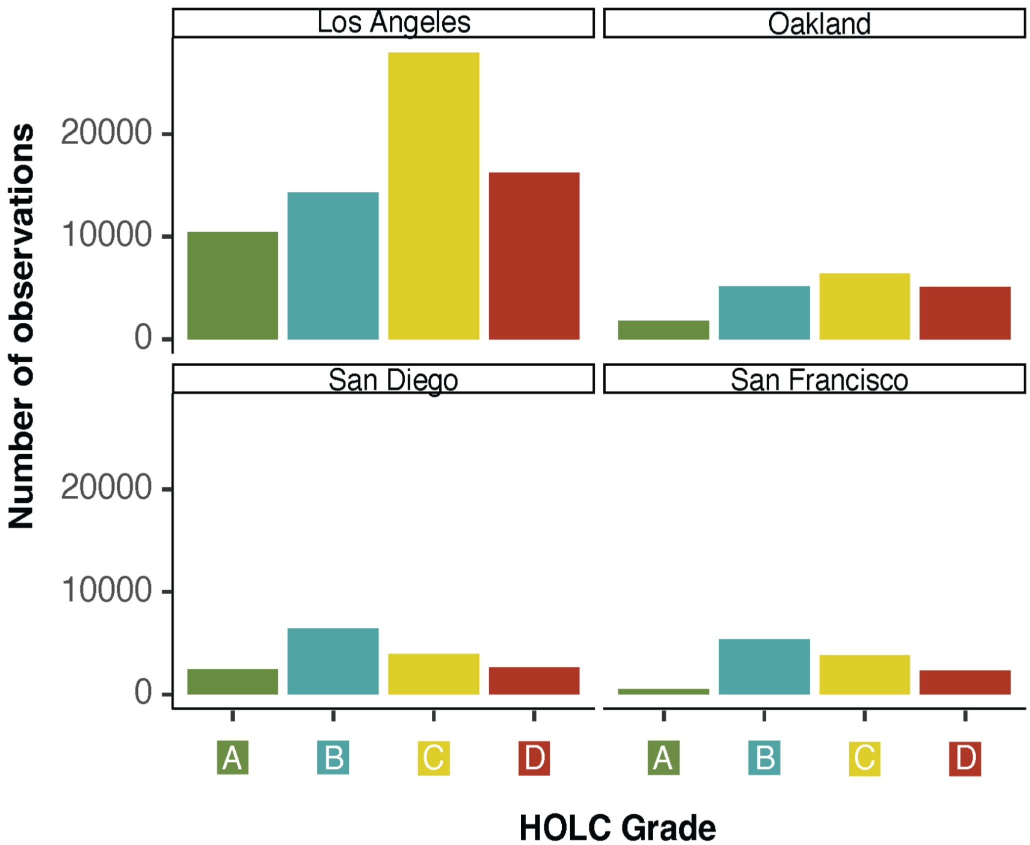

Figure S9. iNaturalist observations across HOLC grades per city. iNaturalist observations for Los Angeles (top left), Oakland (top right), (C) San Diego (bottom left), and San Francisco (bottom right) for each HOLC grade.

Supplemental Materials 3: Tables

Clade	HOLC Grade	Mean Richness	Mean Native Richness	Mean Nonnative Richness
Mammal	A	1.29 (0.24, 3.83)	0.69 (0.17, 1.76)	1.03 (0.22, 3.01)
Mammal	B	1.58 (0.26, 5.88)	0.81 (0.16, 2.6)	1.52 (0.29, 4.52)
Mammal	C	1.07 (0.18, 4)	0.74 (0.15, 2.23)	0.63 (0.1, 2.69)
Mammal	D	0.53 (0.08, 2.31)	0.29 (0.06, 1.04)	0.39 (0.06, 1.69)
Bird	A	6.91 (1.22, 20.96)	5.96 (1.06, 17.82)	1.05 (0.18, 3.4)
Bird	B	4.88 (0.55, 31.72)	4.03 (0.46, 26.14)	1.07 (0.12, 6.06)
Bird	C	4.15 (0.59, 19.14)	3.49 (0.51, 15.91)	0.85 (0.12, 4.02)
Bird	D	1.75 (0.27, 7.36)	1.46 (0.23, 6.01)	0.36 (0.05, 1.76)
Insect	A	8.91 (1.3, 29.65)	4.5 (0.63, 15.5)	4.7 (0.71, 15.07)
Insect	B	6.27 (0.67, 38.31)	3.17 (0.33, 19.47)	3.39 (0.37, 21.27)
Insect	C	4.88 (0.54, 28.77)	2.52 (0.26, 15.62)	2.57 (0.29, 14.54)
Insect	D	2.58 (0.3, 15.25)	1.29 (0.14, 7.84)	1.4 (0.17, 7.87)
Arachnid	A	1.72 (0.25, 5.83)	0.63 (0.09, 2.43)	1.5 (0.32, 4.05)
Arachnid	B	1.74 (0.18, 10.29)	0.85 (0.09, 5.03)	1.56 (0.23, 6.6)
Arachnid	C	1.17 (0.12, 7.39)	0.55 (0.05, 3.85)	1 (0.15, 4.67)
Arachnid	D	0.56 (0.06, 3.97)	0.25 (0.02, 1.96)	0.52 (0.07, 2.96)
Reptile	A	1.37 (0.24, 4.51)	1.42 (0.24, 4.59)	0.36 (0.1, 1.18)
Reptile	B	1.41 (0.18, 6.63)	1.45 (0.19, 6.86)	0.97 (0.16, 3.79)
Reptile	C	0.79 (0.1, 4.63)	0.8 (0.1, 4.69)	0.57 (0.13, 1.91)

Reptile	D	0.4 (0.05, 2.88)	0.43 (0.05, 3.19)	0.16 (0.04, 0.65)
Amphibian	A	0.88 (0.49, 1.53)	0.84 (0.42, 1.56)	0.82 (0.21, 2.99)
Amphibian	B	0.9 (0.28, 2.64)	0.9 (0.25, 2.83)	1.4 (0.22, 8.72)
Amphibian	C	0.5 (0.24, 0.86)	0.5 (0.2, 0.97)	0.47 (0.1, 2.42)
Amphibian	D	0.23 (0.1, 0.52)	0.23 (0.09, 0.55)	0.16 (0.03, 0.99)

Table S1. Overall clade species richness. Species richness for each clade is shown for all cities per HOLC grade (grades A = "best" and "greenlined", B, C, and D = "hazardous" and "redlined"). We show overall species richness, native species richness, and nonnative species richness with mean and 95% credible intervals.

City	HOLC Grade	Mean Richness	Mean Native Richness	Mean Nonnative Richness
Los Angeles	A	4.7 (4.42, 4.99)	2.34 (2.14, 2.56)	2.63 (2.41, 2.87)
Los Angeles	B	8.75 (8.42, 9.09)	4.38 (4.16, 4.62)	4.89 (4.62, 5.16)
Los Angeles	C	4.35 (4.24, 4.48)	2.32 (2.23, 2.41)	2.27 (2.18, 2.36)
Los Angeles	D	2.98 (2.85, 3.12)	1.52 (1.43, 1.62)	1.62 (1.52, 1.73)
Oakland	A	5.17 (4.64, 5.77)	2.24 (1.91, 2.6)	2.43 (2.05, 2.87)
Oakland	B	9.83 (9.16, 10.52)	3.73 (3.38, 4.11)	5.32 (4.82, 5.86)
Oakland	C	9.77 (9.22, 10.34)	4.27 (3.94, 4.61)	4.53 (4.16, 4.91)
Oakland	D	2.95 (2.72, 3.18)	1.29 (1.15, 1.43)	1.36 (1.22, 1.52)
San Diego	A	21.71 (19.54, 24.1)	12.81 (11.05, 14.76)	8.95 (7.67, 10.4)
San Diego	B	8.46 (7.91, 9.04)	4.88 (4.44, 5.34)	3.68 (3.34, 4.04)
San Diego	C	4.64 (4.31, 4.99)	2.72 (2.45, 3)	2 (1.79, 2.22)
San Diego	D	1.77 (1.61, 1.94)	1.09 (0.96, 1.24)	0.71 (0.62, 0.81)
San Francisco	A	16.18 (13.5, 19.2)	10.3 (7.94, 13.22)	8.01 (6.13, 10.18)
San Francisco	B	2.83 (2.6, 3.07)	2.11 (1.87, 2.36)	1.31 (1.17, 1.47)
San Francisco	C	3.53 (3.27, 3.81)	2.31 (2.07, 2.58)	1.84 (1.65, 2.03)

San Francisco	D	2.91 (2.65, 3.2)	1.64 (1.43, 1.86)	1.74 (1.51, 1.98)

Table S2. City-level mammal species richness. Mammalian species richness is shown for each city per HOLC grade (grades A = “best” and “greenlined”, B, C, and D = “hazardous” and “redlined”). We show overall species richness, native species richness, and nonnative species richness with mean and 95% credible intervals.

City	HOLC Grade	Mean Richness	Mean Native Richness	Mean Nonnative Richness
Los Angeles	A	3.79 (3.53, 4.07)	3.26 (3.02, 3.5)	0.88 (0.73, 1.05)
Los Angeles	B	8.68 (8.3, 9.07)	7.4 (7.04, 7.76)	2.06 (1.85, 2.29)
Los Angeles	C	3.46 (3.35, 3.58)	3.07 (2.96, 3.19)	0.71 (0.66, 0.77)
Los Angeles	D	1.57 (1.49, 1.65)	1.37 (1.3, 1.45)	0.34 (0.3, 0.39)
Oakland	A	3.81 (3.35, 4.33)	3.63 (3.17, 4.16)	0.36 (0.24, 0.53)
Oakland	B	7.19 (6.58, 7.84)	6.26 (5.71, 6.86)	1.03 (0.76, 1.38)
Oakland	C	5.51 (5.15, 5.89)	4.78 (4.45, 5.14)	0.81 (0.65, 1)
Oakland	D	1.35 (1.23, 1.48)	1.14 (1.03, 1.26)	0.25 (0.19, 0.32)
San Diego	A	15.81 (14.23, 17.51)	15.47 (13.84, 17.22)	1.71 (1.19, 2.37)
San Diego	B	7.94 (7.37, 8.55)	7.64 (7.05, 8.26)	1.12 (0.91, 1.37)
San Diego	C	4.85 (4.43, 5.3)	4.7 (4.25, 5.17)	0.67 (0.54, 0.83)
San Diego	D	1.81 (1.62, 2.02)	1.82 (1.61, 2.05)	0.21 (0.15, 0.27)
San Francisco	A	11.16 (9.41, 13.11)	9.45 (7.92, 11.2)	1.33 (0.63, 2.67)
San Francisco	B	1.21 (1.12, 1.31)	0.98 (0.9, 1.06)	0.34 (0.26, 0.43)
San Francisco	C	3.52 (3.23, 3.82)	2.9 (2.65, 3.16)	0.78 (0.6, 1)
San Francisco	D	2.36 (2.12, 2.62)	1.95 (1.73, 2.18)	0.46 (0.34, 0.6)

Table S3. City-level bird species richness. across HOLC grades. Avian species richness is shown for each city per HOLC grade (grades A = “best” and “greenlined”, B, C, and D = “hazardous” and “redlined”). We show overall species richness, native species richness, and nonnative species richness with mean and 95% credible intervals.

City	HOLC Grade	Mean Richness	Mean Native Richness	Mean Nonnative Richness
Los Angeles	A	4.7 (4.42, 4.99)	2.34 (2.14, 2.56)	2.63 (2.41, 2.87)
Los Angeles	B	8.75 (8.42, 9.09)	4.38 (4.16, 4.62)	4.89 (4.62, 5.16)
Los Angeles	C	4.35 (4.24, 4.48)	2.32 (2.23, 2.41)	2.27 (2.18, 2.36)
Los Angeles	D	2.98 (2.85, 3.12)	1.52 (1.43, 1.62)	1.62 (1.52, 1.73)
Oakland	A	5.17 (4.64, 5.77)	2.24 (1.91, 2.6)	2.43 (2.05, 2.87)
Oakland	B	9.83 (9.16, 10.52)	3.73 (3.38, 4.11)	5.32 (4.82, 5.86)
Oakland	C	9.77 (9.22, 10.34)	4.27 (3.94, 4.61)	4.53 (4.16, 4.91)
Oakland	D	2.95 (2.72, 3.18)	1.29 (1.15, 1.43)	1.36 (1.22, 1.52)
San Diego	A	21.71 (19.54, 24.1)	12.81 (11.05, 14.76)	8.95 (7.67, 10.4)
San Diego	B	8.46 (7.91, 9.04)	4.88 (4.44, 5.34)	3.68 (3.34, 4.04)
San Diego	C	4.64 (4.31, 4.99)	2.72 (2.45, 3)	2 (1.79, 2.22)
San Diego	D	1.77 (1.61, 1.94)	1.09 (0.96, 1.24)	0.71 (0.62, 0.81)
San Francisco	A	16.18 (13.5, 19.2)	10.3 (7.94, 13.22)	8.01 (6.13, 10.18)
San Francisco	B	2.83 (2.6, 3.07)	2.11 (1.87, 2.36)	1.31 (1.17, 1.47)
San Francisco	C	3.53 (3.27, 3.81)	2.31 (2.07, 2.58)	1.84 (1.65, 2.03)

San Francisco	D	2.91 (2.65, 3.2)	1.64 (1.43, 1.86)	1.74 (1.51, 1.98)

Table S4. City-level insect species richness. Insect species richness is shown for each city per HOLC grade (grades A = “best” and “greenlined”, B, C, and D = “hazardous” and “redlined”). We show overall species richness, native species richness, and nonnative species richness with mean and 95% credible intervals.

City	HOLC Grade	Mean Richness	Mean Native Richness	Mean Nonnative Richness
Los Angeles	A	1.35 (1.15, 1.58)	0.41 (0.31, 0.54)	1.48 (1.23, 1.77)
Los Angeles	B	2.27 (2.07, 2.48)	0.85 (0.72, 1)	2.14 (1.92, 2.37)
Los Angeles	C	1.02 (0.95, 1.09)	0.5 (0.45, 0.57)	0.83 (0.76, 0.9)
Los Angeles	D	0.68 (0.61, 0.76)	0.32 (0.26, 0.39)	0.57 (0.5, 0.65)
Oakland	A	0.66 (0.5, 0.87)	0.18 (0.12, 0.28)	0.65 (0.45, 0.92)
Oakland	B	2.57 (2.1, 3.11)	0.79 (0.57, 1.07)	1.94 (1.48, 2.49)
Oakland	C	2.39 (2.04, 2.77)	0.85 (0.65, 1.08)	1.63 (1.34, 1.97)
Oakland	D	0.78 (0.63, 0.96)	0.27 (0.2, 0.37)	0.58 (0.43, 0.77)
San Diego	A	4.09 (2.92, 5.59)	2.27 (1.26, 3.74)	3.07 (1.89, 4.69)
San Diego	B	1.91 (1.56, 2.31)	0.99 (0.71, 1.34)	1.95 (1.51, 2.48)
San Diego	C	1.06 (0.87, 1.28)	0.83 (0.6, 1.12)	0.83 (0.64, 1.06)
San Diego	D	0.21 (0.16, 0.26)	0.14 (0.1, 0.2)	0.18 (0.13, 0.24)
San Francisco	A	2.25 (1.25, 3.65)	1.51 (0.7, 2.88)	1.42 (0.59, 3.19)
San Francisco	B	0.88 (0.71, 1.09)	1.54 (1.06, 2.15)	0.62 (0.47, 0.81)
San Francisco	C	0.66 (0.54, 0.8)	0.45 (0.32, 0.61)	0.68 (0.53, 0.87)
San Francisco	D	0.56 (0.44, 0.72)	0.34 (0.24, 0.48)	0.73 (0.5, 1.02)

Table S5. City-level arachnid species richness. Arachnid species richness is shown for each city per HOLC grade (grades A = "best" and "greenlined", B, C, and D = "hazardous" and "redlined"). We show overall species richness, native species richness, and nonnative species richness with mean and 95% credible intervals.

City	HOLC Grade	Mean Richness	Mean Native Richness	Mean Nonnative Richness
Los Angeles	A	0.96 (0.79, 1.16)	0.88 (0.71, 1.07)	0.32 (0.17, 0.62)
Los Angeles	B	1.65 (1.46, 1.86)	1.53 (1.34, 1.73)	0.68 (0.44, 0.99)
Los Angeles	C	0.6 (0.54, 0.66)	0.53 (0.48, 0.59)	0.44 (0.32, 0.58)
Los Angeles	D	0.32 (0.27, 0.37)	0.31 (0.26, 0.37)	0.12 (0.09, 0.17)
Oakland	A	0.21 (0.14, 0.31)	0.22 (0.14, 0.33)	0.22 (0.08, 0.58)
Oakland	B	0.43 (0.3, 0.61)	0.45 (0.31, 0.64)	0.47 (0.03, 1.89)
Oakland	C	0.45 (0.33, 0.6)	0.43 (0.31, 0.59)	0.5 (0.19, 1.39)
Oakland	D	0.26 (0.15, 0.43)	0.32 (0.18, 0.53)	0.11 (0.03, 0.43)
San Diego	A	3.62 (2.49, 5.1)	3.51 (2.38, 4.98)	0.32 (0.12, 1.05)
San Diego	B	1.46 (1.13, 1.84)	1.39 (1.07, 1.77)	1.33 (0.41, 4.58)
San Diego	C	0.54 (0.4, 0.7)	0.48 (0.35, 0.64)	0.41 (0.2, 0.77)
San Diego	D	0.18 (0.14, 0.24)	0.16 (0.11, 0.21)	0.11 (0.06, 0.18)
San Francisco	A	1.19 (0.47, 2.74)	1.06 (0.42, 2.43)	0.41 (0.1, 1.63)
San Francisco	B	1 (0.52, 1.74)	0.86 (0.42, 1.57)	1.41 (0.32, 4.81)
San Francisco	C	0.61 (0.33, 1.02)	0.58 (0.29, 1.05)	0.66 (0.2, 1.69)
San Francisco	D	0.25 (0.16, 0.38)	0.22 (0.13, 0.34)	0.24 (0.06, 1.08)

Table S6. City-level reptile species richness. Reptile species richness is shown for each city per HOLC grade (grades A = “best” and “greenlined”, B, C, and D = “hazardous” and “redlined”). We show overall species richness, native species richness, and nonnative species richness with mean and 95% credible intervals.

City	HOLC Grade	Mean Richness	Mean Native Richness	Mean Nonnative Richness
Los Angeles	A	0.85 (0.59, 1.21)	0.79 (0.51, 1.17)	0.79 (0.34, 1.76)
Los Angeles	B	1.53 (1.06, 2.14)	1.63 (1.07, 2.38)	1.05 (0.49, 1.95)
Los Angeles	C	0.5 (0.4, 0.63)	0.56 (0.41, 0.75)	0.34 (0.2, 0.54)
Los Angeles	D	0.21 (0.15, 0.29)	0.23 (0.15, 0.35)	0.15 (0.08, 0.27)
Oakland	A	1.36 (0.91, 2.01)	1.34 (0.85, 2.08)	1.27 (0.3, 6.19)
Oakland	B	1.91 (1.42, 2.52)	2 (1.48, 2.66)	2.13 (0.31, 9.82)
Oakland	C	0.81 (0.63, 1.02)	0.83 (0.65, 1.06)	0.81 (0.22, 2.71)
Oakland	D	0.29 (0.2, 0.41)	0.3 (0.2, 0.42)	0.25 (0.02, 4.22)
San Diego	A	0.68 (0.41, 1.24)	0.68 (0.38, 1.4)	1.22 (0.3, 5.89)
San Diego	B	0.79 (0.41, 1.37)	0.84 (0.44, 1.45)	2.03 (0.11, 55.02)
San Diego	C	0.35 (0.18, 0.53)	0.34 (0.16, 0.54)	0.88 (0.16, 6.67)
San Diego	D	0.13 (0.06, 0.23)	0.14 (0.06, 0.25)	0.22 (0.04, 0.69)
San Francisco	A	0.56 (0.32, 1.26)	0.55 (0.3, 1.4)	0.04 (0.01, 0.68)
San Francisco	B	0.21 (0.15, 0.3)	0.21 (0.14, 0.29)	0.12 (0.01, 2.47)
San Francisco	C	0.31 (0.21, 0.49)	0.32 (0.21, 0.5)	0.02 (0, 0.77)
San Francisco	D	0.22 (0.13, 0.37)	0.23 (0.13, 0.37)	0.01 (0, 0.27)

Table S7. City-level amphibian species richness. Amphibian species richness is shown for each city per HOLC grade (grades A = "best" and "greenlined", B, C, and D = "hazardous" and "redlined"). We show overall species richness, native species richness, and nonnative species richness with mean and 95% credible intervals.

Species	City	A-B	A-C	A-D	B-C	B-D	C-D
All	All	**$p < 0.05$**	**$p < 0.001$**	**$p < 0.001$**	**$p < 0.001$**	**$p < 0.001$**	**$p < 0.01$**
All	Los Angeles	**$p < 0.01$**	**$p < 0.001$**	**$p < 0.01$**	**$p < 0.01$**	**$p < 0.001$**	**$p < 0.05$**
All	Oakland	$p = 0.068$	$p = 0.053$	**$p < 0.05$**	**$p < 0.05$**	**$p < 0.05$**	$p = 0.221$
All	San Diego	$p = 0.508$	**$p < 0.05$**	**$p < 0.05$**	$p = 0.761$	$p = 0.508$	$p = 0.761$
All	San Francisco	$p = 0.0922$	**$p < 0.01$**	**$p < 0.001$**	$p = 0.0708$	**$p < 0.001$**	**$p < 0.01$**
Native	All	**$p < 0.01$**	**$p < 0.001$**	**$p < 0.001$**	**$p < 0.001$**	**$p < 0.001$**	**$p < 0.05$**
Native	Los Angeles	**$p < 0.01$**	**$p < 0.001$**	**$p < 0.01$**	**$p < 0.01$**	**$p < 0.01$**	$p = 0.0707$
Native	Oakland	$p = 0.073$	**$p < 0.05$**	**$p < 0.05$**	**$p < 0.05$**	**$p < 0.05$**	$p = 0.363$
Native	San Diego	$p = 0.619$	$p = 0.091$	$p = 0.091$	$p = 0.886$	$p = 0.696$	$p = 0.696$
Native	San Francisco	$p = 0.2626$	**$p < 0.05$**	**$p < 0.001$**	$p = 0.0557$	**$p < 0.001$**	**$p < 0.05$**
Nonnative	All	$p = 0.26967$	**$p < 0.001$**	**$p < 0.001$**	**$p < 0.001$**	**$p < 0.001$**	**$p < 0.01$**
Nonnative	Los Angeles	$p = 0.0972$	**$p < 0.001$**	**$p < 0.01$**	**$p < 0.01$**	**$p < 0.001$**	**$p < 0.01$**
Nonnative	Oakland	$p = 0.326$	$p = 0.326$	**$p < 0.05$**	$p = 0.089$	**$p < 0.05$**	$p = 0.197$
Nonnative	San Diego	$p = 0.630$	$p = 0.071$	**$p < 0.05$**	$p = 0.630$	$p = 0.376$	$p = 0.936$
Nonnative	San Francisco	**$p < 0.05$**	**$p < 0.01$**	**$p < 0.001$**	$p = 0.3210$	**$p < 0.01$**	**$p < 0.05$**

Table S8. Beta diversity pair-wise comparisons. Pair-wise comparisons for beta diversity via PERMANOVA for each city is shown for all species, native species, and nonnative species. We used a PERMANOVA with 10000 permutations to determine which specific HOLC grade dyads (e.g., A vs. C, A vs. D, etc.) significantly differed in species assemblage with a Benjamin-Hochberg correction. Significant comparisons are bolded.