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Review

The importance of biome in shaping urban biodiversity

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Humanity is urbanizing, with vast implications on natural systems. To date, most research on urban biodiversity has centered on temperate biomes. Conversely, drylands, collectively the largest terrestrial global biome, remain understudied. Here, we synthesize key mechanistic differences of urbanization's impacts on biodiversity across these biomes. Irrigation shapes dryland urban ecology, and can lead to greener, sometimes more biodiverse, landscapes than local wildlands. These green urban patches in drylands often have a different species composition, including many non-native and human-commensal species. Socioeconomic factors – locally and globally – can mediate how biomes shape urban biodiversity patterns through the effects of irrigation, greening, and invasive species. We advocate for more research in low-income dryland cities, and for implementing biome-specific, scientifically grounded management and policies.

Highlights

Research effort on the effects of urbanization on biodiversity is biased towards temperate biomes. Drylands are understudied even though urbanization differentially shapes their biodiversity compared with temperate biomes.

Dryland cities support higher relative species richness (compared with local species pools) than temperate cities. Composition of native and non-native species across urban mosaics differs between biomes mostly due to the influence of irrigation. Focusing solely on species richness can mask these patterns.

In drylands, greenspaces benefit non-native species while gray- and yellowspaces differentially benefit native species. Socioeconomic factors can exacerbate these impacts within and across cities.

Biome, socioeconomics, and culture interact with local ecologies and urbanization to shape biodiversity. These drivers must be considered together in research and management.

Importance of biome-specific approaches for biodiversity patterns: the case of urban drylands

The world is becoming more urbanized [1] with grave implications for biodiversity [2]. To date, most impactful urban biodiversity research has focused on temperate biomes [3–5] (Box 1). This biogeographical bias can have serious conservation consequences [5,6]. Importantly, effects of anthropogenic activities can vary across biomes and socioeconomic gradients [7–9]. These socioeconomic variations within and across cities can also manifest differently across biomes [10]. Consequently, generalizations and policy applications of 'broad' urban biodiversity patterns from one biome (e.g., temperate) to another (e.g., **drylands**; see Glossary)) could be misleading, and potentially lead to counterproductive or even harmful interventions. Drylands collectively comprise the largest global terrestrial biome, encompassing over 40% of terrestrial Earth, and are expanding with worsening climate change [11,12], yet remain disproportionately unprotected [13]. While often viewed as 'barren' or 'unproductive' [14,15], drylands have rich, highly endemic, and threatened biodiversity [16,17]. Drylands are also rapidly urbanizing, which causes habitat conversion, destruction, and other anthropogenic disturbances [18,19]. These anthropogenic changes can directly and indirectly impact biodiversity both in and outside cities [18,19]. However, cities in drylands are understudied, and urban dryland knowledge is biased towards wealthy countries (e.g., USA), mirroring major knowledge gaps between biomes in ecology generally [4,20,21] (Box 1).

Here we propose a framework to better understand the differential impacts of the urban mosaic on biodiversity across biomes and socioeconomics. We contrast dryland biomes with primarily forested temperate (hereafter: 'temperate') and tropical regions. We center our discussions on drylands as a counterpoint to well-discussed trends and mechanisms from temperate biomes across the literature. We primarily focus on more arid dryland subtypes (i.e., semi-arid, arid, and hyper-arid, following [22]).

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Ecological dynamics in drylands

Drylands are defined by their shortage of water, and water controls the patterns and processes of life in these arid, harsh conditions [23]. As a result, resources and biotic interactions are generally strongly driven by resource limitations (e.g., 'bottom-up control') but can rapidly shift to consumer-driven control (e.g., 'top-down control') for short periods [24]. Ecosystems in consistently wet environments, particularly those with higher temperatures, are more likely to have top-down controls, likely driven by high and consistent primary productivity [25]. Dryland species are often marked by adaptations to sparsely vegetated, low-precipitation landscapes, and for hot climates and extreme temperatures [26–28]. For example, hot-adapted dryland species may be outcompeting temperate species in drylands due to specializing in tolerating heat and water stress [26,28]. Drylands also experience strong seasonal rainfall variation and a 'boom–bust' resource economy [23]. These ecological dynamics can in turn affect urban biodiversity in drylands differently when compared with temperate biomes. While we focus on the contrast between forested temperate biomes and more arid drylands, we acknowledge that climatic patterns and vegetation cover exist in a continuum across and within biomes (e.g., barren temperate regions and forested drylands).

Urbanization shapes ecological conditions differently across biomes

Urban areas (areas with high human population density and built land cover [29]) differ from natural ones in their physical, chemical, and species composition [29,30]. These compositional changes vary across biomes [20] and their structures vary within and across cities. Across urban areas, built structures replace natural habitats and seal the soil, and anthropogenic disturbances are added (e.g., human and vehicular traffic, noise, light, and chemical pollution). The urban mosaic itself, and its interactions with the surrounding wild or rural habitats, are complex and can vary greatly across different cities globally. Nevertheless, increasing urbanization is often viewed as a threat to native species richness across taxa, and has been associated with the spread of invasive and urban-adapted species, and shifts in species composition and ecological interactions, depending on the urban mosaic and ecological context of a given city

Box 1. Knowledge gaps and biases in urban biodiversity

We aimed to highlight potential biases and gaps in urban biodiversity knowledge (see also Figure I, and the supplemental information online). Initially we conducted a comprehensive literature review of urban ecology publications that yielded 22 877 publications altogether (see full details in the supplemental information online). We decided to focus only on the 50 most highly cited publications within this dataset that directly included biodiversity data because they are most likely more impactful, set the major narratives for urban ecology, and potentially direct global policies. Nonetheless, we acknowledge that lower-impact and non-English papers may also impact policies, especially on local scales. Most of these publications relied on data from temperate regions; only 11% of the mentioned localities represented dryland regions (Figure I). Amongst these dryland localities, representation lowered with aridity: dry sub-humid localities make up 59% of dryland localities, followed by semi-arid (28%), arid (11%), and hyper-arid (1%) localities. Even within drylands, we found a bias towards high-income cities. Most dryland cities are in lower-income countries (Figure I) [10,19] and subsequently have less access to supplemental irrigation. Yet, these areas are drastically underrepresented in the most impactful urban ecology literature (Figure I) and in the English-language literature as a whole (see the supplemental information online). When we specifically explored urban biodiversity research over time, drylands were mentioned in a small fragment of the literature (2%; supplemental information online). High-income countries – particularly the USA – make up the bulk of recent studies (supplemental information online). For example, Phoenix, AZ, USA, a well-irrigated city, is a hotbed of high-impact urban ecology research (Figure I). Within cities, historically redlined neighborhoods subject to structural inequality and injustice are under-sampled in bird biodiversity data [126]. Even in global regions that are considered understudied, such as Africa, studies are biased towards wealthier countries therein [21]. This is extremely relevant to dryland urban ecology; ~90% of drylands are in UN-defined 'developing' countries [10]. These areas also have a strong diversity of surrounding habitat types, from grazing to agriculture to barren land (driven by extractive industries) to wildlands, each potentially filtering the species pools and bidirectional impacts of urbanization in different ways. We acknowledge this gap in the mechanistic understanding of how biomes affect urban biodiversity. Another gap in knowledge relates to the fact that – unlike local studies – global meta-analyses do not often differentiate native from exotic species when exploring biodiversity patterns, often assuming most species as native (e.g., [127]).

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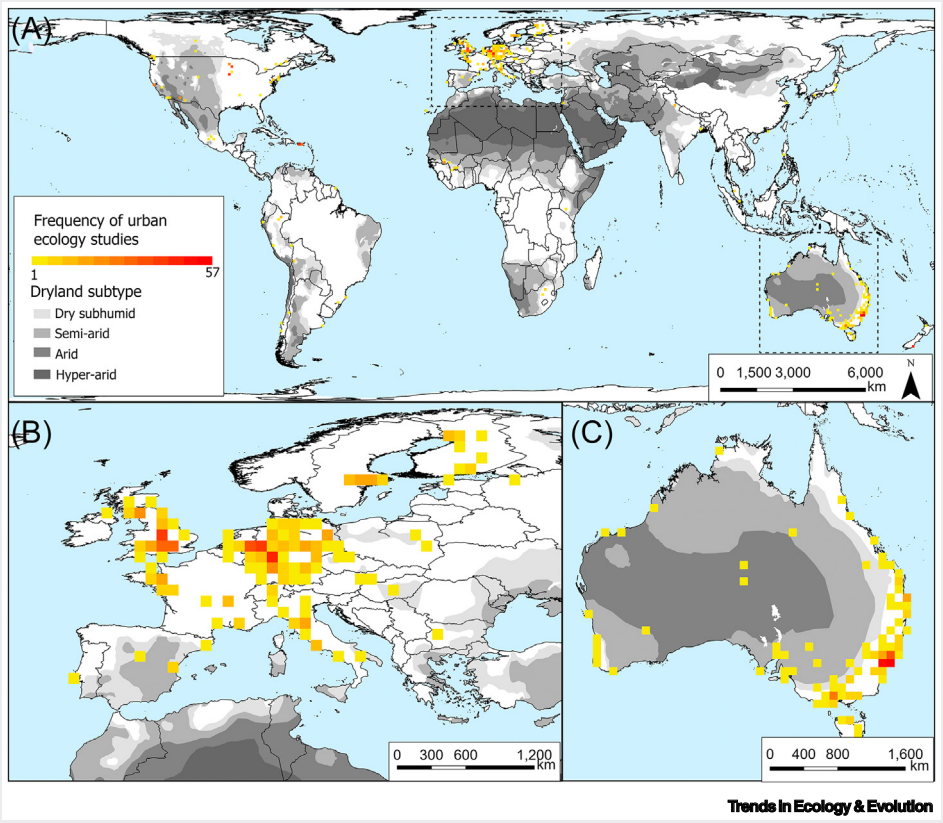

Figure I. Representation of highest impact urban biodiversity data across the globe. These maps display heatmaps (in warm colors) of study locations in the 50 most-cited English-language urban ecology original research papers (that used biodiversity data in their approaches or analyses). Also displayed are the four different UNEP dryland subtypes (in gray [22]). (A) the overall global distribution, (B) and (C) the continents where most research has been conducted (Europe and Australia respectively). Grids are 96.5 × 96.5 km equal area cells in a Behrmann equal area projection (see the supplemental information online for full details on how these maps were constructed).

[13,20,31,32]. This is despite some urban areas being hotspots for certain taxa [33], and others fostering rare species [34] and even increasing species richness across the mosaic, demonstrating the value of conservation within cities [35]. In many cases, cities' surrounding land-uses (e.g., wildlands, agricultural, or industrial rural areas), historic land-uses, and whether it was developed on a biodiversity hotspot can have a great effect on contemporary biodiversity patterns within and across cities [32,36–38]. Regardless, the compositional changes of urban biodiversity and the contrast between urban and non-urban landscapes can vary across biomes [20] and seem to be fundamentally different in drylands from those of temperate biomes (Figure 1).

Within the urban–**suburban** interface, where there is a loss of green space and vegetation and an increase in built cover, there is often an increase of non-native and urban-adapted species associated with species loss across many studied cities [32,36,37]. This process can lead to a peak of biodiversity (both native and non-native) at the interface of cities and surrounding areas ('**peri-urban**' [39]). Moreover, increasing cities' park-space and urban vegetation for both social and ecological benefits also often changes its biodiversity dynamics. Such 'greening' of the urban environment can vary from naturalistic to manicured designs and promote more native/non-

Glossary

Drylands: drylands have different definitions. Here we use the United Nations Environment Programme's (UNEP) definition which is based on an aridity index (ratio of average annual precipitation and potential evapotranspiration) of less than 0.65. The UNEP further divides drylands into hyper-arid, arid, semi-arid, and dry sub-humid lands.
Gentrification: the process in which lower-income and marginalized communities are priced out by higher-income groups.
Green gentrification: gentrification driven by and/or augmented by the addition of greenspaces and green infrastructure.
Greenlined neighborhoods: neighborhoods that were rated positively during redlining practices. These neighborhoods historically, and to this day, have more White inhabitants, are wealthier, and have greater public investments.
Gray space: areas of impermeable ground cover; in urban areas these are often buildings and concrete.
Haussmann Paradox: named after a city planner of Paris, France, this refers to cities where high-income residents live in dense urban cores with limited, highly manicured, less biodiverse greenspace, and lower-income residents live at the edges of cities closer to less-managed, more biodiverse large greenspaces.
Legacy effect: the effects of historical human disturbance on the land that are still impacting its current ecology; in urban ecology the legacy effect often refers to older neighborhoods as having higher biodiversity.
Luxury effect: the pattern in which neighborhood affluence is positively associated with biodiversity in cities (i.e., higher wealth is associated with higher biodiversity).
Mesic: areas or habitats that are defined by or require relatively constant moisture.
Peri-urban: the interface between the urban core and surrounding habitats.
Redlining: race-based exclusionary practices in the USA during the mid-1900s where neighborhoods were graded as 'more' to 'less' risky for investment and loan qualification (from a scale of 'A' to 'D') by the Home Owners' Loan Coorperation (HOLC), marked by the racial, ethnic, and religious make-up

native species respectively [33]. These intracity spatial dynamics, land-use types, and different 'greening' management schemes can also alter urban biodiversity in drylands very differently than temperate biomes (Figure 1 and Box 2).

Patterns of urban biodiversity differ between dryland and temperate biomes

Vegetation diversity and abundance in cities is mediated by human cultivation and spontaneous growth, and partially shape faunal biodiversity. Supplemental irrigation can substantially increase vegetation cover of dryland cities, compared with their surroundings, and cause fundamental changes to their most limiting resource – water. Conversely, urbanization in temperate biomes predominantly causes a decrease in vegetation. Supplemental irrigation is vital to the understanding of dryland urban ecological conditions [40,41]. Year-round supplemental irrigation supports urban greening, gardening, and exotic plants, with strong cascading effects [41–43]. For example, vegetation patterns in metropolises in southwestern USA are decoupled from seasonal precipitation due to supplemental irrigation [40,41]. Moreover, the **urban heat island effect** can function differently in dryland cities, with a reversal of the daytime urban heat island found in some dryland cities globally [44,45]. This reversal may partially be due to a lack of vegetation in dryland native habitats [45,46] compared with effects of managed vegetation on urban cooling [45,47].

Urban biodiversity in drylands

Urbanization is often associated with lower species richness of vertebrates and invertebrates in both temperate biomes and drylands [48–51] (see the supplemental information online). Here, we focus on biodiversity loss through urbanization with reference to wildland, rural, and/or historic species pools of a given area. We note that agricultural areas often surround cities, which threaten biodiversity [52]. Patterns of decline in cities are not as extreme in drier climates in comparison to wetter ones [53–56] (see the supplemental information online). Patterns of declining richness are not universal; some dryland urban areas have similar richness and/or diversity of birds and insects to their natural surroundings [57–59], and some even higher [35,58,60,61]. Globally, a higher proportion of regional bird species are represented in dryland urban species assemblages when compared with wetter biomes [56]. Specifically, birds in urban riparian sites had higher species diversity than desert riparian sites in Phoenix, AZ, USA [60]. Native bird diversity increased with urbanization possibly due to the artificial extension of riparian habitats in Reno, NV, USA [61]. Soil invertebrate abundances increased across more arid cities and declined in wetter cities globally likely because of the impact of supplemental irrigation in drylands [31]. There have also been instances of increased abundance of invertebrates [31], rodents [62], and herpetofauna [63] in dryland urban areas. Seasonality may also affect patterns of richness and biodiversity differently in dryland cities than in their surroundings. For example, this has been found for bees in villages across the Jordan Rift Valley in Israel [42].

Species composition across the urban mosaic

Urban areas are highly heterogeneous in landscape and vegetation [64], which shape their overarching biodiversity richness and abundance patterns. Species composition patterns, though, differ between dryland and non-dryland urban mosaics because of how patches compare to native wildland ecological conditions [65] (Figure 1). In dryland cities, green, **mesic** patches are often occupied by cultivated, irrigated, ornamental vegetation with strikingly different plant species composition and diversity from native habitats [66–69]. These patches can be mismatched with the ecology and attractors of dryland species, and attract more non-native fauna, as has been found in birds and invertebrates [50,59,70]. Consequently, animal species composition of mesic patches often differs from local wildlands. Dryland species may benefit from urban cooling and resources in vegetated urban patches [8,47,71]. However, **synanthropic** and non-native

of the population. Those with lower ratings were also underserved and under-resourced by city services and financial institutions. While illegal since 1968, legacies of redlining on structural racism in cities remains strong to this day, from exposure to pollutants, health outcomes, park distribution, and biodiversity. Redlined (as opposed to 'greenlined') neighborhoods are US neighborhoods that were poorly rated, historically under-resourced, and marginalized as a form of structural racism, and continue disproportionately to house lower-income residents and residents of color.

Suburban: residential tracts or districts within a metropolitan area, yet distant from city centers, at the edges of or outlying cities. These development zones are marked by low-density sprawl.

Synanthropic: associated with and benefits from humans and their environmental changes.

Urban heat island effect: the phenomenon in which the built environment and the urban core is hotter than surrounding undeveloped land.

Xeric: areas or habitats that are very dry and require little moisture.

Xeriscape: landscaping design for arid regions that requires little to no supplemental irrigation.

Yellowspace: remnant dryland wildlands and xeriscaped managed land in cities.

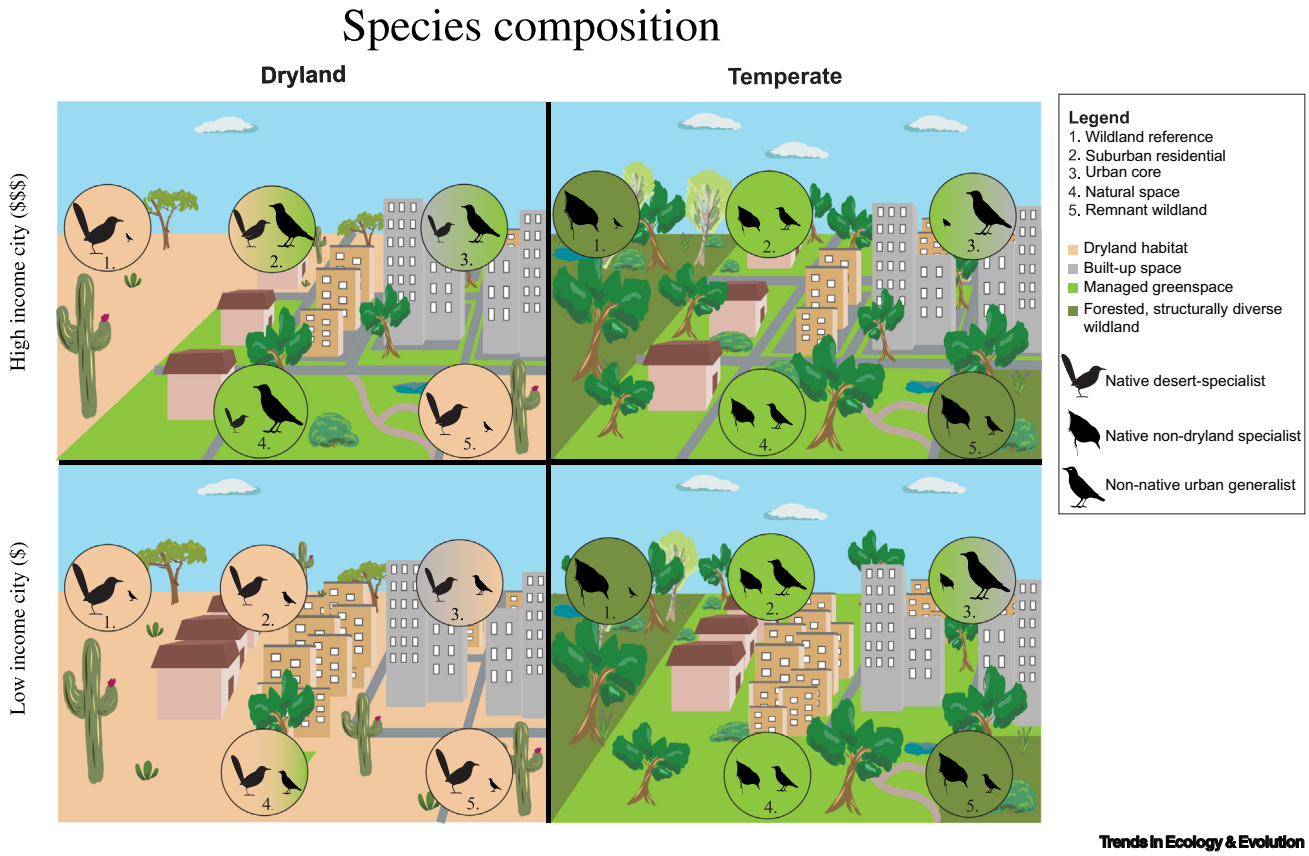

Figure 1. Conceptual and simplified representation of urban biodiversity patterns within cities, between biomes, and across city wealth levels when compared with native wildlands. Conceptual diagram representing species assemblages relative to wildlands across the urban mosaic in drylands (left column) and temperate regions (right column), in high-income cities (upper row) and low-income cities (bottom row). Within each mosaic, species composition of native versus non-native species is represented in (1) a wildland reference, (2) suburban residential, (3) urban core, (4) nature space (be they green or yellow), and (5) remnant wildland patches. Note that complexities such as variations in cities' structure, sprawl, size, and patch types have been omitted from this figure to maintain visual clarity. Please see inset figure legend for symbols.

Box 2. The social construction of nature should not just be 'green'

Greenspaces are thought of as important for urban biodiversity and conservation in cities, fostering native species, and being spaces for human–nature connections. This principle is biased towards temperate and tropical biomes where greenspaces more closely resemble non-urban habitats and foster more native species than the urban grayspace. Even language around 'nature' and sustainability focus on 'green' spaces or 'green' solutions rather than on more inclusive terms such as 'urban nature' or 'urban wilderness' (e.g., [85,128,129]). This is represented in the UN's Sustainable Development Goal 11.7 target of providing 'universal access to safe, inclusive and accessible, green and public spaces' [130]. Deserts are also often described as 'barren' or 'wasted' landscapes rather than their own complex and sensitive ecosystems, with cascading effects in and from European nations and cultures [14,15]. This view may partially be responsible for deprioritizing drylands in conservation, and why they are made to be 'green' in cities and in afforestation efforts. Viewing nature as green, and as separate from the urban experience, can be limiting and exclusionary as the extinction of nature experiences is felt by urbanites. Yet, it is important to recognize that nature – and potential nature experiences – exists in both urban and non-green places. In dryland cities, the idea of nature as greenspaces, and greenspaces as places that have non-native species, may impact human–nature experiences and self-reinforce a connection with non-native species and landscapes rather than native ones. In drylands, it is particularly important to focus on expansive place-based experiences in human–nature connectedness (rather than greenness and greenspaces per se) [131], including the diverse and multiple experiences of place across cultures that incorporate the social and ecological [132–134], culturally shifting how nature experiences are defined and experienced. We propose using the term 'nature spaces' to refer to landscaping features that benefit local ecological conditions in urban environments (be they greenspaces or yellowspaces). These terms denote the existence of vegetation and nature, but do not emphasize greenness per se.

fauna may have even greater competitive advantages over dryland species in greenspaces, which may lead to their overrepresentation in those patches [72]. Thus, while richness in urban green patches may be similar to wildlands (and sometimes even higher), they often support different species compositions [7,54,55,70]. Such is the case for ant communities in Tucson, AZ, USA, where irrigated urban areas have a similar richness and higher abundance to deserts, yet have compositions that are associated with cooler, wetter habitats [7]. In the case of birds in urban drylands, non-native species are associated with non-native vegetation and native species are associated with native vegetation in Nevada, AZ, USA [70]. Notably, some migratory birds appear selectively to stop in urban greenspaces or settlements rather than the desert due to irrigation and/or other resources [70,73]. Supplemental vegetation and year-round irrigation can also impact species interactions and ecological dynamics in urban dryland mosaics. Trophic dynamics shift in urban ecosystems because of human inputs in Phoenix, AZ [42]: stable vegetation in these mesic patches supports higher invertebrate abundances [31,74,75], can decrease their predators' water stress [76], which in turn supports higher predator abundances [42,77]. Ultimately, food webs there can shift from primarily bottom-up control to top-down control [42,76], more akin to temperate climates [25].

Contrasting dryland and non-dryland cities provides evidence for mechanistic drivers of species composition differences in vegetated urban patches. In cities in temperate regions, greenspaces and their designs have long been recognized in urban biodiversity management and conservation (e.g., [3,78–80]). Conversely, dryland urban diversity of some taxa is relatively higher within cities compared with their rural or wildland references. For example, the relative bird biodiversity (when compared with adjacent rural species pools) was higher in dryland cities than more forested cities across Argentina [54,81]. These trends are likely due to higher primary productivity in dryland cities [54]. Nevertheless, variation in bird species richness in Argentina along the urban gradient was associated with vegetation in both biomes [55]. In this study, peri-urban desert sites exhibited higher richness than natural desert sites, yet peri-urban forested sites had substantially lower richness than natural forest sites [55]. Bird species composition in Argentina and Brazil was found to differ between forested and dryland urban-rural contrasts. Dryland urban and natural species composition contrasts were less similar than that of a forested contrast, potentially due to the high prevalence of exotic vegetation in the dryland city compared with the non-dryland city [75]. Together, while vegetation is positively correlated with species richness across biomes, species composition patterns often differ in vegetated urban areas between biomes.

The built environment can differentially benefit native species in dryland versus temperate cities (Figure 1). Dryland species are adapted to sparse vegetation, low habitat complexity, and high heat, whereas most species in temperate biomes are not. 'Barren' hot urban cores, marked by high **gray space** and low vegetation, may be differentially suitable for dryland species beyond the most extreme 'universal' urban exploiters and/or a subset of temperate specialist species adapted to hot-dry patches in temperate zones (e.g., [53,55,72]). In such gray patches, artificial structures and anthropogenic resources can further benefit native dryland species [8], and may even foster species compositions of invertebrates and birds more akin to nearby native dryland habitats compared with dryland urban greenspaces [53,59,65,82]. However, not all native dryland fauna can occupy such complex habitats [83]. Conversely, in studies on avian and butterfly species in the built environment of temperate cities, species composition has been found to be less similar to that of native habitats compared with urban green patches [36,72,84]. The greater habitat complexity of greenspaces itself in more forested cities often supports native species, making species pools of such patches more similar to nearby native habitats [3,80,85]. For example, built features benefit all birds (including 'urban avoiders') in Guyana's savannahs, but in Guyana's forested habitats, built features negatively impacted urban-avoidant birds [72].

Therefore, while species composition in the urban core is dissimilar to the surrounding native habitats, these differences can be less pronounced in drylands [55]. Importantly, gray spaces are understudied across biomes [86].

The importance of 'yellowspaces' in drylands

Remnant dryland wildlands and **xeric** managed spaces (hereafter: '**yellowspaces**') can maintain species compositions more similar to those of local wildlands, including dryland specialists [87–89] (Figure 1). Yellowspaces have been positively associated with native bird abundance in Phoenix [90]. Patches with drought-tolerant plants fostered higher insect species richness and abundance than those without them in Los Angeles, California, USA [89]. Remnant wildlands have even been identified as potential biodiversity refugia from climate change across biomes [91]. Nevertheless, yellowspaces may still differ in faunal species composition compared with wildlands due to anthropogenic stressors [92].

Collectively, we posit that heterogeneity of urban drylands and the size of yellowspaces – rather than the amount of 'green' space per se – can impact how urbanization impacts local biodiversity, and a city's ability to support dryland specialists, or, alternatively, potentially act as sources of and refugia for non-native species, including invasive species (Figure 1). In turn, total species richness patterns may mask important biodiversity metrics for conservation priorities and the effects of urbanization on native biodiversity (Box 1). Downstream effects of urban biodiversity differences across biomes on ecoevolutionary dynamics, zoonotic pathogen spread, species interactions, and bidirectional effects on biodiversity outside of the city require further study.

Socioeconomics affect urban ecological conditions differently and more strongly in dryland biomes

Cities are fundamentally socioecological systems; the cultural and sociopolitical structures of humans, past and present, impact the ecology of and in cities [29,93,94]. Urban biodiversity across biomes can be differentially affected by various factors including (i) wealth, (ii) demography, (iii) **legacy effects** (i.e., historical land management), (iv) spatial configuration of the above factors, and (v) environmental injustice and **gentrification**. Intra- and intercity dynamics within countries, and global trends across cities, can be explored to understand how these factors are interrelated and interact with each other.

The impact of income inequality and social injustice on vegetation and biodiversity within cities

Irrigation and vegetation choices across the urban mosaic are a key mechanism driving urban biodiversity patterns across drylands. Irrigation is, fundamentally, a costly endeavor especially where water is scarce. Who has access and how these water resources are managed is a function of social systems, including power structures and social order [95]. The **luxury effect** is stronger with increasing aridity across biomes likely because of supplemental water use in drylands [43,96] (Figure 1). Indeed, the term was coined to describe variation in plant diversity across a wealth gradient in Phoenix [97]. Wealthier neighborhoods have higher plant diversity due to increased irrigation supporting preferences for exotic species [97]. This was also shown in Argentine cities across climatic gradients [98]. In Argentine arid cities, more vegetation was geographically associated with higher-income groups, yet in non-arid cities less vegetation was associated with high-income groups [98]. This is likely driven by wealth allowing for supplemental irrigation and vegetation whereas unmanaged vegetation is limited in dryland cities, yet unmanaged vegetation is the dominant form in temperate cities [98].

The legacies of historic land-use and urban planning policies can affect contemporary urban ecology. This phenomenon is defined as a 'legacy effect'. For example, older neighborhoods have

higher bird and plant biodiversity in the temperate city of Vitoria-Gasteiz, Basque Country, Spain [99]. Longer-established residents and older housing blocks in Phoenix reflect a desire for an 'oasis' in the desert, preferring highly-irrigated grassy lawns and exotic plants rather than native or **xeriscape** vegetation, leading to higher biodiversity in older housing developments [97,100]. Legacy effects can also interact with wealth in noteworthy ways. These interactions can be driven by policy and socioeconomics, shaping contemporary urban ecological conditions. For example, the luxury effect only existed when coupled with legacy effects in Los Angeles: older, wealthier residential plots had higher plant biodiversity [101]. Interactions with policy become clear in studies on the contemporary effects of historic **redlining** in Los Angeles. Historically redlined neighborhoods have fewer greenspaces and street trees than neighborhoods that were 'greenlined' [102,103]. **Greenlined neighborhoods** have higher greenspace and diversity across animal taxa [104]. Legacies of structural racism persist in greenspace inequality across racial and economic lines in South Africa, as well, due to its historic Apartheid policies [105]. Gentrification in the USA increases mammal biodiversity when impervious surfaces are accounted for [106]. Nonetheless, spatial configurations of wealthy versus impoverished neighborhoods can change across countries and cultures. For example, unlike Southwest USA, wealthier communities in Argentina live in city centers rather than in residential tracts outside the urban core [98]. Spatial configuration effects on the links between wealth and biodiversity are also present in temperate regions [96]. For example, the urban core in Paris, France, is home to wealthier residents yet has lower biodiversity (e.g., the '**Haussmann Paradox**') [96,107]. Importantly, this pattern has only been found in temperate regions [96]. These socioecological dynamics are not one-directional; new green infrastructure and greenspaces in cities often lead to **green gentrification** exacerbating environmental injustices [108].

The impact of inequality on vegetation and biodiversity across cities

Socioeconomic effects on biodiversity can also manifest themselves between cities, either within or across countries. To date, this has been studied with respect to the links between greenspaces and wealth/development, accounting for the impacts of climate [43,109]. The relative amount of urban greenspace and vegetation has been found to increase with city wealth within and across countries [110,111]. However, little is known specifically about the interactions between wealth, biome, and biodiversity across cities (Box 1; see also the supplemental information online). Nevertheless, we can speculate how biodiversity may manifest itself with respect to wealth across cities based on understanding of biodiversity patterns within the urban mosaic and the impact of wealth on biodiversity patterns within cities (Box 1; see earlier text), though these ideas should be further tested. Broadly, effects of wealth on biodiversity should be higher in urban dryland cities rather than in temperate ones. Moreover, wealthier dryland cities should have more dissimilar species composition to nearby wild habitats compared with temperate cities (Box 1). In temperate biomes, water is less important for supporting vegetation. Thus, we expect these compositional effects to be more muted. Indeed, in some temperate cities, a lack of management may increase native habitat intrusion into the city [112].

The importance of culture on vegetation and biodiversity

Beyond the major differences across biomes and wealth in how biodiversity manifests within and across urban systems, it is important to acknowledge the key role that culture has in shaping urban dryland biodiversity, which may interact with socioeconomic effects. Culture, coupled with wealth, shapes urban design and vegetation choices by residents and city planners [113]. For example, ornamental vegetation in residential yards and public greenspaces have been driven by aesthetic values in high-income cities such as those in the United Arab Emirates and the USA,

in order to mimic temperate and semi-temperate landscapes within drylands [66,114]. These choices may cause native species' decline in some cities due to strong ecological mismatches, even if species richness sometimes increases [66,114]. Furthermore, European colonialism and culture have exported French and British gardening aesthetics to global dryland cities, including non-native plants [14]. However, in some cities in the USA, sociocultural differences have led to xeriscaping and cultivating native plants [113].

Traditional agroecosystems and gardening can support native species amongst communities that value them, with residents choosing cultivars and allowing plants to grow spontaneously for utilitarian purposes [115]. For example, in Chihuahua, Mexico, urbanites highly value desert plant species. This leads to culturally mediated conservation of historic plant communities within the urban matrix [116]. Bedouin communities of South Sinai, Egypt, cultivate traditional agricultural gardens – including non-native fruiting trees – through rainwater harvest practices [117]. While these gardens include non-native plants, they have high native plant diversity and high functional complexity, including rare native plant species and a similar abundance of native shrub species as the unmanaged desert [118]. These practices provide oases that can serve as the only stopping points for migratory birds in a hyper-arid desert [119]. Similarly, traditionally managed oases in the Western Sahara have a higher biodiversity that is dissimilar from managed 'modern' oases. These traditionally managed oases provide habitats similar to the desert environment, with more complex habitat structure, and consequently attract bird assemblages including both desert specialists and birds that do not occupy the open desert [120]. Ultimately, not all managed greenspaces are equal; context-dependent costs and benefits must be evaluated between different forms of gardening practices – particularly when considering traditional practices deeply rooted in place in comparison to aesthetics-driven choices dependent on high supplemental irrigation and exotic species. Thus, cultural understandings of 'what is nature' and value systems also shape urban biodiversity patterns (Box 2).

Concluding remarks

We propose a general framework to understand how urbanization, coupled with socioeconomics, differentially impacts species composition and richness across biomes, with an emphasis on differences between temperate and dryland urban biodiversity (Figure 1). This contrast demonstrates how climatic and socioeconomic contexts can exert strong downstream effects on the impacts of urbanization on biodiversity globally. Data from urban drylands are nonetheless deficient, particularly from lower-income countries. As urban biodiversity patterns across biomes manifest differently, applying knowledge and insights from cities in temperate biomes to those in drylands can lead to inappropriate management recommendations. We acknowledge that we have only touched upon a few key elements that shape biodiversity across biomes, and that others (e.g., city size, history, heterogeneity, surroundings, taxa) need further exploration. We propose research questions to begin bridging these gaps (see Outstanding questions). We caution that the widespread emphasis on urban 'greening' can lead to inappropriate interventions in dryland cities and cause harm, much like potential deleterious effects of 'greening', 'blooming', and afforesting dryland native habitats [121–123]. Ultimately, selecting native species in managed patches and protecting remnant wildlands (be they green or yellow) is key for management across biomes [72,124]. Management may also lead to unique human–nature conflicts in dryland cities that will need to be solved, particularly between human interests, culture, and needs (such as prioritizing between highly dense urban vegetation versus supporting native dryland species). There is an urgent need to incorporate knowledge-based strategies in the next iterations of global assessments and recommendations (such as the IPBES [125]) to manage biodiversity threats and opportunities in urban environments while explicitly considering cities' biomes and

Outstanding questions

How does the strong softening of seasonality (caused by different mechanisms, i.e., supplemental irrigation or reduced effects of extreme climates) impact species interactions and ecoevolutionary dynamics within and between biomes? One can explore how biodiversity patterns across trophic levels in urban patches and ex-urban patches vary seasonally, and if these differences lead to selective differences between irrigated and non-irrigated patches. These patterns can be compared between biomes.

How do the surrounding land-uses affect biodiversity within cities between biomes? Do socioeconomic characteristics impact these patterns? The urban/non-urban interface is essential in understanding the impacts of urbanization on biodiversity regionally. We propose testing how land-use at the interface differs ecologically from the wildlands and the city. We expect land-use to vary by socioeconomic characteristics of a city, and the ecological effects to vary by biome because of differences in native wildland characteristics.

Are there greater behavioral mismatches between native and urban habitats for species adapted to particular biomes? Hot-dry specialized species may be preadapted to tolerating the urban core. We propose assessing urban tolerance and habitat selection within cities in comparison with climate specialization.

What is the degree of dependency of different species on managed oases in drylands, either traditional or modern? How will this dependency change with projected climatic changes? We propose assessing the use of oases by different species, the uniqueness of species to these oases, and temperature differences and thresholds across arid and hyper-arid drylands.

How do urban characteristics (i.e., size, heterogeneity of green and gray spaces, and surrounding areas) interact with biome to impact the spread of invasive species both within and outside cities? Modeling approaches, comparisons across cities and species, and fine-scale data from invasive species movements can be leveraged to begin answering this question.

socioeconomics in unison. Dryland species are less protected than non-dryland species, and are threatened by intensive land conversion, climate change, and invasion [13]. Desertification and urbanization are co-occurring, and climate change is simultaneously threatening and expanding drylands worldwide. Together, these threats challenge how urban areas can act as potential sources of invasion or refugia for dryland species. To tackle these challenges efficiently, we need to acknowledge the interplay between social, cultural, and climatic effects on biodiversity for the benefit of both people and nature.

How and should we shift embedded value systems for 'what is nature' (i.e., greenspaces versus yellowspaces) to shape urban biodiversity? How do people's interactions with nature within cities (and not just in 'designated natural spaces') shape their understanding of and interactions with urban nature across biomes? Interdisciplinary approaches across environmental psychology, sociology, and conservation are needed to better understand human–nature relationships across biomes and cultures.

How does 'greenification' beget gentrification, and gentrification beget greenification, in dryland cities versus temperate cities, and what policies and incentives can be instituted to focus on integrating yellowspaces into dryland cities? Quantitative data around income level and urban planning can begin answering whether greenification and gentrification present similarly across biomes. Thereafter, transdisciplinary approaches are needed to understand how human communities can be integrated and protected in the process of integrating yellowspaces in dryland cities.

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Declaration of interests

The authors declare no competing interests.

Supplemental information

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