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Christopher M Swan, Bryan Brown, Dorothy Borowy, Jeannine Cavender-bares, Alienor Jeliaskov, et al.. A framework for understanding how biodiversity patterns unfold across multiple spatial scales in urban ecosystems. *Ecosphere*, 2021, 12 (7), pp.e03650. 10.1002/ecs2.3650 . hal-03290303

HAL Id: hal-03290303







<https://hal.sorbonne-universite.fr/hal-03290303>

Submitted on 19 Jul 2021

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A framework for understanding how biodiversity patterns unfold across multiple spatial scales in urban ecosystems

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Citation: Swan, C. M., B. Brown, D. Borowy, J. Cavender-Bares, A. Jeliakov, S. Knapp, Z. Lososová, J. Padullés Cubino, S. Pavoine, C. Ricotta, and D. Sol. 2021. A framework for understanding how biodiversity patterns unfold across multiple spatial scales in urban ecosystems. *Ecosphere* 12(7):e03650. 10.1002/ecs2.3650

Abstract. Whether cities are more or less diverse than surrounding environments, and the extent to which non-native species in cities impact regional species pools, remain two fundamental yet unanswered questions in urban ecology. Here we offer a unifying framework for understanding the mechanisms that generate biodiversity patterns across taxonomic groups and spatial scales in urban systems. One commonality between existing frameworks is the collective recognition that species co-occurrence locally is not simply a function of natural colonization and extinction processes. Instead, it is largely a consequence of human actions that are governed by a myriad of social processes occurring across groups, institutions, and stakeholders. Rather than challenging these frameworks, we expand upon them to explicitly consider how human and non-human mechanisms interact to control urban biodiversity and influence species composition over space and time. We present a comprehensive theory of the processes that drive biodiversity within cities, between cities and surrounding non-urbanized areas and across cities, using the general perspective of metacommunity ecology. Armed with this approach, we embrace the fact that humans substantially influence β -diversity by creating a variety of different habitats in urban areas, and by influencing dispersal processes and rates, and suggest ways how these influences can be accommodated to existing metacommunity paradigms. Since patterns in urban biodiversity have been extensively described at the local or regional scale, we argue that the basic premises of the theory can be validated by studying the β -diversity across spatial scales within and across urban areas. By explicitly integrating the myriad of processes that drive native and non-native urban species co-occurrence, the proposed theory not only helps reconcile contrasting views on whether urban ecosystems are biodiversity hotspots or biodiversity sinks, but also provides a mechanistic understanding to better predict when and why alternative biodiversity patterns might emerge.

Key words: alpha diversity; beta diversity; cultivated species; dispersal; species co-occurrence; species turnover; urban ecosystems.

Received 27 February 2021; **accepted** 8 March 2021; **final version received** 11 May 2021. Corresponding Editor: Debra P. C. Peters.

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INTRODUCTION

The rapid expansion of urban areas (Chen et al. 2020) is one of the leading causes of habitat degradation and loss, causing declines, and local extinctions of many species (Grimm et al. 2008, Newbold et al. 2015, IPBES, 2019). Yet urban systems are also capable of supporting diverse communities of species, often composed of novel combinations of native and non-indigenous species (Kowarik 2008, Niinemets and Peñuelas 2008, Aronson et al. 2014). Whether cities are more or less diverse than surrounding landscapes, and the extent to which the presence of non-native species in cities due to human actions (e.g., cultivation, accidental escape from pet transport or private zoos, deliberate abandonment of exotic pets in nature) impacts regional species pools, remain two of the most fundamental and uncertain questions in conservation biology. Prior studies have found that urbanization can have both positive and negative effects on biodiversity, with outcomes depending on the specific context (e.g., cities' historical development; Hahs et al. 2009), spatial scale (La Sorte et al. 2007, Pautasso 2007), and taxonomic breadth (Aronson et al. 2016) of analyses. One explanation for the seeming discrepancies among studies in the influence of urbanization on biodiversity is that the mechanisms generating biodiversity patterns in urban systems are not well understood (Shochat et al. 2006, McDonnell and Hahs 2013): Different outcomes across studies are produced by the same underlying mechanisms operating in different contexts. A unifying framework for understanding the mechanisms that generate biodiversity patterns across taxonomic groups and spatial scales in urban systems is important to establish.

There have been a few attempts to conceptualize the variety of mechanisms that drive biodiversity patterns in the urban environment. Investigations of urban biodiversity patterns have been typically constrained by spatial or temporal scales, with the majority of studies

focusing on mechanisms operating at the level of the city (Williams et al. 2009, Kowarik 2011, Concepción et al. 2015), across regions (Groffman et al. 2014), or locally within a specific habitat at a single point in time (Ramalho and Hobbs 2012, but see Johnson et al. 2015). This specificity of focus has limited our understanding of urban community dynamics and has precluded our ability to predict future changes (Williams et al. 2009, Kowarik 2011, Swan et al. 2011, Groffman et al. 2014, La Sorte et al. 2014, Aronson et al. 2016, Pearse et al. 2018, Cavender-Bares et al. 2020). However, one commonality between these efforts is the collective recognition that species co-occurrence locally is not simply a function of natural colonization and extinction processes, but instead are consequences of human actions that are governed by a myriad of social processes occurring across groups, institutions, and stakeholders. Although the explicit incorporation of humans into the study of ecology has resulted in a rich body of urban literature, a mechanistic understanding of urban ecosystems has not been fully considered or explored (Shochat et al. 2006). Here, we expand upon previous frameworks to explicitly consider how human and non-human mechanisms interact to control urban biodiversity and influence species over space and time. Only through a mechanistic understanding can the field reconcile contrasting views on whether urban ecosystems are biodiversity hotspots or biodiversity sinks, and whether they have significant influence on non-urban biodiversity and composition. Most importantly, a mechanistic understanding can allow us to predict when and why alternative biodiversity patterns might emerge, and how they can lead to changes in the delivery of key ecosystem services.

A primary theme of this paper is the recognition that, while urban ecosystems are unique in some of their specific properties, their uniqueness does not remove them from the reach of well-developed ecological frameworks—like meta-community theory—for understanding and predicting biodiversity patterns (Swan et al. 2011).

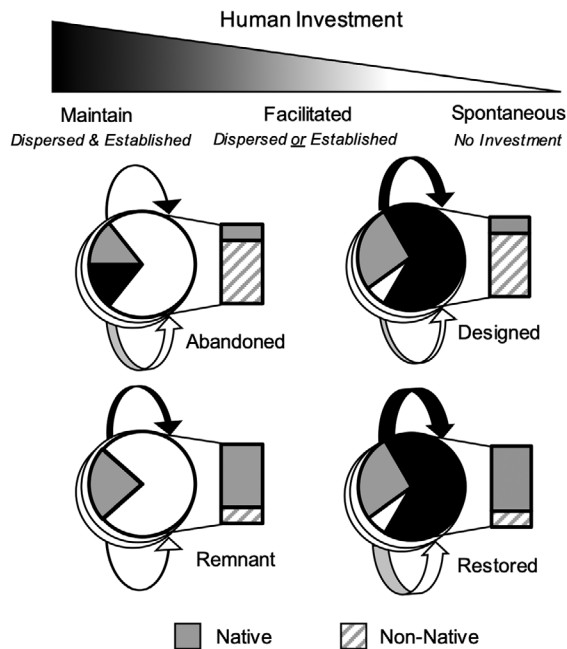


Fig. 1. Biodiversity changes in urban habitat patch types over time. Shaded pie slices indicate the different degrees of human investment in each patch type, ranging from maintained (black), facilitated (gray), and spontaneous (white), as indicated by the top triangle. Arrows represent past (white) and present (black) human investment. Arrow thickness represents the degree of past and present human investment—thick arrows reflect high levels of investment, whereas thinner arrows represent little or no human investment. Bar inserts show contemporary outcomes of human investment on the relative proportion of native (solid gray) and non-native (diagonal gray hatch) species in each urban patch type. This framework simultaneously considers a number of factors. Sources of species: whether species originate from the natural regional biota or from the human-managed breeding pool. Primary types of drivers: whether environmental drivers or human dispersal and management are the major factors dictating relative abundances in local communities. Species groups: The primary groups of species that can roughly be classified as Native Spontaneous; Non-Native Spontaneous; Cultivated or Bred/domesticated or human dependent; the latter pool can also include native and non-native species that are cultivated. Attributes of species: These attributes include species functional traits related to abiotic stress, dispersal, pollination, competitive ability, showiness, and attractiveness to humans, but also their degree of

plasticity. These traits mediate how species are sorted ecologically, disperse, and how human preferences affect their prevalence. Types of assembly process: Ecological sorting which includes abiotic environmental filtering and species interactions, dispersal (both natural and anthropogenic), and human care such as feeding, planting, provisioning, and nurturing. Evolution and adaptation to the urban environment can also contribute to the species sorting process. Attributes of the urban environment: What habitat types are represented in the urban matrix (e.g., forest, grasslands, wetlands, xeric areas, areas dominated by impervious surfaces) and how patch-level heterogeneity of these habitat types influences β -diversity within cities. Additionally, aspects of the built environment including energy and materials that flow through it (e.g., toxicity, wind, sunlight, temperature, waterflow) can affect local community composition by delivering resources, serving as migration corridors, or creating a patchwork of sources and sinks for species.

The same three general categories of factors that are considered to be fundamental to metacommunity dynamics—local factors such as species interactions and environmental conditions, regional processes largely driven by dispersal, and disturbances (Leibold et al 2004)—drive biodiversity patterns in both natural and urban systems. However, urban ecosystems present the challenge of incorporating the human element to a greater extent than more natural systems. For example, while investigators need only to consider the natural dispersal of organisms in pristine environments, in an urban context, they must also consider human-assisted dispersal (Fig. 1). While these human-associated characteristics of urban ecosystems may be unique, they still fall within the purview of metacommunity theory, and thus, the logic, predictions, and analytical tools of this well-developed framework can be used in the study of urban biodiversity across systems and scales as effectively as in more natural ecosystems (Chase et al. 2020, Table 1).

Our work is motivated by the need for a multi-scale approach that integrates consideration of both the drivers of, and measurement of, diversities within and across urban systems (Pautasso 2007). We embrace a detailed examination of spatial properties in urban systems (i.e., the urban

Table 1. Forces structuring communities in natural environments vs. urbanized landscapes.

Factors	Natural	Urbanized
Local	<ul style="list-style-type: none"> • Species interactions • Local environmental conditions 	<ul style="list-style-type: none"> • Species interactions • Local environmental conditions, including anthropogenic modifications • Localized management activities
Regional	<ul style="list-style-type: none"> • Dispersal of organisms 	<ul style="list-style-type: none"> • Dispersal of organisms • Anthropogenic movement of organisms • Modification of habitat connectivity • Autocorrelation between local management regimes that influence biodiversity
Disturbance	<ul style="list-style-type: none"> • Natural disturbance regimes 	<ul style="list-style-type: none"> • Natural disturbance regimes • Anthropogenic disturbance

Note: Forces in boldface are those largely associated with built/urbanized environments.

mosaic) and offer a conceptual framework for how they influence biodiversity in urban ecosystems and outlying regional areas to elaborate on this gap in knowledge.

THE NECESSITY OF ADOPTING A MULTI-SCALE APPROACH FOR MEASURING AND UNDERSTANDING THE DRIVERS OF BIODIVERSITY IN URBAN ECOSYSTEMS

Urban ecosystems are characterized by a highly heterogeneous mosaic of habitat patches, emphasizing approaches that take multiple spatial scales into account, from individual patches to the whole urban mosaic (Tratalos et al. 2007). Additionally, urban conservation targets usually go beyond single patches of urban areas and aim at protecting whole areas that aggregate diverse habitat types, including designed greenspaces (Table 2). Despite these clear needs for a multi-scale perspective, many urban studies focus on a single spatial scale of analysis of large sections of urban areas, either the local patch scale (e.g., Angold et al. 2006, Łopucki and Kitowski 2017) or the regional scale (e.g., Clarkson et al. 2007, Łopucki and Kitowski 2017). To incorporate the potential for multi-scale biodiversity dynamics,

from patches to regions, into studies of urban systems, there are two possible approaches. The first is focusing on a single patch type, for example, urban green spaces, and aggregating across all patches in a region of that patch type, while an area within the greater urban landscape, aggregating across diverse patch types. Here we focus on the first approach.

Understanding the drivers of diversity in a regional urban area goes beyond simply summing multiple facets of local scale diversity; it also includes compositional differences between localities (McKinney 2006, Beauvais et al. 2016). Metacommunity perspectives generally recognize that diversity occurs on three broad spatial scales: α -diversity, which is the diversity of a patch or local community; β -diversity, the variation in species composition among patches or local communities; and γ -diversity, which is the total diversity in a region. These metrics are generally considered to be related such that $\alpha \times \beta = \gamma$ (Whittaker 1960, Jost 2007), though other formulations have also been proposed (Lande 1996, Veech et al. 2002); see Tuomisto 2010 and Chao et al. 2012 for further information about the partitioning of β -diversity). Thus, regional diversity is connected to local diversity by the turnover in composition between locations. In practice, the spatial extent of local and regional are investigator-defined, though in urban ecosystems their definitions may be slightly more practical than in more natural systems, with a city block corresponding to local and an entire urban area corresponding to regional. However, experienced urban investigators will quickly recognize that even these broad generalizations are too facile, since not every habitat patch in urban systems occurs in neat blocks (e.g., parks and waterways), and the boundaries of a regional urban area are almost never discrete except on political maps which have little relevance to non-human organisms (e.g., Wilbanks 2006). Regardless, metacommunity concepts have been applied widely and successfully to natural ecosystems despite the inherent fuzziness of the definitions of local and regional and that application will be no less useful—and potentially more useful—in urban ecosystems.

Since patterns in urban biodiversity have been extensively described at the local or regional

Table 2. Designed greenspaces in urban environments.

Patch type	Nature of ownership	Main purpose	Degree of individual habitat investment	Control over species composition
Lawns	Individual	Recreation/esthetic	High	High
Gardens				
Vegetable	Individual	Food	High	High
Ornamental	Individual	Esthetic	High	High
Botanical	Institutional	Esthetic/education	High	High
Zoological	Institutional	Esthetic/education	High	High
Orchard	Individual	Food	High	High
Parks	Institutional	Recreation	Low	Medium
Paved/sealed areas				
Roads	Governmental	Mobility	Low	Low
Buildings				
Residential	Individual	Dwelling	High	High
Commercial	Institutional	Business	High	High
Industrial	Institutional	Business	Low	Low
Institutional	Institutional/governmental	Services/education	Medium – high	Medium
Stormwater detention	Governmental	Flood control	Low	Low
Bioswales	Governmental	Flood control	Low	High
Commercial landscaping	Institutional	Esthetics	Medium	High
Recreational				
Athletic	Institutional	Recreation	Low - medium	High
Golf courses	Institutional	Recreation	Low - medium	High
Railways	Governmental	Mobility	Low	Low
Green roofs	Individual	Flood control/esthetic	Medium - high	High
Powerlines	Governmental	Services	Low	Low
Agriculture	Individual	Food	High	High
Buried streams (pipes)	Governmental	Flood control	Low	Low
Cemeteries	Institutional	Services	Medium	Medium
Landfills	Governmental	Services	Low	Low
Sea Walls	Governmental	Flood control	Low	Low
Levees	Governmental	Flood control	Low	Medium
Fountains	Individual	Esthetics	Medium – high	High
Recreational ponds	Governmental	Recreation	Medium – high	Medium
Reservoirs	Governmental	Food/service	Low	Medium

scale (but see Jokimäki and Kaisanlahti-Jokimäki 2003, Clergeau et al. 2006, Catterall et al. 2010), we suggest that studying the β -diversity component in urban systems brings unique insights. As urban ecosystems are characterized by extreme spatial heterogeneity in habitat types, it seems obvious β -diversity needs to be quantified and understood. It may also be that a lack of consideration of β -diversity may be the source of many inconsistencies regarding the effect of drivers of changes on biodiversity (e.g., Hillebrand et al. 2017). But what information does β -diversity hold that can inform researchers about urban biodiversity and urban planning? Data from

simulation models (Mouquet and Loreau 2003) and model systems (Cadotte 2006) provide general expectations regarding the influence of dispersal on the α , β , and γ components of biodiversity, given all other processes and environments remain constant. As dispersal increases, given all other processes and environments remain constant, patterns in all three components shift. At low dispersal, α -diversity is low, while β -diversity is high, owing to little or no movement of species between localities, maintaining compositional divergence in localities. As dispersal increases, α -diversity increases as species increasingly colonize localities, but β -

diversity declines as fewer species differ between localities. These two situations maintain high γ -diversity. However, at very high dispersal, competitive dominant species often exclude other species locally, reducing α -diversity and producing regional (γ) diversity declines. Since urban systems are identified as supporting species with high dispersal rates (Kowarik and von der Lippe 2011), this mechanism has been invoked to be one of the explanations why urban systems are species-poor, at least in habitats experiencing ambient, human-unassisted, dispersal (Fig. 1).

The relative influences of dispersal and local habitat filtering, overlaid by the influences of disturbance events and the functional traits of species, lead to a wide range of dynamics that are responsible for assembling local communities (Leibold et al. 2004, Logue et al. 2011). When strong habitat filters, strong species interactions, or influential disturbances are present in a locality, communities can be structured in classic niche-based fashion (Hutchinson 1957, MacArthur and Levins 1964). However, given a strong influence of dispersal, relative neutrality among species, or disturbance regimes that do not favor particular taxa, communities may be assembled more through dispersal-driven dynamics or even chance events, leading to far more stochastic outcomes than niche-based assembly (Leibold et al. 2004, Hubbell 2005, Chase 2007). Generally, niche-based assembly is expected to produce lower β -diversity than dispersal-driven or stochastic assembly, except when habitat heterogeneity of local patches is high (Chase 2014, Viana and Chase 2019).

In urban ecosystems, human action affects which assembly mechanisms are most prevalent through a variety of avenues, including deliberate control over species composition (e.g., planting, weeding, pest control), habitat modification, and altering the frequency and intensity of disturbances (Avolio et al 2018). Therefore, understanding the drivers of biodiversity in urban ecosystems requires understanding how humans affect these assembly processes at multiple spatial scales (Norfolk et al 2013). For example, in designed habitats (Table 2), modification can have contrasting effects on diversity at different scales. At the local scale, α -diversity might be predicted to decrease in designed patches since they are often poor habitat for most organisms,

and humans often exert strong influence over the local species assemblage. Though in some cases, like plant diversity in domestic gardens, this prediction might not hold (Norfolk et al 2013), again because of the pervasive human influence (Kendal et al. 2012). However, even for designed patches that do not support high local diversity, the high spatial heterogeneity in urban ecosystems can drastically increase β -diversity because species turnover is high across localities. Effects of habitat modification on γ -diversity in designed patches will depend on whether or not species losses are compensated for by dispersal and/or human-driven augmentation of the regional species pool (Dullinger et al 2017).

THE DETAILED SPATIAL PROPERTIES OF URBAN SYSTEMS (I.E., THE URBAN MOSAIC) AND HOW THEY SHAPE BIODIVERSITY

The evaluation of biodiversity in urban systems can span multiple scales, from a single patch within an urban mosaic, to multiple patches of the same type, to a true urban mosaic comprising numerous patches of diverse types. We have discussed the properties of several general patch types in urban ecosystems in isolation. Here we scale up to multi-patch systems in two ways: (1) by considering the metacommunity properties of multiple connected patches of the same type and (2) by considering the true urban mosaic, that is, connected patches of differing types. For (1), we offer a set of predicted patterns based on metacommunity theory. For (2), specific predictions are difficult to produce, not because metacommunity theory cannot accommodate the spatial heterogeneity of the true urban mosaic, but rather because the multifarious ways in which urban patch types can be combined precludes generalization. We therefore provide a general set of hypotheses and guidelines for investigating these more complex arrangements of urban patches. We emphasize a need to better identify and integrate human and non-human drivers of biodiversity, with the counsel to be more explicit on processes that drive native and non-native urban species co-occurrence. Furthermore, we offer a multi-scale approach that considers biodiversity in terms of α , β , and γ diversities. We emphasize addressing scales in two ways: the scale at which we measure diversity and the scale at which we

measure drivers. Finally, we agree with contemporary community ecology that there is a need to integrate multiple dimensions of biodiversity—taxonomic, trait, phylogenetic—into our predictions (Webb et al. 2002, McGill et al. 2006).

Diversity across multiple patches of the same type

To assess diversity across patches, one can use pairwise community dissimilarities as a measure of β -diversity. We predict spatial and temporal patterns in community similarity (CS) to vary among urban patch types as a function of their distance from one another (D), the degree of environmental similarity (ES), spatial heterogeneity (SH), and time (T). CS is a standard measure of β -diversity that compares species composition between two localities. There is not a single standard metric for CS, but rather a suite of metrics that focus on different properties of assemblages (reviewed in Anderson et al. 2011), of which the most commonly used is the Bray Curtis metric which expresses the proportion of species that are shared between two sites based on relative abundance data (Legendre and Legendre 2003). ES is akin to CS but expresses the degree of congruence in environmental variables between two sites. SH, as used in our predictions, is the overall average variability in environmental conditions among all sites. While human influence is not an explicit predictor in our hypotheses, it is implicit in several variables. Humans clearly directly affect ES and SH in the urban environment, but they also affect CS both directly and indirectly by manipulation and management of species pools and by acting as dispersal vectors for many species.

Remnant urban patches.—Remnant urban patches represent areas that have not been dramatically altered in the process of urbanization and thus reflect relatively low degrees of past human investment (Kowarik and von der Lippe 2018). Current management practices in remnant urban patches are minimal, with efforts focused primarily on maintenance of natural or semi-natural conditions, including the removal of invasive species. Remnant habitats exhibit community assembly patterns that are governed primarily by natural dispersal and stochastic extinction (Fig. 1). Examples of urban remnant patches include remnant woodlands, riparian habitats, and meadowlands.

Spatial patterns.—Among remnant patches of the same type, we expect variations in dispersal potential to govern patterns in CS as a function of D and ES, though we expect that the length of the environmental similarity gradient will be short (indicated by length of arrows on axis, Fig. 2). Namely, CS will decrease with D when dispersal potential is low and species are limited in their ability to access distant sites. When dispersal potential is high, we expect little or no change in CS with distance between patches (Fig. 2a). CS will increase with increasing ES when dispersal potential is low, due to the combined effects of species' limited ability to colonize sites and differences in environmental conditions within remnant patches that determine which species can persist over time (i.e., species sorting). ES will have little or no effect on CS at high rates of dispersal, due to mass effects, which override the influence of habitat selection on diversity patterns (Fig. 2b). Likewise, we expect ES to decrease with D as remnant patch characteristics will tend to exhibit clustering related to underlying environmental gradients (Fig. 2c). In contrast, we expect managed residential yards and gardens to show high CS as a consequence of convergent human management practices, especially those that override climatic limitations (Groffman et al. 2017, Wheeler et al. 2017, Pearse et al. 2018, Padullés Cubino et al. 2019b, 2020).

Temporal patterns.—CS (Fig. 2d) and SH (Fig. 2e) will not change over T and will be low relative to other patch types as remnant habitats represent fragments of native land cover types that have not been dramatically altered by humans and can be managed to maintain native conditions.

Abandoned patches.—Abandoned patches represent areas that are not actively maintained or are minimally maintained, but which had a high level of human investment in the past. These legacy effects continue to influence contemporary patterns in species composition (Johnson et al. 2015, Roman et al. 2018) and are responsible for maintaining high degrees of habitat heterogeneity among abandoned habitats (Fig. 1). Examples of abandoned patches include vacant lots, brownfields, and wastelands.

Spatial patterns.—We expect patterns in CS along gradients of distance between patches and ES to track predicted patterns for remnant habitat types; however, the range of ES will be

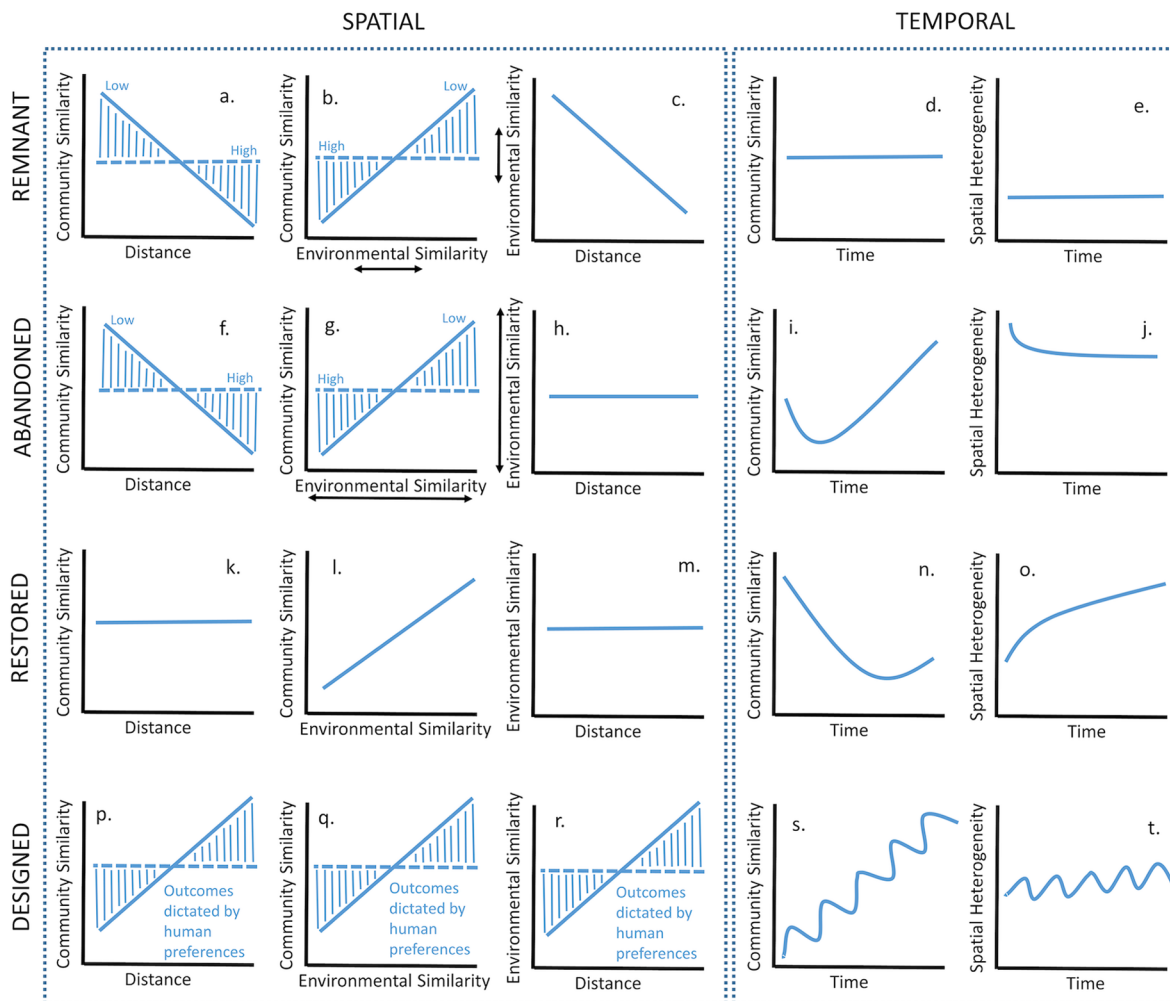


Fig. 2. Predictions for changes in β -diversity (measured as community similarity) across gradients of spatial distance, environmental similarity for four urban patch types (remnant, abandoned, restored, designed) and over time within each patch type. Arrows on the Environmental Similarity axes represent the expected length of the similarity gradient.

greater in abandoned sites due to higher degrees of SH (Fig. 2f, g). Unlike remnant patches, however, we expect ES will not change with D since there is likely to be little spatial correlation between what types of patches are historically abandoned (Fig. 2h).

Temporal patterns.—We expect initial CS will be low due to variations in human land use and habitat types prior to abandonment. As new species arrive at different times from the regional species pool (i.e., priority effects, Chase 2003), CS will decrease. CS will also be influenced by the

localized extinctions of any species that were cultivated or maintained. Over time, community composition will converge, and CS will increase as similar communities of species establish in abandoned habitats (Fig. 2i). Conversely, we expect patch heterogeneity will initially be high post-abandonment, due to differences in human land use and management practices. Patch heterogeneity will decrease and stabilize over time as environmental conditions become more similar once human management pressures are relaxed. Legacy effects, however, will maintain

high heterogeneity among abandoned patches, relative to other patch types (Fig. 2j).

Restored habitats.—Restored habitats are areas where people have assisted in the recovery of an ecosystem that has been degraded, damaged, or destroyed (Palmer et al 2017). They are characterized by relatively low past human investment but high current investment and can include a variety of blue and green ecosystems, including wildlife habitat in private yards, restored river channels, decontaminated soils on brownfield and Superfund sites, and replanted meadows and grasslands. Restored habitats are thus highly heterogeneous, and dispersal is primarily governed by humans (Fig. 1).

Spatial patterns.—We expect CS and ES will not change among restored patches with increasing D as these areas are not spatially arranged in the urban form and can widely vary in form and function (Fig. 2k, m). CS will, however, increase with environmental similarity due to species sorting effects (Fig. 2l).

Temporal patterns.—Degraded urban habitats often share similar environmental conditions including exposed, contaminated soil and water bodies, high proportions of non-native and invasive species, and altered biogeochemical cycles. These general conditions will select for similar pools of species resulting in high CS prior to restoration. As habitats are actively restored to reflect different ecosystem types and conditions, CS will decrease. When restoration efforts cease, CS will increase slightly as species from the regional species pool colonize and establish in restored patches (Fig. 2n). We expect habitat heterogeneity to increase over time among restored habitats, reflecting differences in restoration practices, goals, and success (Fig. 2o).

Designed habitats.—Designed habitats are areas that have been planned, constructed, and maintained by humans to achieve a specific purpose (Nassauer 1988). They include highly developed infrastructure, such as buildings and parking lots, or green spaces that may resemble natural landscapes in form (e.g., gardens, parks, landscaped areas), but which do not function like natural ecosystems. The variation in design types contributes to high SH among patches and dispersal that is mediated primarily by humans (Fig. 1).

Spatial patterns.—CS and ES in designed habitats can show multiple patterns with increasing

distance according to the spatial scale of people's choices (house, block, neighborhood) and patterns in urban design. For example, gardens that represent highly individualized preferences or newly designed urban areas that feature a mixed-use development, which integrates residential, commercial, institutional uses, will exhibit no change in CS with D. However, CS will show strong patterns (increasing or decreasing) with D when socio-economic factors and neighborhood preferences strongly influence landscape design or in older cities that developed as concentric zones of different land use types (Padullés Cubino et al. 2017; Fig. 2p, q). Likewise, we expect CS will either increase with ES, or it will not change depending on whether human preferences and management are strong enough to override environmental effects (Wheeler et al. 2017, Padullés Cubino et al. 2019a; e.g., xeric versus mesic landscaping in Arizona; (Martin et al. 2003, Larson et al. 2017) and at which scale those preferences occur (Fig. 2r).

Temporal patterns.—Among urban patch types, we expect designed areas will exhibit the greatest variability resulting from variations in people's preferences and design types with an overall increase in CS over time due to similarities in the designed species pool (e.g. nursery stock, and pet trade, Cavender-Bares et al. 2020). Conversely, CS may also decrease over time if preferences and designed landscapes vary by neighborhood and cultural group (Fig. 2s). We would not expect SH to show an overall trend with time, though SH may either increase or decrease for intermediate periods of time depending on the degree of spatial autocorrelation in human choice at intermediate and large spatial scales (Fig. 2t).

Diversity in a multi-patch type system

Scaling up to a multi-patch type mosaic presents a large number of possible scenarios depending on how many patches of each type are combined. That complexity makes it difficult to apply the straightforward predictions presented in the last section very difficult. However, we formulated three mechanistic hypotheses supported by theory and empirical patterns that address general properties of the true urban mosaic.

H1: Across-city biodiversity and within-city biodiversity (taxonomic, phylogenetic, and

functional) are governed by different drivers.— Across-city biodiversity is mainly shaped by continental drivers and the regional species pool (La Sorte et al. 2014, Aronson et al. 2016). Within-city biodiversity is mainly shaped by land use (city centers, suburbs, urban parks), environmental heterogeneity, and socio-economic drivers (Aronson et al. 2016, Avolio et al. 2018). We thus expect that large scale natural drivers (e.g., climate) are most important at broad spatial scales (among cities), while human drivers (e.g., degree of habitat alteration) are most important on local and regional scales (within cities).

Biodiversity turnover (species, functional, and phylogenetic) across cities is mainly shaped by climatic drivers, global trade, and the regional species pool. In contrast, biodiversity turnover within cities is mainly shaped by habitat conditions, connectivity, socio-economic factors, and local regulation (Brice et al. 2017, Avolio et al. 2020). Across cities, native species will be driven by climate and the regional pool while non-native and cultivated/domestic species will be driven by global trade and climate (Nobis et al. 2009). Within cities, native and non-native species distributions will be driven by habitat conditions, connectivity, and socio-economic factors. Cultivated and domestic species are known to be regulated by complex interactions between local ecology, local regulations, socio-economic factors, and legacy effects of prior land uses (Cook et al. 2012). As such, turnover in biodiversity (species, functional, and phylogenetic) is an important regulator of how biodiversity emerges at the scale of whole cities. When cities have spatially and temporally heterogeneous habitats, and variable human preferences, species diversity increases, which translates to high γ -diversity.

H2: Different components of urban biodiversity (spontaneous native, spontaneous non-native, human-assisted native, and non-native) are shaped by different mechanisms operating at different scales.— Between cities, differences in regional climates and the regional pool of native species are the most important drivers of turnover in biodiversity (Lososová et al. 2011, 2012, Kalusová et al. 2019). In addition, the importance of factors driving species turnover will vary across sources of urban biodiversity (spontaneous native, spontaneous non-native, cultivated native, and

cultivated non-native; Knapp et al. 2012, Cavender-Bares et al. 2020). For example, reduced trade connectivity will be associated with higher biodiversity turnover among cities for both cultivated native and non-native species. Differences in state- or national-level regulations—for example, differences in biosecurity or biodiversity management in surrounding landscapes—will be associated with higher biodiversity turnover among cities. Differences in human preferences at state or national levels will drive species pool composition resulting in shifts toward species that are visually appealing or that perform key functions, resulting, in many cases, in ecological mismatches between selected species and local habitat conditions. In addition, heterogeneity in regional climate, government regulations, and trade will result in high β -diversity at the cross-city scale.

Within-city species and functional diversity are highest in spatially and temporally heterogeneous urban landscapes where the variety of local environmental conditions increases the variety of niches and therefore species' trait expressions. We thus expect that gamma diversity for a city will be highest when there is high patch heterogeneity. However, this general prediction may not be validated if higher habitat heterogeneity coincides with high levels of habitat fragmentation. In such a case, individual urban habitat patches would become small and isolated, leading to a decrease in patch-level diversity (Prevedello et al. 2016, Fletcher et al. 2018). The overall result of such a scenario would be a unimodal relationship between patch heterogeneity and gamma diversity.

H3: For native and spontaneous non-native species within cities, taxonomic (TD) and functional diversity (FD) are driven by environmental heterogeneity of habitats while, for phylogenetic diversity (PD), increasing urbanity is more influential than heterogeneity.— Cultivated species will not depend on environmental heterogeneity but their diversity will be higher when the degree of human preferences for different cultivars is high. Phylogenetic diversity decreases with increasing urbanization due to the loss of evolutionary distinctive species belonging to lineages that have been evolutionarily less successful. Therefore, semi-natural land use types within urban areas (e.g., forests) are expected to

have a higher phylogenetic diversity (PD) than more human-dominated land use types (e.g., lawns), and the difference should increase with the degree of urbanization.

It is often assumed that differences in PD and FD in urbanized environments compared to the surrounding non-urbanized environments are mainly driven by changes in species loss. Indeed, it is expected that a loss of TD drives a decline in PD and FD just by chance (but see Knapp et al. 2017; Concepción et al. 2016). However, differences in TD, PD, and FD can also be affected by the type of species traits under consideration (Concepción et al. 2016). The reason for this connection is that some attributes of species influence their success in settling, establishing, and spreading into cities and, hence, they largely determine how many species persist in the community and which functions they possess (Williams et al. 2015). It follows that species richness in a city will depend on the prevalence of traits that allow persistence in the novel environment (Duncan et al. 2011). The filtering of species according to adaptive traits will also lead to a disproportionate loss of PD, as traits that confer success in urban environments are likely to be phylogenetically conserved and represented across a few clades.

In many ways, aggregating across multiple patches of the same type within an urban mosaic is an unrealistic scenario and probably has limited utility on its own, though one exception may be studies of the collectives of diversity in urban green spaces in a region. However, the major utility of this section is in demonstrating how metacommunity theory and approaches can be directed at urban areas. The same approaches can be used in a multi-patch type mosaic once the distribution and arrangement of patch types are known, but the approach cannot be generally illustrated here because of the multitude of possible scenarios of patch compositions.

RECOMMENDATIONS FOR FUTURE RESEARCH

Research on urban biodiversity has made enormous strides in the last few decades, from the recognition that urban areas are ecosystems worthy of study (McKinney 2006, Pickett et al. 2008, Sukopp 2008) to detailed descriptions of biodiversity patterns within and across cities (e.g., Duncan et al. 2011, Beninde et al. 2015, King

et al. 2016), and an explicit incorporation of humans into our understanding of urban ecology (e.g., Knapp et al. 2012, Avolio et al. 2018). However, much of this progress has been directed at describing pattern rather than understanding the mechanisms behind biodiversity patterns in urban ecosystems (Shochat et al. 2006). We do not intend to diminish these contributions; description of pattern is exceedingly valuable and is a key step in the scientific process. However, mechanistic understanding is a prerequisite for effective conservation and management (Levin 1992). Therefore, the primary intention of this paper is to encourage a focus on mechanistic understanding of biodiversity in urban systems, based on a multi-scale approach. Here we propose several avenues of research that can strongly contribute to that understanding.

Testing mechanistic hypotheses about the drivers of diversity in urban areas

If mechanistic understanding of urban biodiversity is to be achieved, direct testing of hypotheses regarding the drivers of urban biodiversity is necessary. This paper presents a number of hypotheses regarding the drivers of diversity in urban areas and the processes that produce those patterns. While we strongly encourage evaluation of these hypotheses, we also recognize that the scope of our hypotheses is not exhaustive and encourage the development of additional mechanistic hypotheses. However, we do emphasize the need for a focus on the mechanisms that produce well-documented patterns.

Drivers of diversity patterns within cities

Much of the biodiversity research in urban areas has focused on comparisons of either diversity across city types or comparisons of diversity of urban areas to surrounding natural areas. However, if urban ecosystems are considered worthy of study in their own right, understanding the mechanisms that drive biodiversity patterns *within* cities is fundamental. What are the relative roles of local habitat and dispersal-driven patterns? How does the human influence on regional species pools translate into local diversity in urban patch types? To what degree is the biodiversity in an urban area influenced by remnant natural habitat (Kowarik and von der Lippe 2018)?

How do the drivers of diversity patterns change across scales?

It has been argued that scale is the central problem of ecology (Levin 1992, Willis and Whittaker 2002, Chase et al. 2018) and understanding the processes that generate biodiversity patterns in urban environments is no exception. Processes that dictate community composition at the scale of a city block are not the same processes that drive differences in biodiversity between cities (Aronson et al. 2016). To this end, we encourage synchronized multi-scale investigation in urban systems that can separate the effects of spatial scale from patch-specific effect. Metacommunity theory provides a roadmap of concept and technique for multi-scale investigation and many techniques that have been employed in the study of more naturalistic systems are relevant to the study of urban ecosystems.

Toward an urban biogeography

Urban areas are not uniform; they differ in size, construction, age, and history (Hahs et al. 2009). Over 300 yr, the scientific discipline of biogeography evolved in approach to incorporate both historical and contemporary drivers of diversity in explaining species' distributions. Biogeography effectively combines historical legacy effects with contemporary forces of local habitat filtering and the traits of species. Because urban areas are heterogeneous in their histories and in their current construction, incorporating both sets of effects will be a key in understanding the mechanisms that drive biodiversity in urban ecosystems.

ACKNOWLEDGMENTS

This paper resulted from the sUrBioCity working group funded by sDiv, the Synthesis Centre of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, funded by the German Research Foundation. CMS acknowledges support from NSF LTER grant no. DEB-1027188. The opinions and findings expressed in this paper are those of the authors and not of the National Science Foundation.

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