



# Gentrification drives patterns of alpha and beta diversity in cities

Mason Fidino<sup>a,1</sup>, Heather A. Sander<sup>b</sup>, Jesse S. Lewis<sup>c</sup>, Elizabeth W. Lehrner<sup>a</sup>, Kimberly Rivera<sup>a</sup>, Maureen H. Murray<sup>a</sup>, Henry C. Adams<sup>a</sup>, Anna Kase<sup>a</sup>, Andrea Flores<sup>a</sup>, Theodore Stankowich<sup>d</sup>, Christopher J. Schell<sup>e</sup>, Carmen M. Salisbury<sup>f</sup>, Adam T. Rohnke<sup>g</sup>, Mark J. Jordan<sup>h</sup>, Austin M. Green<sup>i</sup>, Ashley R. Gramza<sup>j</sup>, Amanda J. Zellmer<sup>k,l</sup>, Jacquie Williamson<sup>m</sup>, Thilina D. Surasinghe<sup>n</sup>, Hunter Storm<sup>o</sup>, Kimberly L. Sparks<sup>p</sup>, Travis J. Ryan<sup>f</sup>, Katie R. Remine<sup>q</sup>, Mary E. Pendergast<sup>r</sup>, Kayleigh Mullen<sup>s</sup>, Darren E. Minier<sup>t</sup>, Christopher R. Middaugh<sup>p</sup>, Amy L. Mertl<sup>u</sup>, Maureen R. McClung<sup>v</sup>, Robert A. Long<sup>q</sup>, Rachel N. Larson<sup>b</sup>, Michel T. Kohl<sup>w</sup>, Lavendar R. Harris<sup>w</sup>, Courtney T. Hall<sup>x</sup>, Jeffrey D. Haight<sup>y</sup>, David Drake<sup>z</sup>, Alyssa M. Davidge<sup>aa</sup>, Ann O. Cheek<sup>bb</sup>, Christopher P. Bloch<sup>n</sup>, Elizabeth G. Biro<sup>cc</sup>, Whitney J. B. Anthony<sup>dd</sup>, Julia L. Angstmann<sup>ee</sup>, Maximilian L. Allen<sup>ff</sup>, Solny A. Adalsteinsson<sup>cc</sup>, Anne G. Short Gianotti<sup>gg</sup>, Jalene M. LaMontagne<sup>ah</sup>, Tiziana A. Gelmi-Candusso<sup>ii</sup>, and Seth B. Magle<sup>a</sup>

Edited by Karen Seto, Yale University, New Haven, CT; received October 24, 2023; accepted January 30, 2024

**While there is increasing recognition that social processes in cities like gentrification have ecological consequences, we lack nuanced understanding of the ways gentrification affects urban biodiversity. We analyzed a large camera trap dataset of mammals (>500 g) to evaluate how gentrification impacts species richness and community composition across 23 US cities. After controlling for the negative effect of impervious cover, gentrified parts of cities had the highest mammal species richness. Change in community composition was associated with gentrification in a few cities, which were mostly located along the West Coast. At the species level, roughly half (11 of 21 mammals) had higher occupancy in gentrified parts of a city, especially when impervious cover was low. Our results indicate that the impacts of gentrification extend to nonhuman animals, which provides further evidence that some aspects of nature in cities, such as wildlife, are chronically inaccessible to marginalized human populations.**

alpha diversity | beta diversity | camera trap | gentrification | mammals

In urban areas, the processes that cause unequal access to environmental resources among people have ecological consequences (1–4). Gentrification, the process of neighborhood change by which White, more educated, and higher-income residents displace under-resourced residents in disinvested neighborhoods (5), exemplifies such a process. Ecologically, gentrification may alter which species are locally present in various ways (i.e., species richness or alpha diversity). First, as gentrification brings an influx of wealthier residents to a neighborhood, alpha diversity could increase as residents invest more resources into landscape management [i.e., the luxury effect, (6)]. Second, gentrification can accompany an influx of green infrastructure such as city parks, which can also increase alpha diversity (7, 8). Yet, gentrification also displaces the people who previously lived in the area, further intensifying inequities with people's experience with biodiversity (9). Thus, identifying whether gentrification leads to higher alpha diversity would 1) further demonstrate how changes in human populations contribute to changes in biodiversity and 2) provide evidence that some aspects of nature, such as wildlife, are chronically inaccessible to marginalized human populations.

Simply hypothesizing links between gentrification and alpha diversity, however, would fail to fully recognize how biodiversity responds to changes in human populations and urban design. For example, species assemblages in gentrified versus nongentrified areas may have similar alpha diversity (i.e., same number of species) but differ in species composition (i.e., high beta diversity). This could exacerbate environmental equity issues if species present in gentrified areas are considered desirable (e.g., songbirds), while those that persist in nongentrified areas are considered nuisance species (e.g., rats) that are likely to generate human–wildlife conflict (10) or spread zoonotic disease (11). Furthermore, cities are not identical, and thus, the relative impact of gentrification on biodiversity likely differs among cities (12). Therefore, disentangling the effect gentrification may have in exacerbating environmental inequities requires us to quantify how gentrification affects multiple species diversity metrics across cities.

To understand how changes in biodiversity are linked to gentrification, we tested the hypothesis that gentrification is associated with changes in alpha and beta diversity of medium to large mammals (>500 g). Mammals are an excellent focal group to explore changes in biodiversity that accompany gentrification because they respond strongly to urban landscape heterogeneity (12) and are often conservation and nuisance management targets (13). Given that gentrification-induced changes to a neighborhood could be associated with both alpha and beta diversity, we evaluated three competing predictions

## Significance

To increase environmental equity in cities, it is imperative to better understand social–ecological disparities in biodiversity. Our analysis demonstrates that gentrification, coupled with variation in impervious cover, shapes mammal distributions across US cities such that gentrified parts of cities have 1 to 2 more species on average. Because gentrification also displaces less-affluent human residents, our results provide further evidence that aspects of nature are less accessible to some people. Thus, cities need to develop equitable policies to avoid displacement and nature dispossession of marginalized communities.

Author contributions: M.F., H.A.S., J.S.L., T.S., C.J.S., and S.B.M. designed research; M.F., H.A.S., J.S.L., E.W.L., K.R., M.H.M., H.C.A., A.K., A.F., T.S., C.J.S., C.M.S., A.T.R., M.J.J., A.M.G., A.R.G., A.J.Z., J.W., T.D.S., K.L.S., T.J.R., K.R.R., M.E.P., K.M., D.E.M., C.R.M., A.L.M., M.R.M., R.A.L., R.N.L., M.T.K., L.R.H., C.T.H., J.D.H., D.D., A.M.D., A.O.C., C.P.B., E.G.B., W.J.B.A., J.L.A., M.L.A., S.A.A., and S.B.M. performed research; M.F. analyzed data; and M.F., H.A.S., J.S.L., E.W.L., K.R., M.H.M., H.C.A., A.K., A.F., T.S., C.J.S., C.M.S., A.T.R., M.J.J., A.M.G., A.R.G., A.J.Z., J.W., T.D.S., H.S., K.L.S., T.J.R., K.R.R., M.E.P., K.M., D.E.M., C.R.M., A.L.M., M.R.M., R.A.L., R.N.L., M.T.K., L.R.H., C.T.H., J.D.H., D.D., A.M.D., A.O.C., C.P.B., E.G.B., W.J.B.A., J.L.A., M.L.A., S.A.A., A.G.S.G., J.M.L., T.A.G.-C., and S.B.M. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

Copyright © 2024 the Author(s). Published by PNAS. This article is distributed under [Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 \(CC BY-NC-ND\)](https://creativecommons.org/licenses/by-nc-nd/4.0/).

<sup>1</sup>To whom correspondence may be addressed. Email: mfidino@lpzoo.org.

This article contains supporting information online at <https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2318596121/-DCSupplemental>.

Published April 15, 2024.

on the relative contribution gentrification could have on these diversity metrics (Fig. 1). Briefly, in gentrified and nongentrified parts of cities, we predicted that mammal communities could be fully distinct and therefore share no species (Fig. 1A), that gentrified areas could gain more species than they lose (Fig. 1B), or that gentrified and nongentrified areas could be nested subsets (Fig. 1C).

To test our hypothesis and evaluate our predictions across a variety of urban landscapes, we used camera-trap data from 23 cities in the United States that are part of the Urban Wildlife Information Network [UWIN; (14)], a systematic multicity biodiversity monitoring survey. Overall, we compiled 3 y of data between 2019 and 2021, which represented 188,909 camera trap days at 999 sites across 23 cities that span the contiguous United States (Fig. 2). Our analysis included 21 mammal species across 11 families (see *SI Appendix, Table S1* for the species in our analysis and *SI Appendix, Table S2* for a summary of species detected across cities). This unique dataset allowed us to quantify variation in how gentrification influenced alpha and beta diversity across a wide range of North American mammals distributed over diverse urban landscapes and compare city-specific estimates to our predictions.

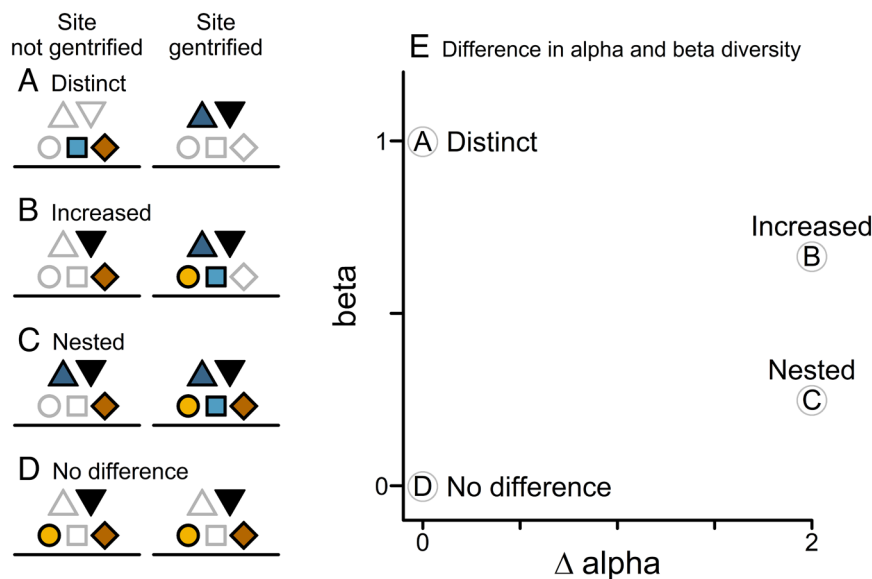
## Results

**Alpha Diversity Results.** We used a log-linear model that accounted for uncertainty in species richness estimates to quantify associations between alpha diversity and gentrification (see *SI Appendix, Tables S3–S10* for additional information on how we quantified gentrification). The model included two covariates: a binary covariate to indicate whether a site was within 500 m of a gentrified Census tract and an urban intensity metric: the proportion of impervious cover within a 1 km buffer of each site. Additionally, we included the interaction between these covariates and used city-level random effects for all intercept and slope terms. Among cities, the minimum impervious cover at gentrified sites was 22.5%

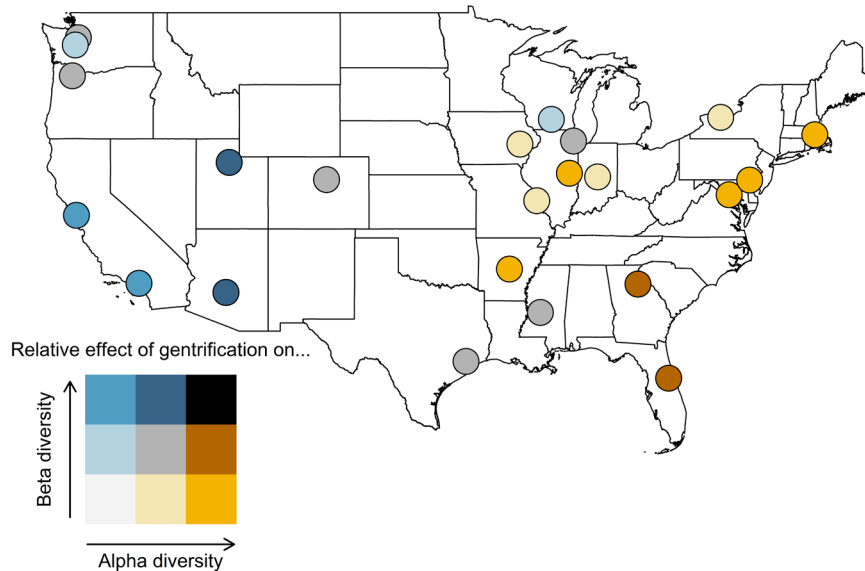
on average. The expected alpha diversity at nongentrified sites with 22.5% impervious cover was 7.73 species (90% CI = 6.67, 8.95), while alpha diversity at a similar gentrified site was about 13% higher (8.74 species; 90% CI = 7.13, 10.69). This difference equates to roughly 1 to 2 more species at gentrified sites than nongentrified sites within a city. The among-city model parameters agreed with this pattern: Gentrification was likely associated with higher alpha diversity ( $\beta_{gent} = 0.17$ ; 90% CI = 0.02, 0.33; Fig. 3), and the interaction term suggested this effect was strongest at lower levels of impervious cover ( $\beta_{gent \times imp} = -0.22$ ; 90% CI = -0.48, 0.04, *SI Appendix, Table S11* and Figs. S2–S24). Conversely, impervious cover had a strong negative effect on alpha diversity ( $\beta_{imp} = -0.49$ ; 90% CI = -0.67, -0.31). Therefore, the effect of impervious cover on alpha diversity was roughly 2.87 times greater than that of gentrification, and alpha diversity decreased by about 3.5 species when impervious cover at a site increased from 0 to 80%. Regardless, that gentrification was estimated to affect biodiversity even while accounting for impervious cover suggests that impervious cover alone is insufficient to explain biodiversity patterns within cities.

At the city level, 10 of 23 cities had >0.9 probability that gentrification and alpha diversity positively covaried, whereas impervious cover was associated with decreased species richness in 18 of 23 cities (*SI Appendix, Table S13*). Furthermore, cities in which we detected a gentrification effect on alpha diversity were predominantly located in the eastern and central United States (Fig. 4).

**Beta Diversity Results.** We used a generalized dissimilarity model that accounted for uncertainty in pairwise dissimilarity between pairs of sites within each city. Our response variable was Sørensen's dissimilarity index, where a value of 0 means that species composition at a pair of sites was identical, and 1 means that the two sites shared no species. We included impervious cover and a binary covariate to indicate whether a site was near a gentrified Census tract as covariates, controlled for geographic distance between sites within a city, and used city-level random effects for



**Fig. 1.** Four theoretical ways that mammal richness (i.e., alpha diversity) and differences in community composition (i.e., beta diversity) could change in response to gentrification, where filled-in shapes in subfigures (A–D) represent the presence of different species. (A) Alpha diversity could remain constant but species assemblages could completely differ between gentrified and nongentrified areas, resulting in no difference in alpha diversity but the highest beta diversity. (B) More species could be gained than lost in gentrified areas, resulting in a large increase in alpha diversity and a smaller increase in beta diversity relative to fully distinct communities. (C) Communities in nongentrified areas could be a nested subset of those in gentrified areas, which could result in large increases in alpha diversity but low beta diversity. (D) The null prediction: no difference; gentrification is not associated with differences in alpha and beta diversity. (E) The difference in alpha diversity (x axis) as well as beta diversity, where a value of 0 indicates identical communities at a pair of sites and 1 indicates completely different communities at a pair of sites (y axis).



**Fig. 2.** Locations of the 23 cities used to assess differences in mammal communities among gentrified and nongentrified parts of a city. Cities are represented by dots. The dot color illustrates the relative effect of gentrification on alpha and beta diversity at average sites in each city that vary in their gentrification status. Gentrification had a more pronounced effect on alpha diversity overall. However, gentrification in more western cities had a stronger effect on beta diversity, central US cities had a mixture, and East Coast cities had a stronger alpha diversity effect. See *SI Appendix, Fig. S1* for this map with city names included.

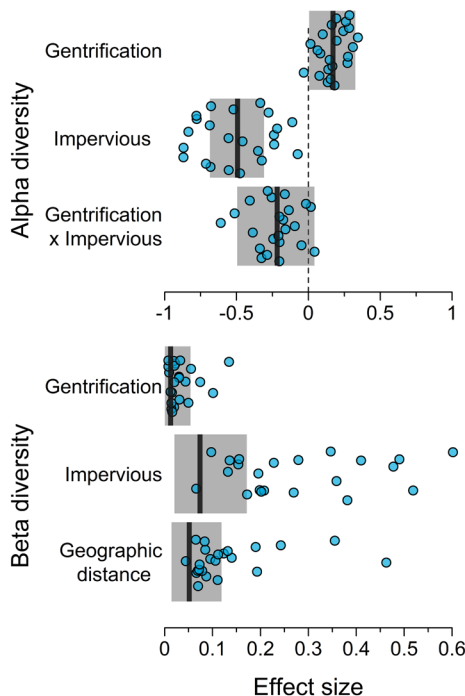
all intercept and slope terms. It is important to note that because the rate of compositional turnover along environmental gradients often varies, generalized dissimilarity models apply I-spline basis functions (i.e., smoothing splines) to continuous covariates to capture nonlinearity in the data if it is present. The use of these splines is beneficial as it provides a flexible way to account for the nonlinear relationship between beta diversity and the ecological

distance between sites, whether that be environmental or spatial. On average, gentrification had a negligible association with beta diversity. For two adjacent sites with identical levels of impervious cover, the among-city difference in beta diversity at gentrified and nongentrified sites was effectively zero (0.01; 95% CI = 0.00, 0.06; 90% CI = 0.00, 0.05).

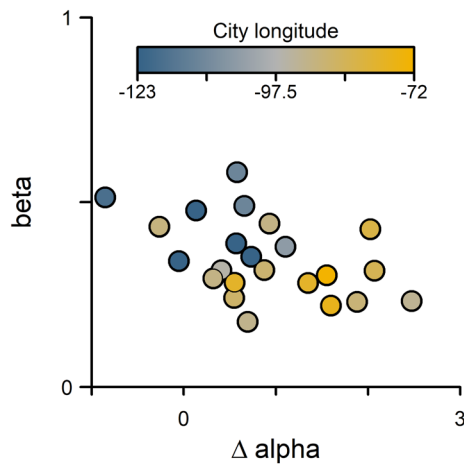
On average, impervious cover had the greatest effect on beta diversity ( $\beta_{imp} = 0.07$ ; 90% CI = 0.02, 0.18), followed by the geographic distance between sites within a city ( $\beta_{distance} = 0.05$ ; 90% CI = 0.02, 0.13), and then gentrification ( $\beta_{gent} = 0.01$ ; 90% CI = 0.01, 0.05; Fig. 3). As such, the average effect of impervious cover on beta diversity was 5.83 times greater than the average effect of gentrification. For example, when comparing sites at opposite ends of the impervious cover gradient (e.g., high vs. low impervious cover), beta diversity was almost two times greater than sites with the same level of impervious cover (e.g., low vs. low impervious cover). While holding the other covariates in this model at their mean, the beta diversity between sites with the highest (80%) and lowest (0%) impervious cover was 0.16 (90% CI = 0.08, 0.29) whereas sites with the same level of impervious cover was 0.09 (90% CI = 0.03, 0.21).

While the average among-city estimates indicated a minimal association of gentrification with beta diversity, beta diversity did strongly covary with gentrification in some cities (Figs. 1 and 3 and *SI Appendix, Fig. S2–S24*). Overall, it appears that gentrification in West Coast cities had a greater association with beta diversity than alpha diversity: four of the five largest associations between gentrification and beta diversity were observed on the West Coast (Fig. 4). Los Angeles, California, for example, had the strongest association between gentrification and beta diversity (median of summed spline coefficients = 0.13; 90% CI = 0.09, 0.18). In Los Angeles, the beta diversity between gentrified and nongentrified sites was 1.28 times greater than sites with the same gentrification status (90% CI = 1.18, 1.38). In other words, sites in Los Angeles that only differed in their gentrification status had mammal communities that were about 60% similar, while sites that did not differ in their gentrification status were about 69% similar.

Finally, cities varied in their relationship between impervious cover and beta diversity. Phoenix, Arizona, had the largest effect



**Fig. 3.** Impervious cover had a stronger effect than gentrification on alpha and beta diversity. Alpha diversity, however, was likely greatest in gentrified areas with lower impervious cover because of the negative interaction term. Vertical black lines represent among-city estimates, the gray-filled rectangles are 90% credible intervals, and blue dots are city-specific estimates for each model parameter. Alpha diversity model parameters are on the log scale, while beta diversity model parameters are on the clog scale (i.e.,  $-\log(1 - x)$ ). As a result, the beta diversity model parameters are constrained to be greater than 0.



**Fig. 4.** Western cities (more negative longitude) had smaller differences in alpha diversity but greater beta diversity, while the remaining cities had greater differences in alpha diversity and lower beta diversity. Dots represent the expected beta diversity and difference in alpha diversity between an average gentrified and nongentrified site in each of the 23 cities. The x axis represents the change in alpha diversity as a function of gentrification, with positive values indicating greater species richness at gentrified sites. The y axis is Sørensen's dissimilarity index, where 0 and 1, respectively, represent completely identical and distinct communities between sites.

(median of summed spline coefficients = 0.79; 90% CI = 0.73, 0.85). Beta diversity between a pair of sites at opposite ends of Phoenix's impervious gradient was 0.72 (90% CI = 0.70, 0.73), while the beta diversity between sites with identical levels of impervious cover was 1.91 times lower (median = 0.38; 90% CI = 0.36, 0.39). Conversely, Indianapolis, Indiana, had the smallest effect (median of summed spline coefficients = 0.07; 90% CI = 0.03, 0.11). When making the same comparison in Indianapolis, the estimated beta diversity for sites at opposite ends of their impervious cover gradient was 0.27 (90% CI = 0.25, 0.29) which was similar to the estimated beta diversity between sites with identical levels of impervious land cover (median = 0.22; 90% CI = 0.25, 0.29). For more city-specific beta diversity results, see *SI Appendix, Figs. S2–S24*.

**Species that Covaried with Gentrification.** As the alpha and beta diversity estimates were compiled from the posterior of a multicity multispecies occupancy model, we also quantified how each species responded to gentrification. Of the 21 species we analyzed, 11 positively covaried with gentrification at the 0.90 credible level (Fig. 5). As we centered and scaled impervious cover, negative parameter estimates for the interaction between gentrification and impervious cover indicate that many of these species were more likely to occupy gentrified areas when impervious cover was low (Fig. 5). See *SI Appendix, Tables S11–S36* for parameter estimates from all models.

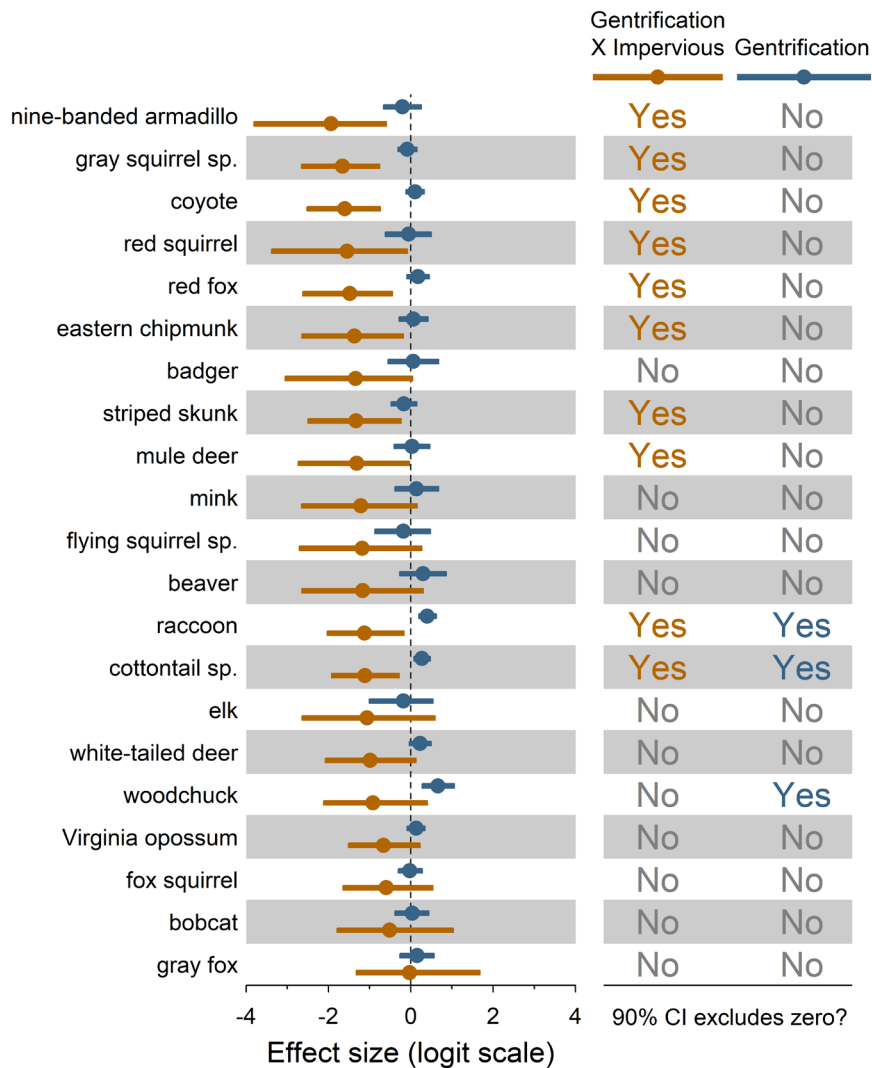
## Discussion

Our results indicate that gentrification, coupled with impervious cover, shape mammal diversity across United States cities. While impervious cover was the dominant form of environmental variation that impacted mammal distributions and greatly reduced alpha diversity, gentrification represented a secondary axis that may ameliorate the negative effect of impervious cover on mammals. This finding emphasizes the often-overlooked role socioeconomic dimensions play in understanding urban biodiversity patterns (15). Such gentrification-induced changes to the mammal community are likely due to wealth-associated increases in

vegetative cover (e.g., street trees), professional landscaping, and irrigation (1, 16), which collectively improve habitat quality for mammals (17). Because gentrification also displaces less-affluent human residents, our results provide further evidence that aspects of nature are less accessible to some urban residents, which underlies the need for cities to develop equitable policies to avoid displacement and nature dispossession of marginalized communities (1–4). That we found gentrification-related shifts in mammal communities across a wide range of cities indicates that the impacts of gentrification extend to nonhuman animals, which highlights the broader implications and importance of this process.

Gentrification may have a smaller effect on mammal diversity than impervious cover for many reasons. First, areas with high impervious cover are likely unsuitable for most mammals (6). In fact, our analysis suggests that gentrification provides the greatest increase in alpha diversity when impervious cover was low. In such locations, higher availability of nonimpervious cover coupled with increased resources (e.g., time, money) likely facilitates greening at the residential parcel level, which scales up to enhance neighborhood wildlife habitat. The lack of nonimpervious cover in intensely urbanized neighborhoods may preclude this effect. Thus, social processes within cities may modulate the effect of the built environment on urban biodiversity. Second, the nongentrified locations we used for comparison represent a mix of sites that were either historically vulnerable to gentrification but did not gentrify or were never vulnerable to gentrification and so could not gentrify (e.g., an already affluent neighborhood). This mix could have made it more difficult to quantify gentrification-induced changes as the sites that were used for comparison varied from one another. Third, this study came about well after UWIN began. As such, our long-term sampling locations were predominately selected to fall along an urban intensity gradient and not gentrification status. While we overcame this issue with our large sample size, more targeted investigations into gentrification and biodiversity should stratify sampling across locations that vary in gentrification status, income gradients, and whether Census tracts were vulnerable to gentrification. Fourth, gentrification is a multidimensional and dynamic process that we distilled into a binary metric for the sake of analysis. As many gentrification metrics exist, all of which quantify gentrification differently, further research is needed to understand gentrification in its different forms across cities (18). Nevertheless, we observed an association between our gentrification metric and patterns of mammal diversity across many US cities. Such results indicate that simple gentrification metrics could be a useful starting point to quantify how gentrification influences other taxa. To facilitate such investigations, we encourage others to tap into the wealth of data products that exist to track demographics over time in cities, beyond what is readily available from the decennial Census. As one example, the Integrated Public Use Microdata Series dataset created by the National Historical Geographic Information System has spatially georectified Census data across many years, making it easier for researchers to conduct large-scale comparative research (19).

We found that our empirical results (Fig. 4) were more nuanced than our predictions (Fig. 1). While some cities experienced different mammal communities in gentrified versus nongentrified areas, we never observed completely distinct communities (i.e., beta diversity never reached a value of 1; Fig. 1A). We also never witnessed large shifts in alpha diversity and high beta diversity simultaneously, which could happen if gentrified areas gained more species than they lost (i.e., the increased prediction; Fig. 1B). Instead, gentrification in many cities was associated with increased alpha diversity but low beta diversity (Fig. 1C) and could indicate



**Fig. 5.** The average effect of gentrification on the occupancy of mammals in this study. Overall, 10 species were more common in gentrified areas when impervious land cover was low, as evidenced by the strongly negative gentrification X impervious slope terms for those species. Three species were more common in gentrified parts of a city overall, and there were no species that negatively covaried with gentrification. Dots represent median estimates for each species, and horizontal lines are 90% credible intervals.

that wildlife communities in gentrified and not gentrified areas are nested subsets of one another. Such a pattern could arise due to the presence of common urban generalists throughout most North American cities, such as Northern raccoon (*Procyon lotor*). These results could also indicate that gentrification is a subtle and ongoing process that likely invokes change over long time periods. Our results may thus identify the start of a process that could become more pronounced over time.

We observed a spatial pattern in the relative association of gentrification with alpha and beta diversity, with western cities showing distinct differences from eastern cities and central US cities representing a mixture of the two (Fig. 2). While socioeconomic-biodiversity relationships among cities could vary along many axes [e.g., temperature, economic inequality, human population density; (20)], it may also be that cities closer to the East Coast are, on average, older and wildlife communities within such cities have become more similar over time (21). As such, gentrification increased species richness but had minimal effects on community composition in these cities. On the other hand, in West Coast cities, which are younger and were affected by extreme weather events during our data collection period (e.g., drought and El Niño), gentrification impacted community composition but not species richness. Such extreme

weather events likely led to more variable wildlife communities as species responded to changes in the availability of resources such as water. It is possible that gentrified parts of a city benefited from additional water resources or cooling provided by trees during droughts (17). This could result in wildlife communities that differed more from nongentrified areas if species responded to such resource allocation. In our analysis, we considered the average wildlife community across sampling periods and seasons, minimizing the potential impact of drought on our results. However, a more detailed and longer-term investigation into how drought influences urban species distributions is warranted. Arid cities, for example, exhibit a stronger correlation between local species richness and per capita income (20, 22), while species in hotter cities are more negatively influenced by urban intensity (23). Exploring how the magnitude of such patterns change during extreme weather events in arid and nonarid cities alike could provide additional insight into how urban biodiversity may respond to a warming climate.

In closing, decades-old land-use decisions in cities can lead to a legacy effect that influences the current distribution of environmental resources available to both humans and wildlife. Similarly, our results show that the socioeconomic process of gentrification influences wildlife communities. These factors shape where species

occur in cities and who can observe or interact with them (negatively or positively). To address these issues, there is a critical need for updated land development and management policies as well as legal mechanisms to prioritize social equity (24). For instance, while urban green space is considered a public good in theory, in practice, it often becomes a commodity primarily accessible to affluent White communities that displaces marginalized communities (25–27). Uncoupling urban green space development from Western capitalism is a challenging task but involves reframing green space development as an essential component of city maintenance rather than an economic development strategy (24). It is crucial to prioritize environmental equity in decision-making processes as the choices we make today will shape our cities for decades to come, particularly because cities will continue to house most of the global human population. Large-scale research networks like UWIN are well positioned to assist decision-makers in understanding social–ecological disparities across different scales, providing valuable insights for building equitable and biodiverse cities.

## Materials and Methods

**Biological Sampling.** We used data from 23 UWIN cities in the United States for this study. Each city followed the same systematic study design, placing motion-triggered camera traps in urban green space along an urbanization gradient (14). Mammal data for this study came from 12 distinct sampling periods between 2019 and 2021. Camera deployments in each sampling period were about 35 d (SD = 13.01) and began on the first of January, April, July, or October of each year. Because UWIN cities joined the network at different times, the number of sampling periods among cities varied (median = 7; minimum = 2; maximum = 12). The median number of unique camera-trapping sites per city was 35 (minimum = 23; maximum = 104).

Mammals in camera trap images were identified to species by trained experts. Depending on the city, trained experts ranged from ecologists with decades of camera trapping experience in their study area, college undergraduates, or volunteers. The latter two examples required multiple experts to classify images before they were considered research grade. However, flying squirrel, gray squirrel, and cottontail rabbit species were summarized to either the subgenus or genus level given challenges in identifying them to the species level from camera trap images (28). For each camera deployment, we counted the number of days each species was detected and the number of operational camera days, which were then used to estimate species occupancy and detectability within our multicity multispecies occupancy model (6, 29).

Overall, 48 mammal taxa were photographed, but—to facilitate model convergence—we restricted our analysis to a total of 21 species that were detected on at least 75 d across a minimum of three cities. Gray squirrels (*Sciurus carolinensis* or *Sciurus griseus*) were detected most often (~41,300 detection days), while flying squirrels (*Glaucomys* sp.) were detected the least (79 detection days). See *SI Appendix, Table S1* for the names of the species included in our analysis and *SI Appendix, Table S2* for a summary of all species detected across cities.

**Social–Environmental Variables.** We calculated two independent variables and included both in all models. First, to represent urban intensity, we calculated the percent impervious cover within 1 km of each site from the 2019 National Land Cover Database imperviousness dataset (30). Second, we determined whether each site was within 500 m of a gentrifying Census tract. To quantify gentrification across a wide range of cities, we modified a two-step process described by Chapple et al. (31). For the first step, we identified Census tracts that were vulnerable to gentrification in 2010 as tracts with at least 500 residents and two of these three qualities: 1) a median income less than the city's median income, 2) a proportion of college-educated residents less than the city median, and 3) a proportion of non-White residents greater than the city median. To calculate gentrification vulnerability, we used the 2010 US decennial Census data via the tidycensus package in R v 4.2.0 (32, 33). For the second step, we used the 2019 American Community Survey (34) data to determine whether a vulnerable Census tract became gentrified. Here, vulnerable tracts from the first step were identified

as gentrified if they experienced a greater increase in median income between 2010 and 2019 than the average change across a city—after correcting for inflation—as well as one of two qualities: a change in college-educated residents or a change in the proportion of non-Hispanic White residents between 2010 and 2019 that exceeded the average change across the city. For additional details and summaries regarding this gentrification metric, see *Additional Gentrification Metric Details of SI Appendix*, where we provide additional summaries of the variables used to quantify gentrification (*SI Appendix, Tables S3–S10*).

**Associations between Gentrification and Social–Environmental Variables.** Among cities, on average, 25% (SD = 11%) of camera sites were within 500 m of a gentrified Census tract. Sites near gentrified Census tracts generally showed higher impervious land cover (mean = 46%, SD = 20%) than nongentrified sites (mean = 25%, SD = 21%). Within cities, Urbana, Illinois, had the lowest percent of sites within 500 m of a gentrified Census tract (3%), and Phoenix, Arizona, had the highest (50%).

With respect to the 2019 distribution of the variables we used to quantify gentrification across cities, the median per capita income of gentrified Census tracts (mean = \$68,785, SD = \$28,193) was roughly \$30,000 less than nongentrified Census tracts (mean = \$98,678, SD = \$50,777). The proportion of non-Hispanic White residents living in gentrified Census tracts (mean = 0.28, SD = 0.26) was lower than nongentrified Census tracts (mean = 0.48, SD = 0.30), and the proportion of people with a college degree in gentrified Census tracts (mean = 0.34, SD = 0.18) was slightly lower than nongentrified Census tracts (mean = 0.48, SD = 0.23). Thus, gentrified Census tracts still have lower incomes, fewer non-Hispanic White residents, and fewer college-educated residents than nongentrified Census tracts. However, gentrified Census tracts saw greater than average shifts in these variables over time such that the population living there shifted to become whiter, richer, and more educated.

Gentrification may also be associated with an increase in either urban green space or impervious cover. As such, we quantified whether gentrified Census tracts had a greater increase in the proportion of green space (i.e., developed, open space from NLCD data) or impervious cover over the same time frame we used to quantify gentrification (i.e., 2010 to 2019). We did not find this to be true. After averaging the proportional increase in urban green space across gentrified and nongentrified Census tracts in each city, the among-city range in both types of Census tracts was effectively zero (min = −0.01, max = 0.00). Likewise, both gentrified and nongentrified Census tracts had less than a 1% increase in the proportion of impervious over this time frame, although there were a small proportion of Census tracts (103 of 7816) that had a >5% increase. Of those 103 Census tracts that had a relatively large increase in impervious cover, only 11 gentrified.

**Statistical Analysis.** We quantified associations between gentrification and impervious cover and patterns of alpha and beta diversity across United States cities, using a Bayesian approach for all models. To do so, we used a method akin to a meta-analysis, although in our case, we fed the summarized results of our multispecies multicity occupancy model into secondary models. However, unlike more common meta-analyses, which must contend with issues of publication bias that can distort results (35), our analysis used all available UWIN data to parameterize both alpha and beta diversity models, resulting in a more unbiased and data-driven evaluation of our hypothesis. We explain the modeling procedure below; see supporting information for a complete description of each model.

First, we fitted a Bayesian multicity, multispecies occupancy model that included a first-order autoregressive term to account for repeat sampling across primary sampling periods within each city (6, 29). This model had three separate logit-linear functions: one to indicate a species presence within a city's species pool, one for site-level occupancy, and one for site-level detection probability. Following Magle et al. (6), we included the distance of each city to the known margin of a species' geographic range in the first linear predictor, with positive and negative numbers, respectively, indicating cities within and outside a species' range. Range data came from IUCN red list data (36). For site-level occupancy and detection, we included impervious cover, gentrification, and the interaction between the two as slope terms in the model. All species-level parameters shared information among species and cities via their random effect structure. Following a 1,000-step adaptation phase and a 125,000-step burn-in, we sampled the posterior 120,000 times across 4 chains. We thinned chains by 3 for a total of 40,000 posterior samples. For all models, we assessed model convergence through a

visual inspection of traceplots and ensured that Gelman–Rubin diagnostics were  $<1.10$  (37). Following model convergence, we simulated species occupancy at each site across the entire study area from 5,000 random samples of the occupancy model's posterior distribution.

For the alpha diversity model, we calculated 1) the expected species richness at each site and 2) the SD in this estimate across the 5,000 posterior samples. To limit the effect of individual years on these estimates, we calculated species richness at a site across all possible sampling periods. This resulted in one estimate per site across cities. We then fitted a varying intercept, varying slope log-linear model to these data, which treated species richness as the response variable but also incorporated the associated uncertainty in this estimate (38). Intercept and slope terms were treated as city-level random effects. We included impervious cover, gentrification, and their interaction as covariates. Following a 1,000-step adaptation and 10,000-step burn-in phase, we sampled the posterior 160,000 times across four chains. We thinned chains by two for a total of 80,000 posterior samples.

For the beta diversity model, we calculated 1) pairwise community dissimilarity between pairs of sites within each city (i.e., Sørensen's dissimilarity index) and 2) the SD in this estimate across the 5,000 posterior samples (39). Like the alpha diversity model, beta diversity estimates were made across all primary sampling periods. We then fitted a varying intercept, varying slope generalized dissimilarity model to these data, which treated pairwise dissimilarity between each pair of sites in a city as the response variable (40, 41). This model used a log link function and had an inverse link function of  $1 - \exp(-\mu)$ , where  $\mu$  is the linear predictor for one data point. Similar to the alpha diversity model, the beta diversity model incorporated the associated uncertainty in the beta diversity estimate. Intercepts and slopes were treated as city-level random effects. Because community composition may be more similar in nearby sites, we included geographic distance between site pairs as a covariate. We also included differences in impervious cover and gentrification between sites as covariates. However, because this model uses l-spline basis functions to incorporate possible nonlinear responses along environmental gradients, we could not include an interaction between gentrification and impervious cover in this model (40, 41). Following a 1,000-step adaptation and 2,000-step burn-in phase, we sampled the posterior 240,000 times across four chains. We thinned chains by three for a total of 80,000 posterior samples.

**Data, Materials, and Software Availability.** Species detection/non-detection data and relevant code to recreate analysis data have been deposited in <https://github.com/mfidino/uwin-gentrification> (10.5281/zenodo.10413281) (42).

1. M. Leong, R. R. Dunn, M. D. Trautwein, Biodiversity and socioeconomic in the city: A review of the luxury effect. *Biol. Lett.* **14**, 20180082 (2018).
2. C. J. Schell *et al.*, The ecological and evolutionary consequences of systematic racism in urban environments. *Science* **369**, eaay4497 (2020).
3. D. H. Locke *et al.*, Residential housing segregation and urban tree canopy in 37 US Cities. *npj Urban Sustainability* **1**, 15 (2021).
4. K. T. Burghardt *et al.*, Current street tree communities reflect race-based housing policy and modern attempts to remedy environmental injustice. *Ecology* **104**, e3881 (2023).
5. S. J. Halsey *et al.*, The public health implications of gentrification: Tick-borne disease risks for communities of color. *Front. Ecol. Environ.* **21**, 191–198 (2023).
6. S. B. Magle *et al.*, Wealth and urbanization shape medium and large mammalian communities. *Global Change Biol.* **27**, 5446–5459 (2021).
7. I. Angelovski *et al.*, Green gentrification in European and North American cities. *Nat. Commun.* **13**, 3816 (2022).
8. M. Triguero-Mas *et al.*, Exploring green gentrification in 28 global North cities: The role of urban parks and other types of greenspaces. *Environ. Res. Lett.* **17**, 104035 (2022).
9. J. R. Wolch, J. Byrne, J. P. Newell, Urban green space, public health, and environmental justice: The challenge of making cities 'just green enough'. *Landscape Urban Plann.* **125**, 234–244 (2014).
10. P. Hubbard, A. Brooks, Animals and urban gentrification: Displacement and injustice in the trans-species city. *Progr. Hum. Geogr.* **45**, 1490–1511 (2021).
11. 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. Syst.* **53**, 403–426 (2022).
12. M. Fidino *et al.*, Landscape-scale differences among cities alter common species' responses to urbanization. *Ecol. Appl.* **31**, e02253 (2021).
13. S. D. Gehrt, S. P. Riley, B. L. Cypher, *Urban Carnivores: Ecology, Conflict, and Conservation* (John Hopkins University Press, 2010).
14. S. B. Magle *et al.*, Advancing urban wildlife research through a multi-city collaboration. *Front. Ecol. Environ.* **17**, 232–239 (2019).
15. R. J. Moll *et al.*, What does urbanization actually mean? A framework for urban metrics in wildlife research. *J. Appl. Ecol.* **56**, 1289–1300 (2019).
16. L. W. Clarke, G. D. Jenerette, A. Davilla, The luxury of vegetation and the legacy of tree biodiversity in Los Angeles, CA. *Landscape Urban Plann.* **116**, 48–59 (2013).
17. G. H. Donovan, J. P. Prestemon, D. T. Butry, A. R. Kaminski, V. J. Monleon, The politics of urban trees: Tree planting is associated with gentrification in Portland, Oregon. *For. Policy Econ.* **124**, 102387 (2021).
18. S. Easton, L. Lees, P. Hubbard, N. Tate, Measuring and mapping displacement: The problem of quantification in the battle against gentrification. *Urban Stud.* **57**, 286–306 (2020).
19. S. Manson, J. Schroeder, D. Van Riper, T. Kugler, S. Ruggles, IPUMS National Historical Geographic Information System, Version 17.0 (IPUMS, Minneapolis, MN, 2022). <https://doi.org/10.18128/D050.V17.0>. Accessed 25 June 2022.
20. E. R. Kuras *et al.*, Urban socioeconomic inequality and biodiversity often converge, but not always: A global meta-analysis. *Landscape Urban Plann.* **198**, 103799 (2020).
21. A. M. Pidgeon *et al.*, Systematic temporal patterns in the relationship between housing development and forest bird biodiversity. *Conserv. Biol.* **28**, 1291–1301 (2014).
22. D. Chamberlain *et al.*, Wealth, water and wildlife: Landscape aridity intensifies the urban luxury effect. *Global Ecol. Biogeogr.* **29**, 1595–1605 (2020).
23. J. D. Haight *et al.*, Urbanization, climate, and species traits shape mammal communities from local to continental scales. *Nat. Ecol. Evol.* **7**, 1654–1666 (2023).
24. L. E. Mullenbach, B. Breyer, B. B. Cutts, L. Rivers III, R. Larson, An antiracist, anticolonial agenda for urban greening and conservation. *Conserv. Lett.* **15**, e12889 (2022).
25. M. Grove *et al.*, The legacy effect: Understanding how segregation and environmental injustice unfold over time in Baltimore. *Ann. Am. Assoc. Geogr.* **108**, 524–537 (2018).
26. A. Rigolon, M. Browning, V. Jennings, Inequities in the quality of urban park systems: An environmental justice investigation of cities in the United States. *Landscape Urban Plann.* **178**, 156–169 (2018).
27. A. Rigolon, J. Németh, Green gentrification or 'just green enough': Do park location, size and function affect whether a place gentrifies or not? *Urban Stud.* **57**, 402–420 (2020).
28. R. Kays *et al.*, Which mammals can be identified from camera traps and crowdsourced photographs? *J. Mammal.* **103**, 767–775 (2022).
29. C. Sutherland, M. Brambilla, P. Pedrini, S. Tenan, A multiregion community model for inference about geographic variation in species richness. *Methods Ecol. Evol.* **7**, 783–791 (2016).
30. J. Dewitz, U.S. Geological Survey. National Land Cover Database (NLCD) 2019 Products, version 2.0. U.S. Geological Survey. <https://doi.org/10.5066/P9KZCM54>. Accessed 25 June 2022.
31. K. Chapelle *et al.*, *Developing a New Methodology for Analyzing Potential Displacement* (University of California, Berkeley, CA, 2017).

**ACKNOWLEDGMENTS.** We thank all UWIN members for their hard work in collecting these data and Pariveda for making the database UWIN uses. We thank R. Mueller, T. Gallo, L. Bliss-Ketchum, A. Aviles Gamboa, I. Taves, and K. Larson for their contributions during different stages of this project. We thank N. Gilbert and one anonymous reviewer for comments on a previous draft of this manuscript. The Seattle Urban Carnivore Project, coordinated by Woodland Park Zoo and Seattle University, provided data gathered with significant contributions of effort from many Woodland Park Zoo community science volunteers and Seattle University students. The Hidden Life of Houston project, coordinated by University of Houston and Memorial Park Conservancy, thanks E. Lagueux, K. Lugar, K. Plum, S. Sullivan, G. Farfan, R. Sanchez-Ruffra, S. Dreyer, J. Vasquez, and G. Kostecki for leading fieldwork and the many University of Houston biology students who conducted fieldwork and tagged photos.

Author affiliations: <sup>a</sup>Conservation and Science Department, Lincoln Park Zoo, Chicago, IL 60614; <sup>b</sup>Department of Geographical and Sustainability Sciences, University of Iowa, Iowa City, IA 52242; <sup>c</sup>College of Integrative Sciences and Arts, Arizona State University, Mesa, AZ 85287; <sup>d</sup>Department of Biological Sciences, California State University, Long Beach, CA 90840; <sup>e</sup>Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720; <sup>f</sup>Department of Biological Sciences, Butler University, Indianapolis, IN 46208; <sup>g</sup>Department of Wildlife, Fisheries, and Aquaculture, Mississippi State University, Jackson, MS 39275; <sup>h</sup>Department of Biology, Seattle University, Seattle, WA 98112; <sup>i</sup>Science Research Initiative, University of Utah, Salt Lake City, UT 84112; <sup>j</sup>Playa Lakes Joint Venture, Lafayette, CO 80516; <sup>k</sup>Department of Biology, Occidental College, Los Angeles, CA 90042; <sup>l</sup>Arroyos & Foothills Conservancy, Pasadena, CA 91102; <sup>m</sup>Consulting Department, Wildlife Habitat Council, Bethesda, MD 20910; <sup>n</sup>Department of Biological Sciences, Bridgewater State University, Bridgewater, MA 02325; <sup>o</sup>University Honors College, Portland State University, Portland, OR 97201; <sup>p</sup>Research Division, Arkansas Game and Fish Commission, Little Rock, AR 72205; <sup>q</sup>Wildlife Conservation Division, Woodland Park Zoo, Seattle, WA 98103; <sup>r</sup>Sageland Collaborative, Salt Lake City, UT 84101; <sup>s</sup>Conservation Department, Utah's Hogle Zoo, Salt Lake City, UT 84108; <sup>t</sup>Conservation Society of California, Oakland, CA 94605; <sup>u</sup>Department of Natural Sciences and Mathematics, Lesley University, Cambridge, MA 02138; <sup>v</sup>Biology & Health Sciences Department, Hendrix College, Conway, AR 72032; <sup>w</sup>Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602; <sup>x</sup>Conservation Operations Department, Memorial Park Conservancy, Houston, TX 77007; <sup>y</sup>School of Life Sciences, Arizona State University, Tempe, AZ 85287; <sup>z</sup>Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, WI 53706; <sup>aa</sup>Department of Integrative Biology, University of Colorado, Denver, CO 80204; <sup>ab</sup>Department of Biology and Biochemistry, University of Houston, Houston, TX 77004; <sup>ac</sup>Tyson Research Center, Washington University in St. Louis, Eureka, MO 63025; <sup>ad</sup>University of Health Sciences and Pharmacy, St. Louis, MO 63110; <sup>ae</sup>Center for Urban Ecology and Sustainability, Butler University, Indianapolis, IN 46208; <sup>af</sup>Illinois Natural History Survey, Prairie Research Institute, University of Illinois, Champaign, IL 61820; <sup>ag</sup>Department of Earth and Environment, Boston University, Boston, MA 02215; <sup>ah</sup>Department of Biological Sciences, DePaul University, Chicago, IL 60614; and <sup>ai</sup>Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON M5S 3B2, Canada

32. K. Walker, M. Herman, tidy census: Load US Census boundary and attribute data as tidyverse and sf ready data frames version 1.4.4 (2023), <https://CRAN.R-project.org/package=tidy census>. Accessed 12 March 2023.
33. R Core Team, R: A language environment for statistical computing version 4.2.0 (2022), <https://www.R-project.org>. Accessed 23 April 2022.
34. U.S. Census Bureau, 2009–2011 American community survey 3-year public use microdata samples (2012). <https://www.census.gov/programs-surveys/acs/data.html>. Accessed 25 June 2022.
35. S. Nakagawa *et al.*, Methods for testing publication bias in ecological and evolutionary meta-analyses. *Methods Ecol. Evol.* **13**, 4–21 (2022).
36. IUCN, The IUCN red list of threatened species, version 2020-2 (2020), <https://iucnredlist.org>. Accessed 14 July 2020.
37. A. Gelman *et al.*, *Bayesian Data Analysis* (Chapman & Hall/CRC Press, ed. 3, 2014).
38. M. Kéry, J. A. Royle, *Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance, and Species Richness in R and BUGS* (Academic Press, 2015), vol. 1.
39. P. Legendre, L. Legendre, *Numerical Ecology* (Elsevier, 2012).
40. S. Ferrier, G. Manion, J. Elith, K. Richardson, Using generalized dissimilarity modeling to analyze and predict patterns of beta diversity in regional biodiversity assessment. *Diversity Distrib.* **13**, 252–624 (2007).
41. K. Mokany, C. Ware, S. N. Woolley, S. Ferrier, M. C. Fitzpatrick, A working guide to harnessing generalized dissimilarity modeling for biodiversity analysis and conservation assessment. *Global Ecol. Biogeogr.* **31**, 802–821 (2022).
42. M. Fidino, mfidino/uwin-gentrification. Zenodo. <https://doi.org/10.5281/zenodo.10413281>. Deposited 20 December 2023.