

REVIEW SUMMARY

URBAN ECOLOGY

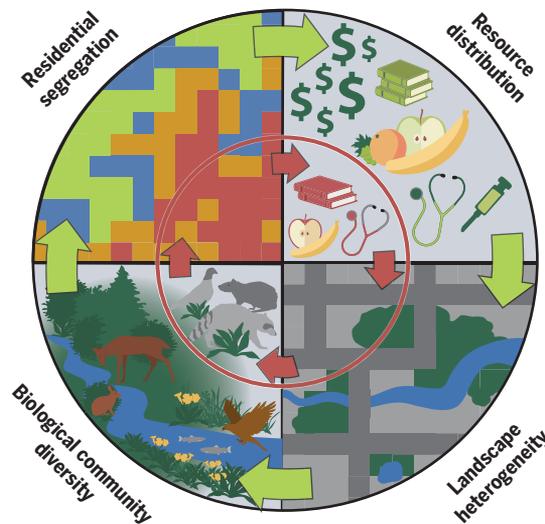
The ecological and evolutionary consequences of systemic racism in urban environments

Christopher J. Schell*, Karen Dyson, Tracy L. Fuentes, Simone Des Roches, Nyeema C. Harris, Danica Sterud Miller, Cleo A. Woelfle-Erskine, Max R. Lambert

BACKGROUND: Human activity and decisions drive all life in cities. Worldwide, cities are characterized by extensive anthropogenic transformation of the landscape, modification of biogeochemical processes, and alteration of biological communities. Underlying all of these characteristics of urban ecosystems is an extraordinary variability in human agency, culture, power, and identity. Though our understanding of cities as ecological systems with distinctive community assemblages and landscape features has broadened considerably, researchers still rarely consider the full range of social drivers that affect landscape heterogeneity. One of the most characteristic attributes of cities is social inequality—specifically the uneven distribution of resources and wealth primarily underpinned by structural racism and classism. Because structural inequalities form the foundation of city infrastructure, urban development, governance, management, and landscape heterogeneity, inequality among humans defines the ecological setting and evolutionary trajectories for all urban organisms. More broadly, systematic inequities have profound impacts on global biological change and biodiversity loss. Many emergent social inequity patterns are principally driven by systemic racism and white supremacy. Hence, centering racial and economic justice in urban biological research and conservation is imperative. Here, we show how social inequalities shape ecological and evolutionary processes in U.S. cities and highlight the need for research that integrates justice perspectives with ecological and evolutionary dynamics.

ADVANCES: Although a rich literature demonstrates how historical and contemporary inequities emerge and persist in human systems, a transdisciplinary perspective that integrates social and cultural processes into an urban eco-evolutionary framework remains unexplored. In today's world, humans often shape the ecological conditions that drive patterns of species distribution and evolution. Distinctive urban landscape features—including reduced habitat patch size, novel plant com-

munities, and increased distance among similar patches—affect key ecological processes such as population dynamics, species interactions, and food web structure. Recent research emphasizes that socioeconomic and demographic factors predict within-city variation in diverse environmental conditions. Humans directly control urban plant, animal, and microbe communities. Further, decisions



Residential segregation and systemic racism have substantial impacts on ecological and evolutionary dynamics in cities. Government-sponsored policies stratify neighborhoods on the basis of race and class (e.g., through “redlining” in the United States, represented here by the red circle), which results in restricted access to social services and environmental amenities for racial and/or ethnic minorities and low-income communities (red arrows). Habitat quantity and quality tend to be greater in wealthier and predominantly white neighborhoods (green arrows), which leads to variations in ecological and evolutionary processes, underscoring the influence of systemic racism and inequality in driving urban landscape characteristics.

about urban resource management are often dictated by a subset of individuals and institutions with social or economic capital. These decisions can bias the distribution of societal benefits derived from nature. Dominant social groups also enact and enforce policies and societal norms that exacerbate social and environmental inequities. Wealthier and predom-

inantly white neighborhoods generally have more green space, more trees, and greater plant diversity than less affluent neighborhoods. In addition, synergies among pollution (e.g., light, noise, chemical), resource distribution, subsidized predators, and non-native species present novel challenges to organisms, which must respond by moving elsewhere, acclimatizing, adapting, or facing local extirpation. These stressors are often stratified according to racial and/or ethnic backgrounds and wealth. Further, intraspecific variation in phenotypic and genotypic traits of urban species may reflect human-induced disturbances. These relationships highlight the potential for both adaptive and neutral evolutionary processes in urban subpopulations to vary across neighborhoods within cities.

OUTLOOK: Stratification of wealth and property ownership shapes the distribution and management of urban spaces, thus constructing the urban ecosystem. Systemic racism and classism drive urban wealth stratification, emphasizing the need to address inequality-driven environmental heterogeneity in urban ecological and evolutionary studies. Residential segregation and colonial annexation (as well as gentrification and displacement) generate predictable ecological patterns in vegetation, air and water quality, microclimate, soils, and the built environment through the rapid influx of resources to specific areas. Accounting for such processes will allow more accurate estimation of the effect of humans on urban organisms. Deconstructing the complex and nuanced attributes of social inequality in affecting biological phenomena can also inform more equitable and sustainable urban planning solutions that implement anti-racist and justice-centered actions. Racial oppression and economic injustice are jeopardizing urban and global ecosystem health and function. Structural racism and classism are further layered with other inequalities, thus necessitating an intersectional approach to urban ecology. Deeper integration across the natural and social sciences is therefore an urgent priority for advancing our understanding of urban ecosystems and developing applied solutions that promote environmental justice, equity, and sustainability. ■

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The ecological and evolutionary consequences of systemic racism in urban environments

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Urban areas are dynamic ecological systems defined by interdependent biological, physical, and social components. The emergent structure and heterogeneity of urban landscapes drives biotic outcomes in these areas, and such spatial patterns are often attributed to the unequal stratification of wealth and power in human societies. Despite these patterns, few studies have effectively considered structural inequalities as drivers of ecological and evolutionary outcomes and have instead focused on indicator variables such as neighborhood wealth. In this analysis, we explicitly integrate ecology, evolution, and social processes to emphasize the relationships that bind social inequities—specifically racism—and biological change in urbanized landscapes. We draw on existing research to link racist practices, including residential segregation, to the heterogeneous patterns of flora and fauna observed by urban ecologists. In the future, urban ecology and evolution researchers must consider how systems of racial oppression affect the environmental factors that drive biological change in cities. Conceptual integration of the social and ecological sciences has amassed considerable scholarship in urban ecology over the past few decades, providing a solid foundation for incorporating environmental justice scholarship into urban ecological and evolutionary research. Such an undertaking is necessary to deconstruct urbanization's biophysical patterns and processes, inform equitable and anti-racist initiatives promoting justice in urban conservation, and strengthen community resilience to global environmental change.

Urban ecosystems encompass complex feedbacks between human activity, built and planted infrastructure, and natural landscapes that drive specific biological processes (1–3). Interactions between social and natural systems produce distinctive biogeochemical and biophysical signatures (4, 5) that alter the demography, life histories, diversity, behaviors, and distributions of non-human species (6, 7). Resultant environmental conditions (e.g., urban heat island effects, food subsidies, and pollution) can drive phenotypic shifts, emigration, or extinction within and across animal and plant populations (8, 9). Cities have, accordingly, become foci for research on biological responses to novel, rapidly changing environments (8–13). Recent urban ecosystems research can inform sustainable solutions that promote biodiversity, human well-being, and urban resilience in the face of global environmental change (3, 14–16). How-

ever, leveraging urban ecosystems as conduits of sustainability, conservation, and innovation, requires a comprehensive understanding of the underlying components, hierarchical structures, and key drivers of urban functions (Fig. 1) (3, 7, 16, 17).

Since its inception, the field of urban ecology has framed cities as quintessential socio-ecological systems (i.e., complex adaptive systems or coupled human and natural systems) where social processes alter ecological properties that reciprocally influence human societies (18–20). These formative urban ecology models placed human decisions and institutions at the core of urban ecosystems, emphasizing the need to quantify spatial and temporal feedbacks within cities (17, 21). For example, the National Science Foundation's urban Long-Term Ecological Research (LTER) programs in Phoenix, Arizona, and Baltimore, Maryland, United States (i.e., the Central Arizona–Phoenix LTER program and the Baltimore Ecosystem Study, respectively) have established links between social and ecological systems by overlaying habitat patch types with demographic information such as neighborhood wealth, housing density, and impervious surface cover (2, 3, 10, 16).

Socioeconomic status has been a standard metric for many socio-ecological studies, as it combines social factors such as culture, race, occupation, education, and societal power into a complex aggregated measure (22, 23). Many social variables that contribute to socioeconomic

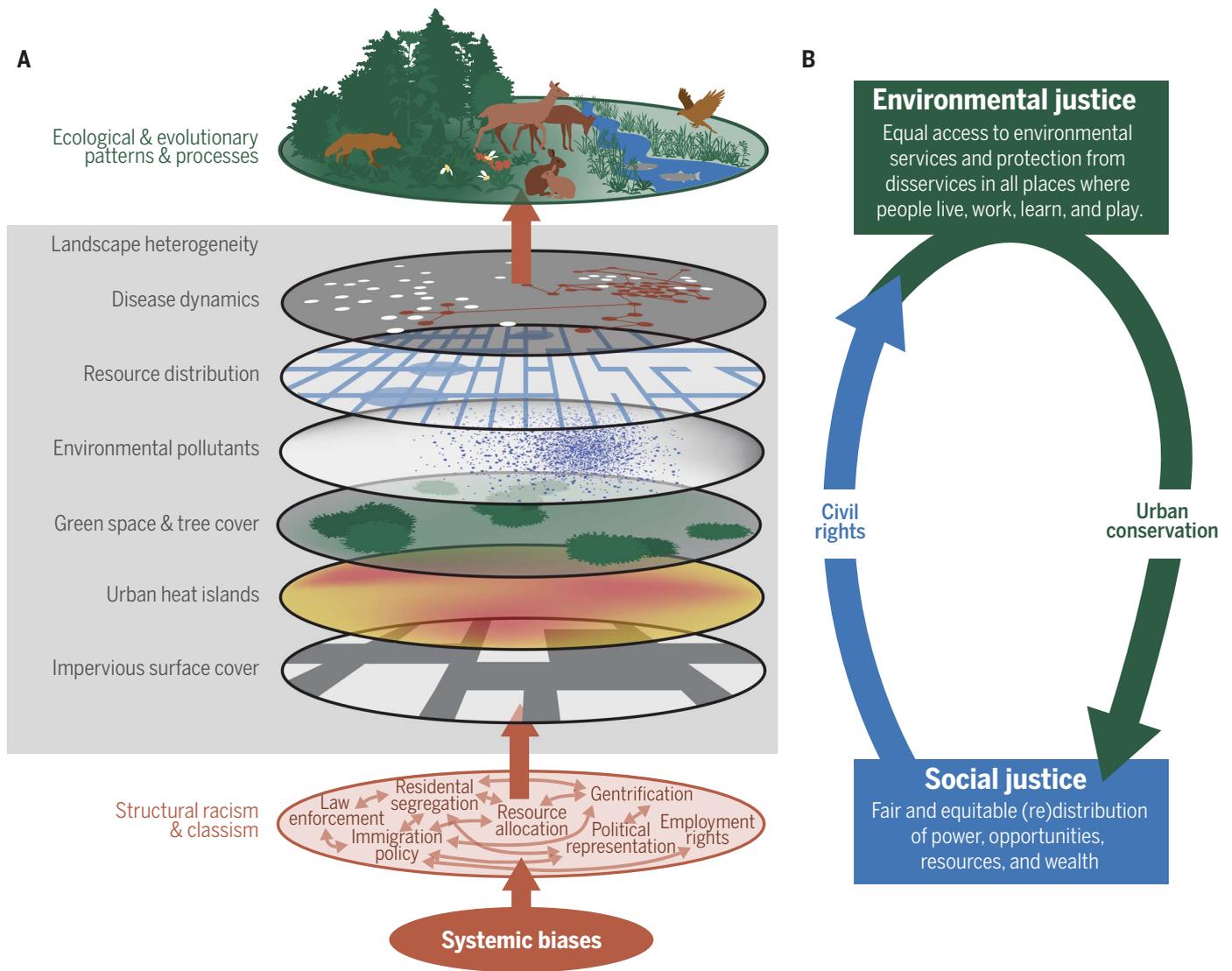
status and related environmental variability are the result of historical government and societal actions (24, 25). Recent studies have begun to address the varied contributions of several social factors (e.g., race, sex, and age) to ecological heterogeneity in cities (25–28). However, social inequality remains insufficiently studied as a key driver of ecological and evolutionary change in cities (Fig. 1) (15, 21, 24). Social inequality is the unequal distribution or allocation of wealth and resources to specific socio-cultural groups. Such imbalances contribute to substantial injustices (i.e., social inequities; Fig. 1) that privilege certain individuals over others (29–31). Inequality and inequity disproportionately affect which individuals own and access land, functionally restricting the people who become the primary drivers of urban ecosystem structure and function (32, 33).

Urban social inequality stems from historical and contemporary power imbalances and produces deleterious effects that are often intersectional, involving race, economic class, gender, language, sexuality, nationality, ability, religion, and age (34). Various ecological attributes in cities are principally governed by the spatial and temporal scale of social inequities (23). For instance, the uneven distribution of urban heat islands (35–39), vegetation and tree canopy cover (27, 28, 40, 41), environmental hazards and pollutants (42–46), and access to healthy waterways (47, 48), as well as the relative proportion of native to introduced species (49, 50), are strongly dictated by structural racism and classism (Fig. 1) (21, 31, 32, 51). Concurrently, the environmental justice literature has long articulated the economic, health, and environmental implications of structural racism in cities (52–55). Integrating the contributions of social inequities to urban environmental structure is therefore crucial for informing our understanding of biological processes in cities (33, 55, 56).

Here we provide a transdisciplinary synthesis on how social inequities—and specifically systemic racism—serve as principal drivers of ecological and evolutionary processes by shaping landscape heterogeneity (Fig. 1). We draw on the social and political sciences to specifically stress how understanding systemic racism and racial oppression, rooted in settler colonialism and white supremacy, is essential for advancing research in urban ecology and evolutionary biology. First, we review the socio-ecological effects of wealth disparities in cities. We then describe how systemic racism drives inequitable patterns in wealth, health, and environmental heterogeneity, noting that intersectionality with other identities (e.g., gender, sexual orientation, and indigeneity) may have additive impacts on urban structure (29, 34, 57). We propose hypotheses linking systemic racism to urban ecological and evolutionary patterns and processes. We close by illustrating how centering

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C Definitions

Inequality: Unequal distribution of wealth and resources across social groups.

Inequity: Unjust allocation of resources driven by power dynamics discrimination, stereotypes, and systemic biases.

Racism: Stereotypical norms that disadvantage communities of color (typically Black, Asian, Latinx, and Indigenous groups), including the interdependent forces of “prejudice plus power” that dictate how racial inequalities persist even after elimination of racist actors or policies.

Classism: Discriminatory actions based on wealth, income, or social class, usually directed at barring people from working class backgrounds from accessing benefits and social spaces dominated by middle or upper classes.

Intersectionality: The intersection, interaction, and compounding of marginalized identities, causing individuals and communities at such intersections to experience greater social inequalities.

Fig. 1. Structural racism and classism underpin landscape heterogeneity in cities.

(A) Conscious and unconscious systemic biases and stereotypes contribute to shaping institutional policies that drive and exacerbate racist and classist structures in urban systems (e.g., law enforcement, residential segregation, and gentrification). The emergent properties of these structural inequalities have substantial impacts on multiple attributes across the urban landscape, including impervious surface cover, urban heat islands, green space and tree cover, environmental pollutants, resource

distribution, and disease dynamics. These physical and biological characteristics have known impacts on the ecological patterns and evolutionary processes of urban organisms. (B) Incorporating environmental justice principles and civil rights into ecological and evolutionary applications is an urgent priority for positively affecting the long-term success of urban conservation and sustainability. (C) Definitions of key terms for understanding the interconnectedness of racism, classism, and intersectionality as related to system inequality.

environmental justice and anti-racist activism in biological research is a priority for urban conservation (55, 56).

Although we predominantly focus on work from North America, the global ubiquity of social inequality and systemic racism across cities suggests that our synthesis is broadly applicable (58–60). Addressing systemic and structural racism in both cities and the scientific community is necessary to comprehensively understand urban ecological and evolutionary dynamics, conserve biodiversity, improve human health and well-being, and promote justice in nature and society.

Socio-ecological effects of wealth

Household and neighborhood wealth are currently the most common social variables that ecologists use to describe within-city biodiversity patterns, especially in residential neighborhoods (26, 61–64). Wealth—specifically median household income—has repeatedly emerged as a key explanatory variable for predicting urban ecological patterns. One of the most well-known and robust hypotheses linking household income and ecology—the luxury effect—suggests that urban biodiversity, and plant diversity in particular, is positively correlated with neighborhood wealth (61, 63).

The wealth–biodiversity covariance is predicated on a fundamental tenet of urban ecosystems: Humans manage urban areas and, as the ultimate ecosystem engineers, can greatly augment or remove resource limitations that favor growth and abundance of some species over others (32, 61). As a result, households with greater discretionary income and capital, higher education levels, and reduced pressure for essential needs exert stronger influence on plant assemblages, establishing a residential ecological mosaic based on socioeconomic (32, 50, 62, 65).

The luxury effect is particularly pronounced in arid ecoregions and biomes and intensifies with increasing urbanization, vegetation loss, and wealth gaps (21, 35). Initial support for the luxury effect came from Phoenix, Arizona, with observed positive correlations between household income and woody perennial diversity (61). Studies investigating the luxury effect globally have implicated wealth as a strong correlate of faunal and floral diversity (26, 63), relative vegetation cover (27, 40), species abundances (49), and the distribution of abiotic attributes [such as urban heat islands (35, 66) and environmental hazards (44)] in cities. Recent meta-analyses have supported the wealth–biodiversity phenomenon yet emphasized that the causal social and political mechanisms behind these patterns are seldom explored (26, 64).

Vegetation cover and biodiversity

Affluent urban residential neighborhoods generally have greater vegetation cover, canopy

cover, and plant diversity than their less wealthy counterparts (27, 63, 67). Public urban forests, recreational parks, and private green spaces also tend to be larger and more established with older trees and vegetation that provide greater niche space to support biodiversity at other trophic levels (49, 68, 69). For instance, strong positive correlations exist between urban tree cover and household income for seven major U.S. metropolitan regions (40). General vegetation cover in Los Angeles, California (27), and the distribution of urban forests throughout Cook County, Illinois (41), are also positively affected by increasing wealth, as well as several other socioeconomic factors (e.g., racial composition, education, and home ownership). In addition, recent work suggests that interactive effects between housing age and income predict tree biodiversity, with more established homes in high-income neighborhoods exhibiting greater diversity (27). Lawns are an unusual case: Wealthier residents intensively manage their lawns to be very green (70) and have few to no species other than turfgrasses (71). As a result, some studies have found neutral or negative wealth–plant biodiversity relationships in these areas (72, 73).

Luxury effects customarily scale from the household to the neighborhood level. A recent study found that yards in wealthier neighborhoods consistently had greater abundances and diversity of flowering plants, trees, and non-native species (65). Similarly, individual homeowners with landscaping priorities primarily driven by cost (i.e., the need for cheaper plants) have lawns with higher relative proportions of non-native plant species with lower functional diversity (50). These recent studies illustrate how socioeconomic drive variation among individuals and therefore influence choices at the household level, which can scale up to affect neighborhood biodiversity. These wealth-driven impacts on patterns of primary producers may have substantial effects on metacommunity composition and dynamics. Luxury effects often scale from the residential to the city-wide level, providing cross-city evidence that wealthier U.S. cities have better-resourced urban park systems (74). Whether such trends in vegetative structure are consistent across cities, or even across biomes, remains unexplored.

Impacts on animal communities

Luxury effects extend beyond primary producers, with recent studies suggesting that colonization, species richness, and abundance of birds are related to neighborhood wealth (49, 75–77). Most prior studies have addressed these relationships in birds in multiple cities across the globe. For instance, bird community richness positively correlates with median household income across multiple urban centers in South Africa (49). However, negative

income–richness relationships in highly urbanized landscapes imply that highly built yet expensive downtown centers can deter or prevent successful colonization and persistence (49). Other studies in Phoenix, Arizona, similarly found that bird diversity was greatest in parks and residential yards in high-income neighborhoods, a pattern primarily explained by an increased relative abundance of native desert species and proximity to undeveloped desert landscapes (75, 76). Further, recent evidence from 45,000 observations of 160 passerine species found across U.S. cities shows that increasing household income predicts greater abundances of migratory species, as well as greater abundances of smaller, shorter-lived birds (77). These results are some of the first empirical examples linking the luxury effect to evolutionary ecology.

Few studies have addressed the luxury effect in other animal taxa, though evidence implies that these effects persist across multiple clades. Evidence for coyotes (*Canis latrans*) and raccoons (*Procyon lotor*) throughout Chicago, Illinois, United States, suggests that carnivores are more likely to colonize and persist in wealthier neighborhoods (68). Household income is also a strong predictor of lizard species richness in Phoenix, Arizona, with other factors such as traffic density and surface temperatures having weak effects (78). Evidence from arthropod research suggests that richness in high-income neighborhoods across North Carolina is greater regardless of vegetation cover at the property level (69).

Wealth–animal richness trends can also extend beyond city limits. Red bat (*Lasiurus borealis*) and evening bat (*Nycticeius humeralis*) activity is positively correlated to household income, regardless of land cover metrics (79). Activity patterns of hoary bats (*Lasiurus cinereus*), however, decrease with increasing neighborhood income, which suggests that luxury effects are more salient for some species than others (79).

Urban heat islands and air pollution

Heat is unevenly distributed within cities: Temperatures are typically greater in lower-income neighborhoods than in higher-income areas (35, 36). Low-income neighborhoods have reduced tree and vegetation cover and increased impervious surface cover, which contribute to higher surface temperatures in Phoenix, Arizona (35, 66); Baltimore, Maryland (36); and other cities worldwide (38, 39, 80). Given the cooling capacity of trees, apparent luxury effects on tree and vegetation cover can substantially impede environmental cooling in low-income neighborhoods, making residents particularly vulnerable to heat-related illnesses (36, 81). Such wealth–tree–heat axes have emerged in other countries as well, including Canada (82), Brazil (83), and South Africa

(84, 85). Heterogeneity in the distribution of urban heat islands, and associated health outcomes, is thus a direct consequence of the luxury effect (24, 35).

Other environmental disamenities, especially pollutants, also reflect the luxury effect. Air pollution sources are often colocated near low-income neighborhoods; consequently, low-income residents frequently have higher risk of exposure to and vulnerabilities associated with air pollutants. For instance, low-income residents throughout North Carolina (44) and multiple cities in the Northeastern United States (86) experience greater exposure to atmospheric particulate matter. Low-income residents also experience greater ambient nitrogen dioxide concentrations in Montreal, Canada, though some high-income areas in the downtown region similarly experience increased ambient concentrations of this pollutant (87). Further, meta-analysis of data from the American Housing Survey suggests that low-income households have elevated indoor concentrations of nitrogen dioxide and particulate matter (42).

Research on heat islands and pollution supports the idea that inequality in neighborhood wealth leads to a diversity of environmental hazards and that these hazards compound to create distinctive, challenging environmental patches.

Limitations of the luxury effect

The luxury effect is far from universal across systems and taxa, and the underlying processes and causal mechanisms that contribute to emergent wealth–ecology relationships are seldom addressed (21, 40). In a meta-analysis of associations between wealth and biodiversity, the directional relationship (positive, negative, or no relationship) between biodiversity and wealth varies markedly according to differences in social conditions, which include cultural norms, individual and community preferences, and municipal policies (26). A pair of similar meta-analyses concluded that relationships between income inequality and urban forest cover are not always noteworthy, with neighborhood racial composition explaining divergent conditions in vegetation cover (64, 88).

The history of urban development, individual-level choices, and societal norms also distorts potential relationships between wealth and biodiversity. For instance, in some cities, wealthier neighborhoods may have a higher relative proportion of high-rise structures and built downtown areas that severely limit the amount of vegetated cover, reducing functional habitat space and biodiversity (26). Wealthier neighborhoods may also enact policies that reduce vegetation diversity and mandate the proliferation of monoculture lawns that yield considerable environmental homogeneity and serve

to similarly reduce biodiversity (26). Moreover, refined analytical approaches may help to disentangle the contributions of wealth, culture, and other socioeconomic factors to ecology. For example, evidence in New York City suggests that residential canopy cover is best explained as a signal of social status (the “ecology-of-prestige hypothesis”) (32). Hence, the convergence among policy, individual choices, and socioeconomic variables may be a better predictor of urban ecological variance than wealth alone (32). Indeed, recent work assessing the plant diversity of residential yards supports this conclusion, suggesting that individual homeowners’ landscaping priorities largely dictate private lawn community composition (50).

Luxury effects have been explored primarily in terrestrial systems, with less work in aquatic habitats. Lack of evidence for aquatic luxury effects in urban ponds, lakes, and rivers may be due to other abiotic factors regulating waterway health that do not necessarily correlate with wealth disparities (63). Small ponds or lakes are also seldom present in lower socioeconomic areas, functionally eliminating potential studies on aquatic luxury effects. Moreover, riverfront or coastal environments have increasingly become hotspots for the wealthy, excluding lower-income communities and thereby compounding ostensible luxury effects. Urban rivers and streams run through and interconnect high- and low-income areas, so downstream habitats may suffer consequences of upstream pollution and erosion.

Characteristically, the luxury effect has also resided at the community and ecosystem level, with few studies investigating how wealth heterogeneity affects organismal and population ecology (68, 79). Prior studies also predominantly address patterns but seldom articulate the underlying sociopolitical processes that contribute to wealth–ecology relationships. Integrating the study of systemic racism and that of environmental justice should emerge as the next development in socio-ecological scholarship.

Beyond wealth: Structural racism, ecology, and evolution

In multiple cases, neighborhood racial composition can be a stronger predictor of urban socio-ecological patterns than wealth (25, 37, 88). For example, exposure to particulate matter in cities such as Los Angeles (43), Phoenix (46), and other cities throughout North Carolina (44) is increased for racial and ethnic minority groups, especially Black, Latinx (i.e., a person of Latin American origin), and Native American populations (43, 45). The geographic distribution of urban heat islands and tree canopy cover in cities is also stratified by race: Multiple studies have repeatedly demonstrated that land surface temperatures are magnified for

racially minoritized groups in many U.S. cities (36, 37, 39), with certain racial groups more vulnerable than others (37, 38). Differential pollutant exposure extends to aquatic systems. For example, decades of neglected pollution in the Flint River led to an ecological disaster for the stream biota and a massive ongoing humanitarian crisis in the predominantly Black community of Flint, Michigan (47, 48). Pressures to save money motivated the local government to switch Flint’s source of drinking water from Lake Huron to the polluted river (89). The calamity of the polluted Flint drinking water is just one example of a larger pattern of minoritized communities bearing the brunt of ecosystem disamenities (48).

Recent studies have begun to reveal some of the underlying structural constructs—especially racism—that contribute to urban heterogeneity beyond household income (28, 37, 88). However, determining the true influence that systemic and structural racism exerts on ecological dynamics remains a novel area of investigation (28). Studies on the resultant evolutionary outcomes are also rare (90). Knowing the relative contribution of structural racism to wealth disparities informs our understanding of complex temporal dynamics in cities, which is not possible in approaches lacking historical context (21, 24). In addition, accounting for structural racism in biological models should improve their predictive value, thereby allowing us to more accurately estimate the effect of urbanization on evolutionary and ecological change. Frameworks that consider systemic and structural racism as principal drivers of urban form advance our ability to predict how and which species may acclimatize and evolve for life in cities (Figs. 2 and 3).

Residential segregation and redlining

Globally, residential segregation—characterized by a physical separation of groups within cities and further compounded by the concentration of government and ecosystem benefits (30)—is an especially potent form of social stratification. Residential segregation shapes ecological conditions along multiple environmental axes that cannot be neatly characterized by variables such as wealth or impervious surface cover (91). This is particularly important because social geographies vary for different racial, ethnic, and cultural groups depending on the historical forms of discrimination experienced by each minoritized group (31). The impact of structural racism on Black geographies in the United States has been particularly well documented, with substantial legacy effects on urban ecological patterns (21, 24, 27, 92).

Perhaps one of the most notorious examples of structural racism is the U.S.-sanctioned policy of “redlining” enacted between 1933 and 1968. This practice segregated urban

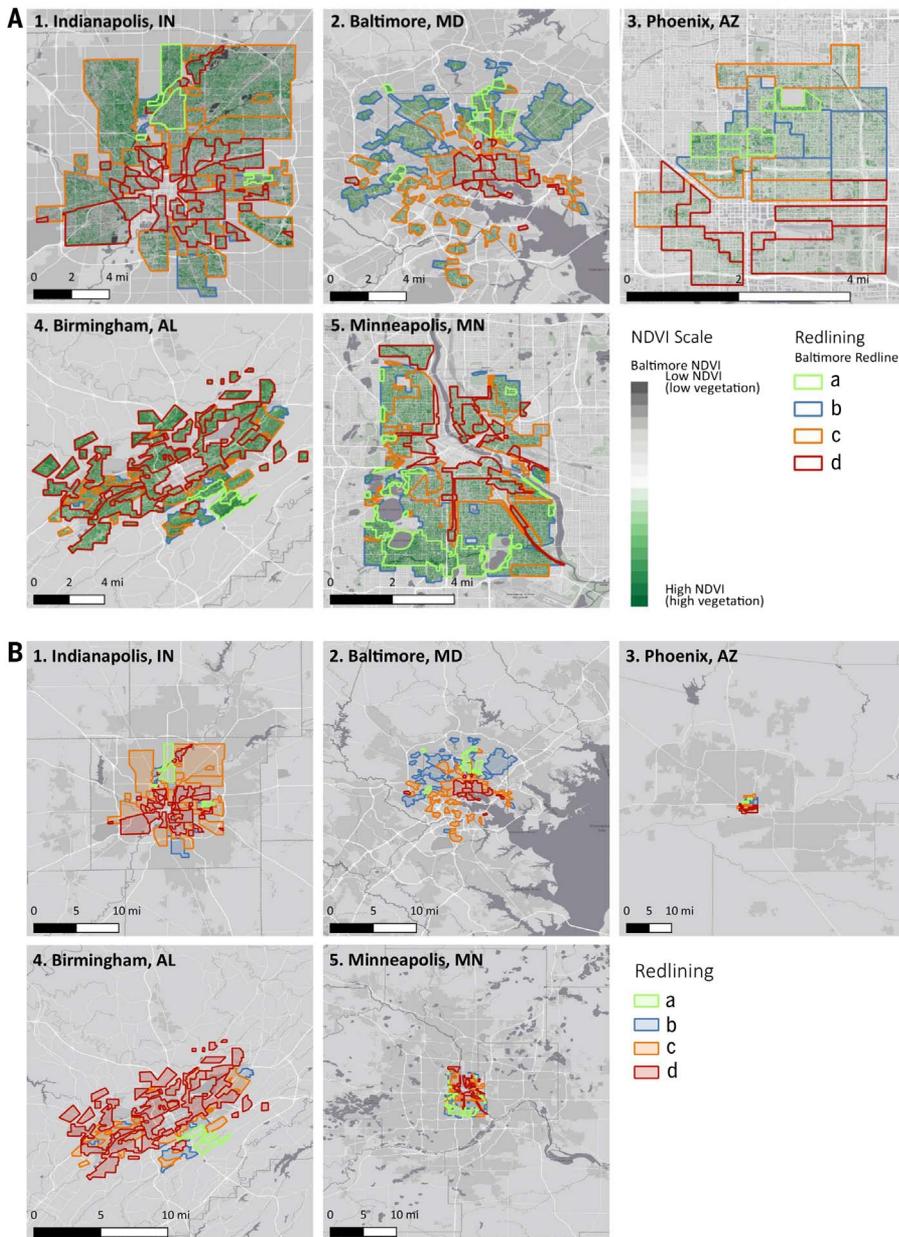


Fig. 2. The practice of redlining in the United States functionally segregated neighborhoods by race and class.

The highest-rated neighborhoods (graded “a” and outlined in green) were wealthier and predominantly white. The lowest-rated neighborhoods (graded “d” and outlined in red) were poorer and predominantly Black. Demographics of intermediate-ranked neighborhoods (graded “b” and “c” and outlined in blue and orange, respectively) were between those of “a” and “d” areas. Segregation practices such as redlining leave lasting marks on urban landscapes. (A) Redlined neighborhoods still have substantially less green space (e.g., trees, parks, and lawns) than higher-graded neighborhoods. Although this pattern is consistent across cities, there is marked variation among neighborhoods and between cities, as seen in the comparison of Birmingham, Alabama, and Baltimore, Maryland. Other environmental amenities, such as urban water bodies in Minneapolis, Minnesota, are also segregated. (B) Historically greenlined or redlined neighborhoods are positioned differently relative to contemporary urban boundaries and access to natural areas outside the urban landscape. In Minneapolis, Minnesota, and Baltimore, Maryland, redlined neighborhoods are concentrated in the city center, far from the urban periphery. These cities have also grown over the past 50 years, meaning that human and nonhuman residents of redlined neighborhoods must travel farther to get out of the city. By contrast, the city extent of Birmingham, Alabama, has grown minimally, and redlined areas are near forested lands. Note that in the background maps, white represents roads, pale gray represents exurban land, gray represents urban land, and dark gray represents water. Redlining data are from the Mapping Inequality collaborative project (<https://dsl.richmond.edu/panorama/redlining/>). NDVI, normalized difference vegetation index.

residential neighborhoods principally by race and was used to formally suppress capital wealth gains of Black Americans (30). Redlining policy graded neighborhoods from most desirable (“a”; outlined in green in Fig. 2) to hazardous (“d”; outlined in red in Fig. 2) according to their perceived amenities and disamenities, including financial riskiness, environmental quality, proximity to industrial facilities, and racial composition (30). Black Americans were refused housing loans and walk-throughs in neighborhoods deemed “a” or “b” quality and were relegated to “c” and “d” areas, which received less governmental support.

Today, the ecological effects of redlining persist. Redlined “d” neighborhoods have, on average, 21% less tree canopy than “a” neighborhoods. Further, “a”-graded areas are frequently more uniformly green, have older tree canopy, and are closer to environmental amenities than redlined “d” neighborhoods (Fig. 2). Although redlining is no longer an active policy, studies have shown that its legacy remains a key driver of contemporary urban landscapes across at least 37 cities in the United States (24, 28, 92).

Ecological effects of structural racism

Redlining may greatly contribute to the asymmetric distribution of habitat that structures bottom-up processes influencing biodiversity (28, 35). Reductions in tree and vegetation cover necessarily diminish niche diversity and quality (63, 93), which frequently coincides with reduced species richness of birds, mammals, and arthropods (94–97). By concentrating Black Americans and other minoritized communities in urban centers, redlining often reduced the proximity of segregated areas to undeveloped landscape beyond the urban boundary (Fig. 2A), and patterns of segregation might have subsequently created variably permeable urban matrices (Fig. 2B). Therefore, we may hypothesize that emergent patterns of species colonization and extinction vary considerably within and among cities as a function of heterogeneous temporal and spatial legacies of racial segregation. A critical question is whether the severity and age of residential segregation affect the number of species co-occurring at a localized site (alpha diversity), a reduction in community composition across sites over space and time (beta diversity), or city-wide regional biodiversity (Fig. 3 and Table 1).

Archived redlined maps may prove valuable for predicting the spatial distribution of niches across cities (Fig. 2). Because redlining predicts the age, abundance, and distribution of urban tree canopy in many cities, it is likely that such maps may also provide substantial resolution to the geographic locations of potential sink habitats and ecological traps in

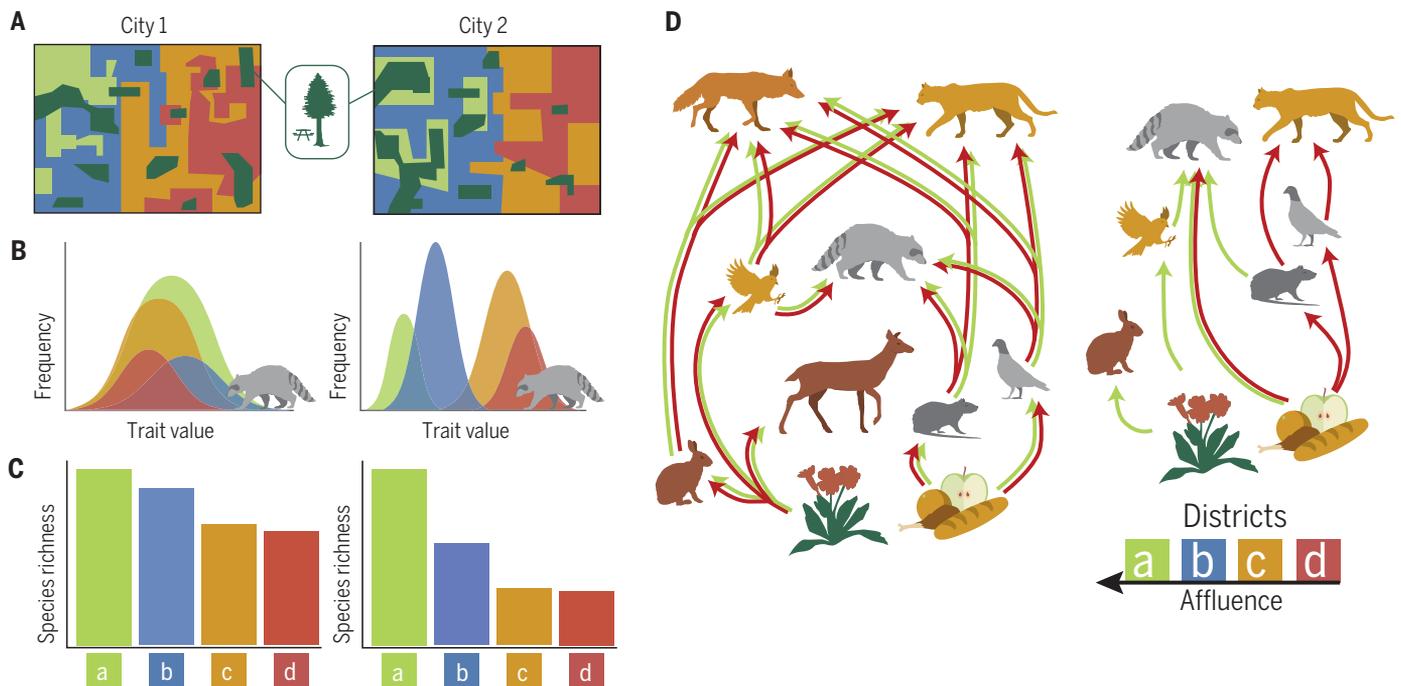


Fig. 3. Conceptual diagram illustrating how between-city differences in segregation may produce disparate ecological and evolutionary outcomes.

(A) In hypothetical city 1, green space is more evenly distributed and continuous from green- to redlined districts (Fig. 2) relative to city 2. (B) Between-city differences in connectivity may result in different selective gradients that contribute to varying distributions of genetic or phenotypic trait values of species found across districts (“a” through “d”). (C) Both cities have near-identical

species diversity and composition in “a” districts, and species diversity and composition decline from “a” to “d” neighborhoods. However, within each jurisdiction, city 2 has substantially less species diversity in “b,” “c,” and “d” districts relative to city 1, potentially as a result of differences in habitat distributions. (D) Food webs may be more diverse and interconnected across districts in city 1 (left) but are more simplified across districts in city 2 (right), owing to the relative differences in structural and functional habitat connectivity.

both terrestrial and aquatic environments (98). Though several studies have addressed the emergence of source and sink habitats (99–102), none have explicitly considered whether heterogeneity in pollutants, heat, and other disturbances shape their geographic distribution (Fig. 1A). The legacy effects of residential segregation could predict the locality and size of potential ecological sinks and traps, thereby helping to identify and predict geographic regions with compounding anthropogenic disturbances that require more sustained stewardship (Table 1).

Recent studies emphasize that the spatial arrangement of vegetation cover can drive evolutionary change (103), fundamentally linking segregation-driven patterns of vegetation cover to evolutionary trajectories of urban populations. Impervious surface is frequently associated with reduced movement of organisms across landscapes and therefore lower gene flow, more subdivided populations, and lower genetic diversity (104–106). Urban tree cover can ameliorate these effects; for example, tree cover facilitates gene flow in native white-footed mice in New York (107, 108). Increased land cover and habitat connectivity, however, may also boost transmission of zoonotic disease (e.g., Lyme disease), and adaptive management solutions to control disease

spread may produce additional evolutionary feedbacks (51, 109). Hypotheses that address the relative contributions of racial segregation and wealth disparities to tree cover can elucidate the socioeconomic attribute that most accurately predicts population genetic structure and connectivity (Table 1).

Evolutionary impacts of structural racism

The compounded impacts of heightened edge effects, smaller patch sizes, reduced niche diversity, and individual human behaviors may predict increased genetic drift in racially minoritized neighborhoods (Fig. 3). Urban development and habitat fragmentation are generally expected to increase drift and reduce genetic diversity (107, 110), and urban green spaces in minoritized communities are customarily fragmented (55). Habitat patches may also experience substantially reduced gene flow if adjacent habitats are not proximal (i.e., isolation by distance) or have barriers that prohibit successful immigration into a desired habitat (i.e., isolation by resistance) (107). Reduced tree canopy cover significantly reduces gene flow for some species (108), and canopy cover is significantly diminished in racially segregated neighborhoods (40). As a result, gene flow of native species may be detrimentally affected, whereas some pest species may

thrive in previously redlined neighborhoods (69, 90). Further, highways and impervious surfaces are formidable urban barriers for a variety of taxa (106, 111, 112), and these built structures tend to be more prevalent in racially minoritized neighborhoods (37). How other aspects of urban habitats (e.g., vacant lots, food availability from pets or waste, and homeless encampments) vary as a function of various forms of structural racism and, consequently, affect gene flow in different taxa remains an area worthy of exploration.

Redlining and similar discriminatory policies (e.g., Jim Crow laws) that increased Black Americans’ proximity to polluting industries (45, 92, 113) and heightened exposure to intensified urban heat effects (36, 39) may have compounded to create strong selective pressures that drive adaptive and maladaptive evolution (Fig. 3B). Increased pollutant exposure can increase the rate of heritable mutations in mice (114) and selection for toxicity-mediating genes and connected signaling pathways in killifish (*Fundulus heteroclitus*) (115), respectively. Recent studies also provide evidence of rapidly evolved thermal tolerance in urban water fleas (*Daphnia magna*) (116, 117), ants (*Temnothorax curvispinosus*) (118), and damselflies (*Coenagrion puella*) (119). To our knowledge, no studies have explicitly explored

Table 1. Key questions integrating systemic racism, ecology, and evolution. A proposed list of potential research questions that integrate social heterogeneity, ecology, and evolution in urban systems. These questions could inform practitioners, planning professionals, and elected officials as to how such processes in cities can be leveraged for positive social change. Colored dots denote the primary research focus of each question (blue, ecological; gold, evolutionary).

Key questions	Research focus
1. How does biodiversity vary with the degree of residential segregation within a city?	●
2. Do socioeconomic and racial stratification predict the locality of ecological traps and source-sink dynamics within cities?	●●
3. How does the severity of economic and racial segregation influence connectivity, dispersal, gene flow, and genetic isolation?	●
4. Does equitable urban greening increase the probability of rescue effects of native species and ecological specialists?	●●
5. Do cities with increasing homelessness rates have reduced species occupancy rates?	●
6. Is functional or structural connectivity reduced in cities with more pronounced economic or racial segregation?	●
7. Are rates of local adaptation or maladaptation higher for urban organisms in redlined neighborhoods?	●
8. How have urban renewal and associated displacement affected habitat fragmentation and ecological disturbances?	●
9. Do carbon sequestration and soil microbial density differ as a function of neighborhood segregation?	●
10. Does selection for non-dispersing seeds in plants vary with socioeconomic and demographic predictors?	●
11. Do numerical responses in predator-prey or pollinator-plant dynamics vary across redlining categories?	●
12. Is natural selection along multiple ecological conditions strongest in redlined or low-income neighborhoods?	●
13. How do sublethal effects (e.g., life-history traits, physiology) vary as a function of pollution proximity and segregation in cities?	●●
14. Are rates of zoonotic disease transmission accelerated or dampened by residential segregation and/or urban renewal?	●
15. Can improvements to public transportation infrastructure and greenways improve habitat connectivity?	●
16. Do anti-displacement policies affect ecological stability and integrity over time?	●
17. Are cities with smaller economic inequality indices (e.g., the Gini coefficient) more biodiverse relative to others?	●
18. Does remediating pollution (air, soil, water) in marginalized neighborhoods enhance biodiversity and organismal abundances?	●

how either neutral or adaptive evolutionary processes operate as a function of heterogeneity that stems from structural racism.

The lack of effective intervention, water sanitation, medical access and resources, and trash management programs due to structural racism may also shape mutation rates and emerging disease dynamics (90, 120).

Racially minoritized and low-income communities witness increased proximity to pest species known to harbor zoonotic diseases (90, 121, 122). For instance, brown rat (*Rattus norvegicus*) abundances negatively correlate with socioeconomic status, such that low-income neighborhoods report more frequent rat sightings across cities globally

(123–127). Racially diverse neighborhoods consistently receive inadequate sanitation services that are compounded with aging infrastructure and overgrown vegetation, all factors that attract brown rats and other non-native rodent pests (125, 128). Inconsistent administration of over-the-counter rodenticides may lead to various levels of immune resistance in local rat populations (129), further exacerbating health and disease risks for marginalized communities (130). Societal neglect underpinned by systemic racism may therefore promote the evolution of rodenticide immunity that heightens zoonotic disease risks in marginalized communities (51).

Infection and mortality rates from coronavirus disease 2019 (COVID-19), caused by severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2), are disproportionately high for Latinx, Indigenous, and Black communities relative to other racial groups in the United States (91, 113, 131–135). Over decades of government policy and economic development, cities have disproportionately situated environmental hazards (e.g., petrochemical industries, waste facilities, and major roadways) near predominantly Black and Indigenous communities (43, 46). Such forms of environmental racism have substantially compromised neighborhood air quality and respiratory health of minoritized communities (43, 87). Recent evidence linking air pollution exposure with COVID-19 mortality risk (134, 136) thus indicates direct connections among environmental racism, air quality, and disproportionate death rates for Black and Indigenous communities. This epidemiological phenomenon is further compounded by reduced access to adequate health care, heightened risks of concomitant health comorbidities (e.g., cardiovascular disease, hypertension, and diabetes), and increased housing density (133). Communities with higher human densities can experience increased viral mutation rates, which subsequently increase the likelihood of viral host jumping (120). An alarming but plausible and insufficiently studied (137) hypothesis is that mutation rates in pathogens such as SARS-CoV-2 are greatest in racially minoritized and low-income communities, creating a pernicious socio-evolutionary loop between increasing virulence and the uneven distribution of social and health inequities in these communities.

Intersecting forms of inequality

Understanding the mechanisms that shape urban inequality and, thus, urban eco-evolutionary patterns and processes requires incorporating intersectional theories of inequality and evaluating accessibility to different spaces (34, 138, 139). The term “intersectionality” emphasizes that various marginalized identities of an individual or community more broadly intersect, compound, and interact, ultimately affecting the magnitude and severity of experienced social

inequities (Fig. 1) (57). For example, discrimination experienced by a queer Black woman in the United States may be intensified relative to that faced by individuals with similar racial, gender, and sexual orientation identities alone. Translating the concept of intersectionality onto the urban landscape can provide a more holistic understanding of the patterns and processes that shape urban ecosystems. For instance, we may hypothesize that characteristic differences between Indigenous ecological practices and those of forestland managers may contribute to variance in native species richness and community complexity (140, 141). Similarly, we may predict that gender differences as related to land cultivation and homeownership shape plant species assemblages and species turnover rates. Further, vegetation removal and increased nighttime lighting to deter LGBTQIA+ (lesbian, gay, bisexual, transgender, queer, intersex, asexual, and other) communities (95) may have subsequent effects on disturbance regimes and local biodiversity that reduce habitat value for multiple species. Though such empirical links are currently speculative and not well established, integration of various inequities in cities may provide additional resolution to understanding how social drivers affect urban ecology and evolution. Although our focus has been on racism and classism, we recognize the need for and encourage intersectional approaches in urban ecology.

Centering justice in urban ecology and conservation

The origins of environmentalism in the United States were heavily influenced by white men who expressed racist perspectives in their efforts to protect nature. Writings by early environmentalists such as Aldo Leopold, John Muir, Madison Grant, Gifford Pinchot, and Theodore Roosevelt argued that nature is most pristine without human influence but should be reserved for white men as a resource for personal improvement (142–144). These early arguments greatly contributed to the exclusion of Black, Indigenous, and non-white immigrant communities from outdoor spaces and environmental narratives (145), despite these communities shouldering the brunt of environmental and climate crises and leading effective movements for environmental and climate justice (53, 146, 147). White-led environmental and climate movements have long marginalized issues of racial justice when crafting policy and legislation (148). In addition, such movements have traditionally considered structural violence to be unrelated to environmental issues, yet state-sanctioned police brutality (149, 150), environmental degradation (113), and the climate crisis (53, 147) all reinforce patterns of racial segregation and criminalization of minoritized people in urban public spaces (151, 152).

Black, Indigenous, Latinx, and immigrant communities possess cultural knowledge, ongoing land and water relations, and effective practices for community and ecological revitalization, honed through generations of struggle with and for the land (140, 141). Systemic racism in environmental policy excludes communities from ecocultural relations with urban ecosystems, urban planning processes, and urban ecological restoration (153, 154). As a result, these communities find that their longstanding and effective practices of managing and advocating for lands, waters, and species are limited. When judges, elected officials, planners, scientists, and others who hold power in environmental governance work in solidarity with frontline communities, urban organisms, ecosystems, and human communities move toward regeneration (155–157).

Racist research and conservation approaches must be challenged and redesigned to include justice, equity, and inclusion (24, 157–159). To do so, ecologists, biologists, and environmentalists must reimagine what is considered an ecological or conservation issue. Increasing economic opportunities, bolstering public transportation infrastructure, investing in affordable housing and health care, and strengthening voting rights and access are issues rarely considered by mainstream environmental organizations. Yet such societal initiatives reduce carbon emissions, dampen environmental hazards, enhance public health, and expand economic mobility of marginalized communities. Moreover, reallocating municipal funds to initiatives that aim to improve home ownership for minoritized communities reduces displacement and promotes local stewardship, which in turn affects overall public and environmental health. Such paradigm shifts will be essential, as accumulating evidence suggests that income inequality predicts biodiversity loss (63, 160). Centering racial and environmental justice that drives equitable policy changes is thus inextricably linked to urban conservation and ecological restoration initiatives (157, 159).

Improving green infrastructure and green-space access, paired with policies that shield against displacement, can greatly enhance community health and wealth (54, 161). Exposure and access to quality natural space in cities improve physical and mental health (162) and buffer against health comorbidities experienced by minoritized groups (31, 92, 161). Justice-centered applications of ecological and evolutionary tools can further spotlight convergences among social inequities and environmental disamenities (e.g., ecological modeling of habitat sinks and sources) to identify areas of high conservation and restoration need. Equitable restoration of urban habitat patches and infrastructure necessarily improves landscape connectivity and refugia to support successful

colonization of native species, guards against local extinctions, and increases urban biodiversity (159). Hence, equity-based ecological restoration will benefit both human and non-human communities (163, 164), but only if the foundation of such initiatives are rooted in anti-racist practices (156, 165). The maintenance of societal integrity should, in turn, lead to capital gains for minoritized communities that translate to ecological stability that positively affects species diversity in cities.

As urban ecologists and evolutionary biologists, we have a responsibility to implement anti-racist strategies that evaluate systems of oppression in how we perform our science. This necessarily means eradicating efforts that perpetuate inequities to knowledge access, neglect local community participation, or exploit community labor in the pursuit of academic knowledge (i.e., the practices of colonial and “parachute” science). Concurrently, increasing representation of individuals of diverse identities is inherently just and enhances our scholarship (166, 167). By directly including a diversity of scholars and incorporating an understanding of systemic racism and inequality, we can more holistically study urban ecosystems. We will not be able to successfully assess how racism and classism shape urban ecosystems, nor address their consequences, without a truly diverse and inclusive scientific community.

Outlook

The decisions we make now will dictate our environmental reality for centuries to come, as illustrated by modern policies such as the Green New Deal proposal (168) and the Paris Agreement (169). Such endeavors are timely as we face a global pandemic that is both affected by and exacerbates the latent structural inequities underpinning modern cities, directly threatening environmental health and biodiversity conservation (170, 171). Concurrently, our contemporary fight for civil rights in the wake of unjust murders and continued racial oppression of Black and Indigenous communities stresses the need to question and abolish systemic racism. The insidious white supremacist structures that perpetuate racism throughout society compromise both public and environmental health, solidifying the need to radically dismantle systems of racial and economic oppression.

Consequently, our capacity to understand urban ecosystems and nonhuman organisms necessitates a more thorough integration of the natural and social parameters of our cities. We cannot generalize human behavior in urban ecosystems without dealing with systemic racism and other inequities. Further, incorporating environmental justice principles into how we perform and interpret urban ecology and evolution research will be essential, with restorative and environmental justice serving

as the foundation for effective ecological restoration and conservation (158, 159, 163). Doing so is both our civic responsibility and conservation imperative for advancing urban resiliency in the face of unrelenting global environmental change (172).

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