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Title: Gentrification drives patterns of alpha and beta diversity in cities

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**Abstract:**

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 (> 500g) to evaluate how gentrification impacts species richness and community composition across 23 U.S. cities. After controlling for impervious cover, gentrified parts of a city had the highest mammal species richness. Change in community composition was only associated with gentrification in a few cities, which were mostly located along the West Coast. Our results indicate that the impacts of gentrification extend to non-human animals, which provides further evidence that some aspects of nature in cities, such as wildlife, are chronically inaccessible to marginalized human populations.

**One-Sentence Summary:** Across the United States, gentrified parts of a city have more mammal species than non-gentrified parts of a city.

In urban areas, the processes that cause unequal access to environmental resources among people have ecological consequences (Leong et al. 2018, Schell et al. 2020, Locke et al. 2021, Burghardt et al. 2022). Gentrification, the process of neighborhood change that includes demographic and economic shifts in historically disinvested neighborhoods whereby whiter, more educated, and higher income residents displace under-resourced residents (UDP 2021), exemplifies such a process. Ecologically, gentrification-induced changes to a neighborhood could alter which species are locally present in various ways (i.e., richness or alpha diversity). First, as gentrification brings an influx of wealthier residents in a neighborhood, alpha diversity could increase as residents invest more resources into landscape management (i.e., the luxury effect, Magle et al. 2021). Second, gentrification can accompany an influx of green infrastructure such as city parks, which can also increase alpha diversity (Anguelovski et al. 2022, Triguero-Mas et al. 2022). Yet, gentrification also displaces the people that previously lived in the area, further intensifying inequities with people’s experience with biodiversity (Wolch et al. 2014). 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 accumulating 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 wildlife respond to changes in human populations and urban design. For example, species assemblages in gentrified versus non-gentrified areas may have similar alpha diversity (i.e., same number of species) but differ in the identity of the species present in those assemblages (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 non-gentrified areas are considered nuisance species (e.g., rats) that are likely to generate human-wildlife conflict (Hubbard and Brooks 2021) or spread zoonotic disease (Murray et al. 2022). Furthermore, cities are not identical, and thus, the relative impact of gentrification on biodiversity likely differs among cities (Fidino et al. 2020). 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 (Fidino et al. 2021) and are often conservation and nuisance management targets (Gehrt et al. 2010). Given that gentrification-induced changes to a neighborhood could be associated with both alpha and beta diversity, we evaluated three predictions on the relative contribution gentrification could have on these diversity metrics (Fig. 1).



**Figure 1.** Four theoretical ways that mammal richness (i.e., alpha diversity) and shifts in community composition (i.e., beta diversity) could change in response to gentrification, where shapes in sub-figures A through D represent different species. A) Alpha diversity could remain constant but species assemblages could completely differ between gentrified and non-gentrified areas, resulting in no change 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 full replacement. C) Communities in non-gentrified 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 change; gentrification is not associated with changes in alpha and beta diversity. E) The change 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).

To test our hypothesis and evaluate our predictions across a variety of urban landscapes, we used camera trap data from 23 US cities that are part of the Urban Wildlife Information Network (UWIN; Magle et al. 2019), a systematic multi-city biodiversity monitoring survey. Overall, we compiled three years 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). 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 own theoretical predictions.



**Figure 2.** Data from 23 cities were used to assess differences in mammal communities among gentrified and non-gentrified parts of a city. Cities are represented by dots. Dot color illustrates the relative effect of gentrification on alpha and beta diversity at average sites in each city that only vary in their gentrification status. Gentrification had a more pronounced effect on alpha diversity overall. However, gentrification in West Coast cities had a stronger effect on beta diversity, central U.S. cities had a mixture, and East Cost cities had a stronger alpha diversity deffect. See fig. SX for this map with city names included.

**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. The model included two covariates: a binary covariate to indicate whether a site was within 500m 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 non-gentrified sites with 22.5% impervious cover was 7.73 species (95% CI = 6.47, 9.22; 90% CI = 6.67, 8.95) while alpha diversity at a similar gentrified site was about 13% higher (8.74 species; 95% CI = 6.85, 11.12; 90% CI = 7.13, 10.69). This difference equates to roughly 1 to 2 more species at gentrified sites than non-gentrified sites within a city. The among-city model parameters agreed with this pattern: gentrification was likely associated with higher alpha diversity (*βgent* = 0.17; 95% CI = -0.01, 0.36; 90% CI = 0.02, 0.33; Fig. 3), and the interaction term suggested this effect was strongest at lower levels of impervious cover (*βgentXimp* = -0.22; 95% CI = -0.53, 0.09; 90% CI = -0.48, 0.04). Conversely, higher levels of impervious cover across cities had the largest and most pronounced negative effect on alpha diversity (*βimp* = -0.49; 95% CI = -0.71, -0.27; 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. Alpha diversity decreased by about 3.5 species when impervious cover at a site increased from 0 to 80%.

A diagram of different types of gentrification

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**Figure 3**. Impervious cover had a greater effect than gentrification on alpha and beta diversity, although there was some indication that alpha diversity was greatest in gentrified areas with lower impervious cover. Vertical black lines represent among-city estimates, the gray-filled rectangles are 95% 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 0.

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. Furthermore, cities in which we detected a gentrification effect on alpha diversity were predominantly located in the East Coast and Central United States (Fig. 4). For more city-specific alpha diversity results, see fig sx-sy.



**Figure 4.** The expected beta diversity and change in alpha diversity between an average gentrified and non-gentrified 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 different communities between sites. West Coast cities (more negative longitude) are those with smaller changes in alpha diversity but greater beta diversity, while the remaining cities (less negative longitude) had greater changes in alpha diversity and lower beta diversity.

**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 the mammal communities at a pair of sites were identical and 1 means the two sites had completely dissimilar mammal communities. 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 all intercept and slope terms. 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 non-gentrified 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 (*β­imp* = 0.07; 95% CI = 0.02, 0.19; 90% CI = 0.02, 0.18), followed by the geographic distance between sites within a city (*βdistance* = 0.05; 95% CI = 0.01, 0.13; 90% CI = 0.02, 0.13), and then gentrification (*βgent* = 0.01; 95% CI = 0.00, 0.07; 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., hi 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 other covariates at their mean, the beta diversity between sites with the highest (80%) and lowest (0%) impervious cover was 0.16 (95% CI = 0.07, 0.31; 90% CI = 0.08, 0.29) whereas sites with the exact same level of impervious cover was 0.09 (95% CI = 0.02, 0.23; 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 (Fig. 1, Fig. 3). Overall, it appears that gentrification in West Coast cities had a greater association with beta diversity than alpha diversity: 4 of the 5 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; 95% CI = 0.08, 0.19; 90% CI = 0.09, 0.18). In Los Angeles, the beta diversity between gentrified and non-gentrified sites was 1.28 times greater than sites with the same gentrification status (95% CI = 1.16, 1.40; 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 (median of summed spline coefficients = 0.79; 95% CI = 0.72, 0.86; 90% CI = 0.73, 0.85). Beta diversity between a pair of sites at opposite ends of Phoenix’s impervious gradient was 0.72 (95% CI = 0.70, 0.73; 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; 95% CI = 0.36, 0.39; 90% CI = 0.36, 0.39). Conversely, Indianapolis, Indiana had the smallest effect (median of summed spline coefficients = 0.07; 95% CI = 0.02, 0.13; 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 (95% CI = 0.24, 0.30; 90% CI = 0.25, 0.29) which was quite similar to the estimated beta diversity between sites with identical levels of impervious land cover (median = 0.22; 95% CI = 0.24, 0.30; 90% CI = 0.25, 0.29). For more city-specific beta diversity results, see Supplemental Material X4.

**Species that covaried with gentrification**

As the alpha and beta diversity estimates were compiled from the posterior of a multi-city multi-species occupancy model, we also quantified how each species responded to gentrification. Of the 21 species we analyzed, 11 of them 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 Supplemental Material X4 for parameter estimates from all models.



**Figure 5.** The average effect of gentrification on the occupancy of the 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 who negatively covaried with gentrification. Dots represent median estimates for each species and horizontal lines are 90% credible intervals.

**Discussion**

Our results indicate that gentrification, coupled with impervious cover, shape mammal distributions across U.S. cities. Compared to gentrification, however, impervious cover is the dominant form of environmental variation that impacts mammal distributions and greatly reduces alpha diversity. Further, sites at opposite ends of the impervious gradient in cities have the greatest beta diversity. While this finding confirms decades of urban ecological research (e.g., McKinney 2008), our analysis shows how generalizable this outcome is across a wide geographic range including multiple U.S. cities. Gentrification, on the other hand, represents a secondary axis that may lessen the negative effect of impervious cover on mammals. Such changes to the mammal community are likely due to wealth-associated increases in vegetative cover such as street trees, professional landscaping, and irrigation (Clarke et al. 2013, Leong et al. 2018), which collectively improve habitat quality for mammals (Donovan et al. 2021). 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-enabled dispossession of marginalized communities (Leong et al. 2018, Schell et al. 2020, Locke et al. 2021, Burghardt et al. 2022). That we found gentrification-related shifts in mammal communities across a wide range of U.S. cities indicates that the impacts of gentrification extend to non-human 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 (Magle et al. 2022). 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 non-impervious 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 non-impervious cover in intensely urbanized neighborhoods may preclude this effect. Thus, social processes that occur within cities can non-linearly modulate the magnitude of effect the built environment has on urban biodiversity. Second, the non-gentrified 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, gentrification is a multidimensional and dynamic process that we distilled into a binary metric for 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 (Easton et al. 2020). Nevertheless, we observed an association between our gentrification metric and patterns of mammal diversity across many U.S. cities. Such results indicate that simple gentrification metrics could be used 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 decadal Census. As one example, the IPUMs 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 (Manson et al. 2022).

We found that our theoretical predictions (Fig. 1) were more extreme than the nuanced results we observed in our data (Fig. 4). While some cities experienced different species assemblages in gentrified versus non-gentrified areas, wildlife communities were never completely dissimilar (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 (Fig. 1B). Instead, gentrification in many cities was associated with increased alpha diversity but low beta diversity (Fig. 1C), and could indicate 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 West Coast cities showing distinct differences from East Coast cities and central U.S. cities representing a mixture of the two (Fig. 2). Cities closer to the East Coast are typically older and potentially more biotically homogenized (Pidgeon et al. 2014); 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 resource availability, such as water. It is possible that gentrified parts of a city benefited from additional water resources or cooling provided by trees during droughts (Donovan et al. 2021). This could result in wildlife communities that differed more from non-gentrified 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 (Chamberlain et al. 2020), while species in hotter cities are more negatively influenced by urban intensity (Haight et al. in press). Exploring how the magnitude of such patterns change during extreme weather events in arid and non-arid 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 socioeconomic processes, such as gentrification influence human demographics and wildlife communities. These factors shape where species occur in cities and who has the opportunity to 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 (Mullenbach et al. 2022). For instance, while urban greenspace is considered a public good in theory, in practice it often becomes a commodity primarily accessible to affluent white communities that displaces marginalized communities (Grove et al. 2018, Rigolon et al., 2018, Rigolon and Németh 2020). Uncoupling urban greenspace development from Western capitalism is a challenging task, but involves reframing greenspace development as an essential component of city maintenance rather than an economic development strategy (Mullenbach et al. 2022). 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 the majority 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.

References and Notes

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Materials and Methods

Supplementary Text

Figs. S1 to S#

Tables S1 to S#

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