Biodiversity and socioeconomics in the city
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The ecological dynamics of cities are influenced not only by geophysical and biological factors, but also by aspects of human society. In cities around the world, a pattern of higher biodiversity in affluent neighbourhoods has been termed ‘the luxury effect’. The luxury effect has been found globally regarding plant diversity and canopy or vegetative cover. Fewer studies have considered the luxury effect and animals, yet it has been recognized in the distributions of birds, bats, lizards and indoor arthropods. Higher socioeconomic status correlates with higher biodiversity resulting from many interacting factors—the creation and maintenance of green space on private and public lands, the tendency of both humans and other species to favour environmentally desirable areas, while avoiding environmental burdens, as well as enduring legacy effects. The luxury effect is amplified in arid cities and as neighbourhoods age, and reduced in tropical areas. Where the luxury effect exists, benefits of urban biodiversity are unequally distributed, particularly in low-income neighbourhoods with higher minority populations. The equal distribution of biodiversity in cities, and thus the elimination of the luxury effect, is a worthy societal goal.

1. Introduction

Most of the history of ecology has focused on aspects of climate and geography as determinants of the abundance, composition and diversity of species found in a place. However, the social systems of humans also influence biodiversity. Even in the earliest cities, socioeconomics had an impact on species distributions and biodiversity. For example, in 1350 BCE Amarna, Egypt, the living areas of labourers hosted different insect species compared to those in affluent neighbourhoods [1]. Similarly, in early public health research in nineteenth century London, Snow found that the distribution of cholera was related to the distance of people from a contaminated well; however, an alternate hypothesis related to a connection between poverty and cholera [2]. More recently, Hope and colleagues [3], identified a curious pattern in Phoenix, Arizona, which they termed the luxury effect, wherein more affluent neighbourhoods have higher plant diversity. Since then, scientists have recognized the luxury effect in cities around the world, exploring various urban ecosystems and measures of plant and animal biodiversity.

2. Where past research has found the luxury effect

When Hope et al. [3] first proposed the luxury effect, they considered patterns of plant diversity in the Central Arizona-Phoenix long-term ecological research

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study area. They sampled all perennial, woody plants in 30 by 30 m plots and then tested the correlation between their diversity and geophysical, geographical and social variables. Along with elevation and land-use history, they discovered that census block median household income was one of the most important predictor variables [3]. Wealthier census blocks tended to have a higher diversity of woody plants. Hope and colleagues sampled both green and non-green parts of the city, so the relationship between biodiversity and affluence they observed included both the effects of affluence on greenness (whether a plot had plants at all) and then for those plots with plants, the number of species present.

The luxury effect has since been found in respect to plant diversity in North America, Burundi, China and Australia [4–9]. Other studies have used the concept of the luxury effect to describe the effect of affluence, not on plant diversity per se, but on the greenness of neighbourhoods in cities, measured using remote sensing tools focused on tree canopy or ground vegetation cover [10–15]. Greenness of cities, particularly canopy cover, sets the template for patterns in the composition and diversity of other species. Socioeconomics has been shown, in some cases, to outperform other biophysical and human factors in predicting plant diversity or vegetation cover [10,14,16]. A caveat to this trend is that we suspect that absence of the luxury effect is underreported. If socioeconomics is not an important variable, its lack of importance is unlikely to be featured.

Humans act directly on urban vegetation, from selecting plants to introduce and maintain to actively eliminating others. Our influence over more mobile taxa is indirect, yet the luxury effect can still be observed in animals, demonstrating the wide reach of socioeconomics. Fewer studies have considered the effects of socioeconomics on animals than on plants, and most of the animal studies have considered birds. Positive correlations between neighbourhood income and bird diversity are common and have been reported in North America, Europe and New Zealand [17–22].

Bird community composition can also be correlated with socioeconomics. Kinzig et al. [17] found that, in Phoenix, the greater diversity of birds in parks in high-income neighbourhoods than parks in low-income neighbourhoods was driven by differences in the number of native bird species. Lerman & Warren [19] also found that the abundance of native, desert bird species was highest in higher-income neighbourhoods in Phoenix. Similarly, Melles [18] found that the diversity of native bird species increased with socioeconomic status in Vancouver, Canada. The effects of socioeconomics on the proportion of native and introduced bird species do not, however, seem general. While Loss et al. [20] found that bird diversity was, indeed, higher in more affluent areas of Chicago, this effect was driven by introduced bird species. Native bird diversity was actually greater in low income neighbourhoods. No general expectation for when affluence might favour native versus introduced biodiversity has emerged, though the Phoenix studies suggest that a template of native plant diversity influences the presence of native bird species [17,19].

Birds depend directly on plant species for food and nesting, so it is possible that their diversity correlating with socioeconomics is, in part, mediated by the effect of affluence on plants. However, animals that are less reliant on vegetation have also exhibited luxury effect patterns, implying that other factors of affluence, independent of vegetation effects, may also influence ecological communities. To date, the biodiversity of both lizards and bats appears to be correlated with affluence in cities. One study, again in Phoenix, by Ackely et al. [23] found increased lizard diversity in affluent areas and that socioeconomic variables proved to be better predictors of diversity than other environmental variables. In Texas, Li & Wilkins [24] found that certain bat species were more often found in high-income neighbourhoods, while other bat species did not demonstrate any relationship with socioeconomics. A study of opossums, coyotes and raccoons in Chicago focused on the abundance or occupancy of individual species rather than overall diversity [25]. Results differed between taxa, but showed that socioeconomic factors performed just as well as the tested environmental factors in modelling distributions [25].

Only one study has considered the effect of affluence on arthropods, despite their diversity and abundance in cities. Leong and colleagues [26] found that homes in wealthier census blocks in North Carolina were more likely to have higher arthropod diversity indoors, regardless of vegetation at the property level. Further, while millions of species of microbes live in cities [27], no studies have considered how affluence might affect their biodiversity. Studies have, however, shown that urban residents of low socioeconomic status have more inflammatory and immune diseases—possibly due to their lack of exposure to microbial diversity that exists in green spaces, animals and agricultural settings [28].

Most of the studies of the luxury effect focus on terrestrial environments, but a few consider aquatic environments. So far, organisms in aquatic environments do not appear to exhibit a luxury effect. In one study, the biodiversity of pond macroinvertebrates around Stockholm, Sweden was unaffected by socioeconomic variables. A study from England actually found that ponds in affluent neighbourhoods have fewer sensitive aquatic invertebrate taxa [29]. The species missing from more affluent areas tended to be those less tolerant of pollutants, leading the authors to hypothesize that more two-car households in affluent neighbourhoods leads to more toxic run-off into nearby ponds [29].

3. Measuring the luxury effect

The luxury effect describes a relationship between ‘wealth’ and ‘biodiversity,’ but there are many ways of measuring these features. Wealth is often measured as a function of median household income, but upon proposing the luxury effect, Hope et al. [3] hypothesized the association between household income and biodiversity could also be due to correlating socioeconomic factors such as education, cultural values and institutional power. Future work, teasing apart the aspects of wealth and socioeconomics that matter most will be important, but in practice, median household income seems to be both a strong correlate of biodiversity and a proxy for many other socioeconomic features.

As with socioeconomics, techniques for evaluating ‘biodiversity’ also vary. Many use α diversity, or richness [3–8,17–20,23,26], whether measured at a single square metre [30] or whole city blocks. Other measurements of diversity that require abundance data, such as community composition, diversity indices, density or evenness are less frequently used [17,20,31]. A few studies of focal taxa, such as bats or other urban mammals, where α diversity is less informative, tend to focus on the abundance or occupancy of individual species to
model how these groups are distributed throughout cities. Few, if any, studies appear to have considered whether the among site (β) diversity or total (γ) diversity of less affluent neighbourhoods differs from that of more affluent neighbourhoods.

Studies of the luxury effect use the term ‘biodiversity’ in a broad sense, and include vegetation studies that do not measure plant diversity on the ground, but instead use remote sensing tools to evaluate canopy and vegetation ground cover (10–15), given the assumption that these indirect measurements still provide information on biodiversity patterns [32]. There is no reason to expect the patterns of ‘biodiversity’ and affluence to be the same for these disparate metrics of biodiversity. It would be useful to compare the affluence effect for one group of organisms at different sampling graineds and with each of many metrics of biodiversity.

4. Factors driving the luxury effect

What explains the relationship between socioeconomics and urban biodiversity where it does occur? Here we argue that the primary links between biodiversity and affluence in cities relate to the area of green space (or canopy cover) which is influenced both by the decisions of individual property owners and city officials. Wealthier individuals and municipalities simply have more resources to allot towards vegetation and habitat. Vegetation in the urban landscape has often been introduced, and in many cases maintained, by human residents. The resultant novel plant community then has cascading effects on the surrounding ecological community. Additional factors of affluence beyond vegetation also contribute to luxury effect patterns.

(a) Private properties

In many cities, private green spaces, including gardens, make up a relatively large proportion of total urban green space [33]. How residents choose to manage their land is influenced by disposable income, culture and individual values [34–36]. The first of these management choices is whether to leave a patch of ground as green/open space. In Hope et al. [3], for example, many plots sampled in lower income neighbourhoods had woody plant biodiversity of zero. Then, if individuals choose to maintain green spaces, they make choices about the identity and origin of the species they plant. While high-income neighbourhoods often have greater plant diversity than low-income neighbourhoods, ornamental plants (which are often exotic) can be favoured such that there is an inverse luxury effect for native plants [37]. Or, in the case where monoculture lawns are favoured, the influence of affluence on biodiversity may actually be negative. Additionally, what is desirable within a society varies—the racial/ethnic make-up of a neighbourhood, in addition to household income, was found to influence the composition of plants in community gardens in LA County [38]. Links between behaviour, culture and biodiversity, provide a mechanism to intentionally shift biodiversity patterns in cities in favour of those beneficial to conservation or ecosystem services to humans [39].

Decisions made at the property level can also impact animal communities. Besides the fact that property-level vegetation provides food, shelter and building materials for animals, human behaviour may also directly influence animal distributions. People around the world engage in wildlife feeding, and the abundance of households that feed birds increases in neighbourhoods of higher socioeconomic status [40]. A higher density of feeding stations is then related to greater abundance of visiting birds [40].

(b) Public spaces

Public spaces, such as parks, medians and public right-of ways, account for much of the green space in urban areas. Socioeconomics affects the creation and maintenance of public green spaces through property taxes and through the effect of affluence on decision makers who determine where green spaces will be placed and maintained. As such, public green spaces are often inequitably distributed [14,41], as are street trees [8]. There is generally less urban tree canopy cover in neighbourhoods with lower income, lower education and more people of colour [14,42,43].

Well-documented environmental equity issues exist in urban environments such that low-income neighbourhoods (and those with higher racial/ethnic minority populations) shoulder greater public environmental burdens, such as exposure to pollutants [44]. This impacts not only human residents, but also other animals. For example, grey squirrels living in low-income neighbourhoods were found to have higher lead concentrations in their kidneys than those from more affluent neighbourhoods [45].

Considering the influence of affluence on the distribution of public green spaces, we predict that the luxury effect may be reduced in more socialist cities, where income inequality is reduced, and urban planning is more focused on the equitable distribution of city resources. In the USA then, where income inequality is among the most extreme in the developed world, the prevalence of the luxury effect may be expected.

(c) Neighbourhood choice

Biodiversity might also be greater in affluent neighbourhoods because people of means may preferentially choose to live in habitats that naturally favour biodiversity [46,47]. Property values may then be higher in biodiverse neighbourhoods due to the increased competition to live there. For example, higher elevation sites in Phoenix are more biodiverse and have higher property values due, in part, to the aesthetics of biodiversity and/or of the conditions associated with it. In addition to being able to choose the best present-day neighbourhoods, affluent individuals have been able to choose the historically best parts of the city to develop their neighbourhoods whether that be near bodies of water, in better microclimates, or on hillsides [46,47].

(d) Legacy effects

Especially in older cities, relationships between socioeconomics and biodiversity may be influenced not only by current patterns in green space and affluence, but also by legacies of land use [48]. Land-use history influences the distribution and composition of species in forests and other ecosystems [49], and may be particularly important in urban landscapes. In some cases, legacy effects modulate which species are influenced by affluence. For example, legacy effects may be larger on species with long generation times (e.g. trees), whereas species with shorter generation times (annuals) might respond more to current patterns in affluence in land use [41]. It generally appears that the luxury effect is amplified as neighbourhoods age because of the
accumulation of established vegetation and the cascading ecological effects [3,9,16].

Social histories of cities also matter, and may explain deviations from expected patterns. While there is generally less canopy cover in neighbourhoods with more people of colour [14,42], regions exhibit contrasting patterns. For example, in the city centre of Detroit, Michigan, remote-sensing data showed that areas with the most increased vegetation over time were associated with the lowest household income [50]. This study, spanning decades, captured this inverse relationship that reflected a history of wealthier residents abandoning the urban centre and migrating to suburbs during the desegregation era.

5. Future directions

Urban affluence effects on biodiversity are common but not ubiquitous. Clearly one future direction is to better understand when they do and do not occur. Comparative studies between varying cities could disentangle the role of correlated factors in driving the luxury effect. For example, population density has a mixed association with the luxury effect [3,54]. Comparing the luxury effect in cities where the wealthiest neighbourhoods are in less population-dense suburbs, to cities where affluent neighbourhoods are in the city centres (ex. USA versus Europe) [55] could elucidate the relationship between population density and the luxury effect. Existing studies that compare cities have focused exclusively on canopy cover [14,15] measured with remote sensing tools. Canopy cover data alone leave unanswered questions about the specifics of plant and animal diversity. Future ground-truthing of canopy cover studies may come from citizen science data collection [56], or even from large-scale efforts at digitizing natural history collections [57].

Another, perhaps more important, future direction is working to better understand the cascading consequences of luxury effect patterns on daily human life. Many studies consider the consequences of biodiversity on human health and on ecological processes. Yet this literature, grounded in the study of wild places, offers many hypotheses yet to be tested in light of biodiversity patterns in cities. Better understanding the ecological processes behind the luxury effect will allow us to make predictions about the resiliency of urban ecosystems. For example: do affluence effects result in top down effects of predators and parasitoids on pests? Are more diverse neighbourhoods more resilient to the arrival of novel pests and pathogens? Overall, are they more resistant to change? The opportunities for new insights are great.

6. Broader implications

Increasingly, the ecosystem services provided by biological diversity are recognized [58]. In cities, these benefits include air and water purification, local climate moderation, CO₂ sequestration, reduction in soil erosion and alleviation of noise pollution. Higher biodiversity is also associated with increased human psychological well-being, stronger social cohesion and community empowerment, and decreased crime. More recently, it has become clear that biodiversity also has beneficial effects on immune health. Higher biodiversity in gardens, for example, is associated with higher biodiversity on the skin of teens and, in turn, reduced allergy and other autoimmune problems [59]. The effects of biodiversity can, of course, also be negative [60] but they generally seem more likely to be positive, particularly at local scales. The luxury effect represents not just an interesting ecological pattern but also yet another layer in the social and structural injustices present in cities. The goal in studying luxury effects should be, in part, to figure out how to get rid of it. Our current understanding suggests that a healthy, ecologically sound city is one in which biodiversity is high and equitably distributed.

Data accessibility. This article has no additional data.

Competing interests. We declare we have no competing interests.

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