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PERSPECTIVE

Predicting the assembly of novel communities in urban ecosystems

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Abstract
Context Ecological communities in urban ecosystems are assembled through ecological processes, such as species interactions, dispersal, and environmental filtering, but also through human factors that create and modify the landscape. These complex interactions make it difficult to untangle the relationships between social–ecological dynamics and urban biodiversity.
Objectives As a result, there has been a call for research to address how human activities influence the processes by which ecological communities are structured in urban ecosystems. We address this research challenge using core concepts from landscape ecology to develop a framework that links social-ecological dynamics to ecological communities using the metacommunity perspective.
Methods The metacommunity perspective is a useful framework to explore the assembly of novel communities because it distinguishes between the effects of local environmental heterogeneity and regional spatial

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processes in structuring ecological communities. Both are shaped by social–ecological dynamics in urban ecosystems.

Results In this paper, we define social, environmental, and spatial processes that structure metacommunities, and ultimately biodiversity, in cities. We then address how our framework could be applied in urban ecosystem research to understand multi-scalar biodiversity patterns.

Conclusions Our framework provides a theoretical and empirical foundation for transdisciplinary research to examine how social-ecological dynamics mediate the assembly of novel communities in urban ecosystems.

Keywords Community ecology theory · Urban ecosystems · Metacommunity · Human–environment interactions · Biodiversity · Social–ecological dynamics

Introduction

Urbanization is increasing globally, both in terms of human population and land use, including the rapid expansion of urban land use in global biodiversity hotspots (Seto et al. 2012). Since the majority of the global population lives in urban areas, cities are a nexus for human–environment interactions, which ultimately shift global biodiversity patterns (Grimm et al. 2008). However, the ecological effects of human activity are highly variable across geographic scales, as well as across taxonomic and functional groups (Chase et al. 2019).

Interactions with social dynamics add a level of complexity to ecological patterns and processes in urban ecosystems (Swan et al. 2011). Management decisions at scales ranging from individuals and households to developers and government entities, shape and reshape the urban landscape mosaic. People shift biodiversity patterns by influencing the environmental composition and spatial configuration of habitat patches across scales (Aronson et al. 2016). In turn, the urban landscape provides ecosystem services and constrains future management decisions (Pickett and Cadenasso 2008). As a result, human–environment interactions drive the landscape mosaic through iterative feedbacks to influence regional patterns of biodiversity and human well-being (Wu 2008).

Beginning in the 1990s, there has been an emergence of interdisciplinary research to understand social-ecological dynamics in urban ecosystems (Machlis et al. 1997; Alberti et al. 2003; Childers et al. 2014; Pickett et al. 2017). These efforts have paved the way for urban ecology concepts that consider people and social institutions as interacting components of ecosystems (Pickett and Grove 2009; Warren et al. 2010). However, the literature lacks a theoretical framework to spatially address interactions between social dynamics and ecological processes that alter ecological communities and associated biodiversity across scales. Here, we use a multi-scalar approach to address the current research challenges in urban ecosystem science presented by Groffman et al. (2017), which are: (1) predicting the assembly of novel ecological communities under altered environmental conditions, and (2) integrating humans as components of ecosystems, rather than separate entities or outside forces. Drawing from interdisciplinary literature (Goddard et al. 2010; Swan et al. 2011; Cook et al. 2012; Aronson et al. 2016), our theoretical framework links social, environmental, and spatial factors to community composition, and therefore biodiversity, to address these research priorities for urban ecosystems (Fig. 1).

The metacommunity perspective applied to urban ecosystems

Here, we use the concept of metacommunities, which combines local and regional process within a spatially explicit context (Leibold et al. 2004), as a basis to understand and conserve urban biodiversity in a spatial, process-based framework. Similarly, the metacommunity perspective's evolving concept has been brought forward as a useful framework to study biodiversity conservation in consideration of human drivers (Chase et al. 2020). The metacommunity perspective offers unique insights to urban ecosystems given the environmentally heterogeneous, spatially structured landscapes associated with human development. Four models have been traditionally used to distinguish the relative effects of spatial and environmental drivers from local to regional scales on metacommunity dynamics and biodiversity patterns:

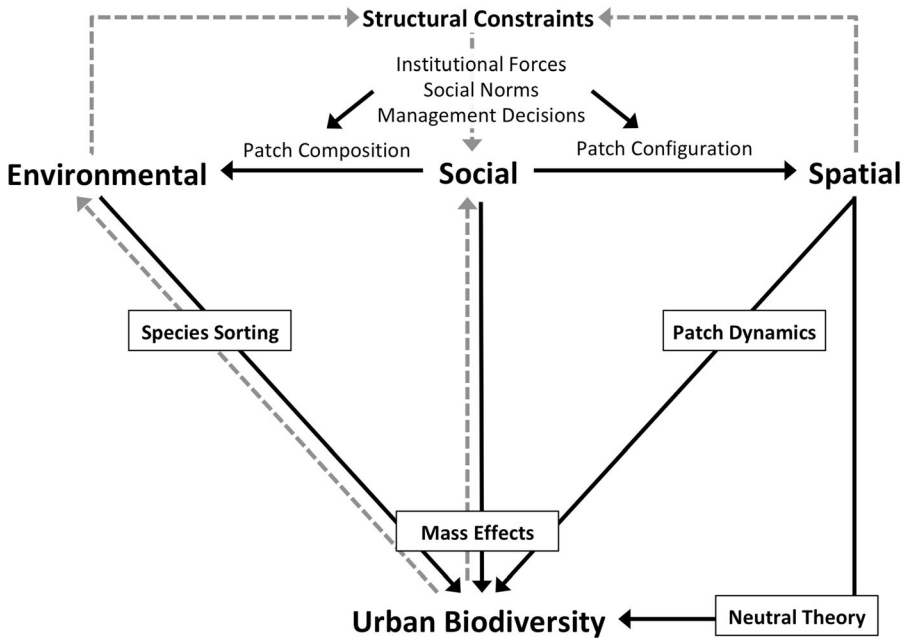

Fig. 1 Local to regional scale processes categorized into environmental, social, and spatial factors, which structure metacommunity dynamics (Species Sorting, Patch Dynamics, Mass Effects, and Neutral Theory) and therefore, biodiversity in urban ecosystems. People (social factors) influence biodiversity through management decisions that disperse biota and shape habitat patch composition (environmental factors) and configuration (spatial factors) across the landscape. Structural constraints, including the environmental heterogeneity and spatial configuration of the urban landscape, constrain management decisions across multiple scales. Grey-dotted arrows indicate feedbacks reproduced in the system, which further influence environmental and social factors over time

patch dynamics, species sorting, mass effects, and the neutral model (Holyoak et al. 2005; Table 1).

The patch dynamics model assumes a homogenous environment and limited dispersal of species, whereby tradeoffs in colonization and competition shape community composition (Slatkin 1974). In contrast, species sorting assumes environmental heterogeneity is a crucial driver of biodiversity patterns through niche partitioning and resource gradients (Whittaker 1962; Aronson et al. 2016). Similar to species sorting, the mass effects model assumes that species are associated more strongly with some habitats over others (Shmida and Wilson 1985). Under mass effects, dispersal between patches structures the ecological community, creating source-sink dynamics (Pulliam 1988). Under source-sink dynamics, a population can persist in less favorable environmental conditions as individuals disperse from suitable habitat elsewhere on the landscape (Holt 1985). Neutral theory assumes species are functionally equivalent, thereby emphasizing random demographic effects and dispersal limitation over environmental heterogeneity (Hubbell 2001). We do not consider these models to be mutually exclusive or encompassing the complexity of processes that structure ecological communities. Instead, we use these foundational models to organize and link social factors that may alter the different assumptions of local to regional scale processes that structure ecological communities in cities (Leibold and Chase 2017a).

We base our framework on concepts from landscape and urban ecology (Pickett and Cadenasso 2017), such as the use of heterogeneous patches spatially distributed throughout the landscape mosaic, to predict the assemblage of novel ecological communities in urban ecosystems through the metacommunity perspective (Teixeira and Fernandes 2020). To expand on the metacommunity perspective, we incorporate the concept of *social factors,* defined as the land management decisions made by individual people and organizations that influence patch composition and spatial configuration. *Social factors* influence both the environmental composition and spatial configuration of the urban landscape. *Environmental factors* are

Table 1 Glossary of key concepts

Foundational metacommunity concepts	
Metacommunity	Ecological communities (plants/animals) linked by habitat patches throughout a landscape. The metacommunity perspective is based on deterministic and stochastic processes from local to regional scales, as well as spatial and temporal heterogeneity
Species sorting	Metacommunity dynamics driven by environmental heterogeneity and resource utilization
Mass effects	Metacommunity dynamics driven by spatial and environmental factors. Source-sink dynamics where species disperse to local patches
Patch dynamics	Metacommunity dynamics driven by spatial effects of dispersal and colonization-competition tradeoffs. Assumes no spatially fixed environmental heterogeneity
Neutral theory	Metacommunity dynamics randomly determined by processes such as speciation and extinction
Factors structuring metacommunity dynamics in urban ecosystems	
Social	Individual people and organizations that interact with local ecological communities and make decisions that impact environmental and spatial factors
Environmental	Biophysical characteristics and heterogeneity of parcels that scale up or down to create habitat patches. Environmental factors include environmental filtering and resource dynamics that influence interspecific interactions and fitness
Spatial	The structure or configuration of habitat patches throughout the landscape. Spatial factors include dispersal, source-sink dynamics, and colonization. People can override spatial structure by facilitating dispersal
Social and ecological processes	
Deterministic	Niche-related processes related to environmental heterogeneity (mass effects and species sorting)
Stochastic	Unpredictability, random, and neutral processes, typically related to spatial structure (patch dynamics and neutral theory)
Structural constraints	The external factors that control management decisions (e.g., socioeconomic status, life stage, social and cultural norms, parcel size, systematic racism, development history)

defined as the biophysical characteristics of a patch (patch composition). *Spatial factors* are characterized by the distribution of patches throughout a landscape (patch configuration) connected by dispersal. Local and regional scale processes structure metacommunity dynamics, and ultimately biodiversity, through these social, environmental, and spatial factors.

Integrating social factors into metacommunity dynamics

Multi-scalar land management

Habitat patches are typically managed along human-constructed boundaries in cities (e.g., private, public, or communal land parcels). However, the scales at which species and ecological communities respond often transcend the social-political boundaries that delineate cities (Cumming et al. 2006). Management decisions made on individual parcels scale up or down to create habitat patches throughout the urban landscape mosaic (Goddard et al. 2010). Additionally, the same individual or entity could control management decisions across spatially distant land parcels. As a result, parcels that are close together may have different regimes based on the variety of landholders making diverse management decisions. However, mimicry, social norms, and other external pressures may also synch management decisions across connected parcels to create habitat patches (Minor et al. 2016). To address these cross-scalar implications, we apply the metacommunity perspective in light of local management decisions that consider the broader scale

forces at neighborhood, municipal, and regional levels. Local land management decisions that influence environmental heterogeneity link social factors to deterministic models of species sorting and mass effects. Conversely, the patch dynamics and neutral theory models, which emphasize the importance of spatial and stochastic processes, connect to social factors through management decisions that structure the configuration of patches throughout the urban landscape.

Different disciplines and research traditions hold varying assumptions on the freedom of choice that goes into land management decisions. The decisions people make based on preferences, priorities, and desires is a common, 'agency-based' approach to understanding how management decisions affect ecological outcomes (e.g., Yabiku et al. 2008; Larson et al. 2010; Harris et al. 2013). However, other arguments posit that external factors, as opposed to preferences and desires, control or constrain decision making (Robbins and Sharp 2003a). The biophysical and social factors that restrict agency in decision making are commonly known as structural constraints (Larson et al. 2010; Roy Chowdhury et al. 2011). Management decisions are constrained by factors reinforced through time, such as financial resources, social and neighborhood norms, current environmental conditions, and local- or broader-scale policies (Cook et al. 2012). As a result, homeowners, developers, governments, and market forces all exert control over one another to influence land-management decisions (Robbins et al. 2001), which in turn structures metacommunity dynamics (Swan et al. 2011).

Local deterministic models vary under the influence of agency versus structure

The social science concepts of agency and structure in land management decisions connect to metacommunity models that assume the importance of deterministic, or environmental, processes. In particular, species sorting assumes that local environmental conditions, not geographic space, structure metacommunity dynamics (Leibold and Chase 2017c). The effects of social-ecological dynamics on urban biodiversity based on local environmental conditions have been explained by internal motivations and landholder characteristics that constrain decision-making (Cook et al. 2012).

The assumptions of species sorting, which emphasizes local environmental factors, could apply to conditions where individual agency was the dominant driver of management decisions based on preferences and internal motivations (Cubino et al. 2020). Here, an individual landholder would make decisions based on their attitudes, beliefs, or emotions (Harris et al. 2013). Individualized experiences with the landscape would then influence one's role tending to their local environment, such as planting wildlife-friendly gardens (Musacchio 2013). Under the model of emphasizing local environmental features, individual management decisions based primarily on the landholder's internal motivations would be decoupled from spatial processes of social norms or broader constraining biophysical factors. For example, management decisions would not be influenced by widespread customs or neighborhood-level effects such as development patterns and mimicry that control spatially structured landscaping choices (Minor et al. 2016). As a result, local decisions that result in extreme environmental heterogeneity would structure metacommunities without the influence of spatial factors.

People and entities are often faced with multi-scalar constraints that prevent them from freely realizing their values and ideals (Roy Chowdhury and Turner 2006; Wheeler et al. 2020). For example, socioeconomic status and life stage can constrain land management decisions (e.g., Avolio et al. 2018). Limited resources—such as time and money (Avolio et al. 2020)—can restrict land management decisions on public and private land (Goodness 2018; Venter et al. 2020). Additionally, intensively managed parcels are often used as a signal to display social status or moral character, known as the ecology of prestige (Grove et al. 2014). Still, other studies have found that external factors, such as environmental gradients and urban density, better explain the relationships between biodiversity and socioeconomic status (Kuras et al. 2020). These findings leave open mechanistic questions that investigate the social-ecological processes that drive biodiversity patterns along social, environmental, and spatial gradients.

Social norms and formalized regulations link local and regional dynamics

Despite the relative importance of individual characteristics (e.g., sociodemographics) and preferences for landscaping choices, social and environmental factors across broader spatial and temporal scales also constrain people from doing what they want (Larson et al. 2010). Developers often plan and install the landscapes of multiple parcels at once, creating a relatively homogenous area of shared biophysical conditions (Pincetl 2012). These original landscaping decisions create spatially structured environmental patterns, which often dictate subsequent management decisions (Larson et al. 2017). For example, if a developer installs a drought-tolerant yard with native landscaping, then the next landholder may be inclined to keep the current conditions in place rather than replace it (Wheeler et al. 2020). Overall, the initial point of development offers a significant opportunity because the subsequent landscaping choices that support urban biodiversity conservation and human well-being are reinforced by the legacy effects of historic environmental conditions.

In addition to development patterns constraining management decisions, factors such as social norms and codified rules from Homeowner's Associations or municipal ordinances also exert control over local management decisions (Roy Chowdhury et al. 2011; Larson et al. 2020). For example, the maintenance of grassy lawns and palm trees in historic preservation districts in Phoenix, AZ are reinforced through time by the expectations of neighbors and through codified rules regulating the preservation of mesic landscaping (Larson and Brumand 2014). As formal regulations are enforced through sanctions, social norms further support formalized constraints through expectations of social obligations and the conceptualization of land management as a civic responsibility (Robbins 2007). As a result, formal institutions, such as municipal ordinances, are both produced and reinforced through social norms to constrain local land management decisions (Nassauer et al. 2009), such as neighbors enforcing weed height restrictions (Sisser et al. 2016).

The mass effects model can explain the relative influence of structural constraints, which are often spatially clustered. Although the mass effects model emphasizes the importance of local environmental factors (or deterministic processes) in explaining metacommunity dynamics, the spatial structure of habitat patches also plays an important role in structuring metacommunity dynamics (Leibold and Chase 2017a). Social norms and mimicry, as well as clustered social factors (York et al. 2011), can result in homogenization (or similar parcels) within a neighborhood, with increased heterogeneity at larger scales between neighborhoods. As a result of external pressures such as social norms, houses closer together have similar community assemblages due to uniform management decisions creating a socially driven spatial structure of local environmental factors (Locke et al. 2018). In landscapes where constraints such as regulations or widespread norms prevail, we can expect spatial structure to influence community composition along with environmental factors, at least within the social boundaries that restrict management decisions (Hunter and Brown 2012).

Regional social-political forces

Multi-level shifts in authority, which regulate how control over the land is exercised and to what extent individuals can actually determine their local environment, result in a dynamic locus of control over management decisions (Grove et al. 2005). Top-down effects, such as land-use institutions (e.g., zoning), shape development patterns and the spatial configuration of the urban landscape mosaic (York et al. 2014). Discriminatory development policies based on race, such as redlining, unequally stratifies urban greenspace and canopy cover (Locke et al. 2020). However, racial discrimination is an important, but vastly understudied, structural driver of biological change and ecological community composition (Schell et al. 2020). In additional to regional controls, bottom-up effects from individual homeowners can also influence social-ecological dynamics that spatially structure the urban environment. For example, support for impact fees in certain neighborhoods controls development at the urban fringe, resulting in more preserved open space (York et al. 2017). Dispersal to and from source habitat of nearby open space could influence ecological community composition in these neighborhoods, linking to source-sink dynamics under mass effects. We may see biodiversity positively associated with open space proximity, where native and specialist species can occupy a patch despite its local

environmental conditions, such as homogenous lawn cover (Davis et al. 2012).

The marketing of landscaping ideals, such as the industrial lawn throughout the United States, is another broad-scale social factor that homogenizes community composition through the enforcement of mesic landscapes in public and private greenspace (Robbins and Sharp 2003a, b). Market and economic pressures dictate the inventory available at nurseries and other commercial stores, influencing the urban species pool (Aronson et al. 2016), which people disperse from nurseries and other nearby sources into local habitat patches (Avolio et al. 2018). The variety and functional traits of plant species offered at nurseries and selected by individuals change over time, which creates temporal turnover in novel ecological communities (Pincetl et al. 2013).

However, even in heavily managed landscapes such as manicured lawns, the occurrence of spontaneous vegetation is widespread (Wheeler et al. 2017; Lerman et al. 2018). These spontaneous plant communities colonize actively managed patches from other habitat patches throughout the urban landscape mosaic, rupturing human control over the ecological processes and disrupting people's expectations and selection for a neat and kempt aesthetic (Head and Muir 2006). Although experiences with urban biota have been linked to health and well-being, potential conflicts—such as the nexus between ecological functioning and perceived tidiness—also raise the question of how-to best balance management practices that support both human use and biodiversity conservation (Raymond et al. 2019).

Environmental and spatial processes driving metacommunity dynamics

Social factors shape the spatial configuration and environmental composition of patches within the urban landscape mosaic through land management decisions (Pickett and Cadenasso 2008). However, these environmental and spatial factors also iteratively constrain management decisions. In the following section, we further investigate how particular management decisions may alter ecological processes—environmental filtering, biotic interactions, disturbance, stochasticity, and dispersal—that structure the assembly of novel ecological communities in urban ecosystems. Under models that assume the importance of local deterministic processes, such as species sorting and mass effects, we would expect local factors to structure ecological communities through environmental filtering (Sattler et al. 2010). However, mass effects also assumes the importance of spatially structured environmental heterogeneity and source-sink dynamics, which partially explains why species can be present in otherwise poor-quality habitats throughout the urban landscape. Stochastic events, such as disturbance, link to patch dynamics and coexistence under competition (Leibold and Chase 2017a). Finally, neutral theory acts as the null model and instead explains random processes not attributed to traits or environmental conditions that drive patterns of community composition. However, random processes may still be spatially structured throughout the landscape.

Environmental filtering

Deterministic processes structure ecological communities through environmental heterogeneity and resource utilization. In particular, models such as species sorting recognize the importance of local effects driven by environmental heterogeneity (Chase and Leibold 2003). However, biophysical features of the local environment, which shape habitat composition, are influenced by human activities in urban ecosystems. Developers, homeowners, commercial property owners, and other urban land managers often remove and replace biophysical features of the landscape during development (Pincetl 2012). Local management decisions then further shape the biophysical characteristics and resource availability of habitat patches. Anthropologists have used the term "niche construction" to describe the historic and ongoing capacity of people to construct, modify, and select components of their environment (Boivin et al. 2016).

By constructing habitat suitable for people, land management practices also create environmental filters that determine the assembly of urban species pools (Aronson et al. 2016). Over time, land management decisions create environmentally and spatially heterogeneous habitat patches throughout the urban mosaic (Cook et al. 2012). Management decisions related to heterogenous landscaping choices and resource inputs have the potential to alter community composition

across the urban landscape through environmental filtering (Nielsen et al. 2014). For example, management regimes in green spaces (e.g., parks, cemeteries, and golf courses) lead to local variation in the biophysical environment of habitat patches, thereby affecting colonization, persistence, and community composition (Gallo et al. 2017).

Deterministic effects can also structure ecological communities in less actively managed land, such as preserved open space or vacant lots (Swan et al. 2011, 2017; Kattwinkel et al. 2011). For example, Johnson et al. (2018) found that previous land-use decisions influencing local environmental heterogeneity in Baltimore, Maryland, carried forward over 20 years to affect current ecological community composition in vacant lots. Ripplinger et al. (2016) found that plant communities became "weedier", with more spontaneous annual vegetation during the Great Recession as a result of people's homes being foreclosed upon.

Biotic interactions

Management decisions influence local interspecific interactions by shifting biophysical constraints imposed by limiting resources in cities. Urban ecosystems often provide greater availability of resources, such as water and nutrients, from human activities (Faeth et al. 2005). As a result, synanthropic—or human-associated—species gain advantage in urban ecosystems, whereas others suffer due to increased competition and risk exposure (Bradley and Altizer 2007; Shochat et al. 2010a), resulting in shifts in species dominance.

Organisms that succeed in cities by taking advantage of the balance between stress and resource availability have been hypothesized to be "living on credit" (Shochat 2004). As a tradeoff, these individuals may have lower fitness than their non-urban counterparts (Shochat et al. 2010b). Urban bird species frequently have higher survival rates (Evans et al. 2015), but smaller clutch sizes compared to rural birds, likely due to the balance of resources and risk in cities (Sepp et al. 2018). Along with differences in reproductive strategies (Ryder et al. 2010), common urban species are also efficient foragers and may even change foraging behavior depending on habitat type (Shochat et al. 2004; Lerman et al. 2012a). Together, interspecific interactions and environmental heterogeneity represent deterministic mechanisms that structure metacommunities, where niche-related dynamics and environmental conditions of the system over time and space predict community assembly. Both species sorting and mass effects rely heavily on deterministic processes, which further links these models to social factors through resource subsidies provided by people.

Disturbance and stochasticity

Spatial factors, such as dispersal limitations and spatially structured stochastic events (e.g., disturbance), can counteract deterministic mechanisms, such as competition (Chesson 1985). Stochastic events causing an externally imposed mortality factor partially explain the high degree of temporal and spatial turnover in cities (Allen et al. 2019), which are more prone to these stochastic disturbances (Sattler et al. 2010). There is support for both the intermediate disturbance and ecosystem stress hypotheses in urban ecosystems (Lepczyk et al. 2008), which emphasize the effects of disturbance on biodiversity (Connell 1978; Rapport et al. 1985; Menge and Sutherland 1987). The intermediate disturbance hypothesis explains the hump-shaped relationship between human-induced disturbance and diversity, whereby areas of intermediate urban land use support the highest levels of diversity (McDonnell and Pickett 1990; Lepczyk et al. 2008; Andrade et al. 2018). In contrast, the ecosystem stress hypothesis suggests a negative relationship between urban development and diversity (Faeth et al. 2011).

Disturbance also influences competition and colonization tradeoffs (Leibold and Chase 2017b). For example, under the ecosystem stress hypothesis, community assemblages will converge around species with high population growth rates that disperse well but are weaker local competitors. Frequent disturbance prevents the persistence of superior competitors and instead favors better disperses that can occupy the patch post-disturbance (Schwartz et al. 2006), which aligns with the colonization-competition tradeoffs in the patch dynamics model. In particular, patch dynamics considers how disturbances allow for species to coexist because both superior competitors and colonizers are prevented from excluding one another (Leibold and Chase 2017a).

Dispersal

The spatial configuration of the landscape mosaic, availability of suitable habitat patches to colonize, and functional traits of an organism can all affect dispersal (Starrfelt and Kokko 2012). In turn, dispersal ability mediates the role of environmental and spatial heterogeneity on metacommunity structure (Padial et al. 2014; Jacobson and Peres-Neto 2010). For example, inferior competitors persist throughout the landscape as a result of dispersal under the model of mass effects. When dispersal is an important factor driving metacommunity dynamics, competition becomes less critical as inferior competitors with high dispersal rates swamp out locally superior competitors (Leibold and Chase 2017a). Although dispersal is unimpeded for some urban adapted species by human-based barriers such as roads (Fey et al. 2015), habitat fragmentation due to roads and fences can also severely limit dispersal (Shepard et al. 2008).

Urbanization limits dispersal for certain groups of organisms, but human activity can also generate unlimited dispersal as people distribute species throughout the landscape (La Sorte et al. 2007). Although human-mediated dispersal can occur across many taxa, it is most applicable to plants owing to their use in landscaping. Human-mediated dispersal can be considered a social-spatial process, where people introduce an organism to a local habitat patch from another source habitat. The importance of dispersal, as in mass effects, can be particularly relevant in urban ecosystems, where people act as a dispersal agent, moving species throughout the landscape, and changing local environmental conditions that support specific organisms (Swan et al. 2011). However, once a species is introduced into the local species pool, organisms are still subject to deterministic and stochastic processes (Cubino et al. 2019), such as speciation/extinction or limitations in dispersal to other patches.

The functional traits related to natural dispersal (such as wing length; Piano et al. 2017), are not necessarily the same species traits that support human-mediated dispersal (Mack and Lonsdale 2001). Instead, human-mediated dispersal is largely driven by traits desirable to people, such as being relatively low maintenance or aesthetically pleasing (Cubino et al. 2019). However, other human-mediated dispersal may be unintentional, such as the movement of insects in untreated firewood (Jacobi et al. 2011). Species traits can also influence resource dynamics when people make management decisions to support specific taxa in local habitat patches, such as putting out food for hummingbirds. As a result, a common and widespread species may have been purposefully attracted and curated as a reflection of its popularity rather than its ability to disperse or compete (Avolio et al. 2015). Thus, human-mediated dispersal directly connects social and spatial factors with biodiversity in urban ecosystems.

Applying the framework

Testing the importance of social, environmental, and spatial factors

The expected importance of social, environmental, and spatial factors in our conceptual model can be tested with a methodology put forward by Chase et al. (2005) using regression techniques (Swan et al. 2011). Using this methodology, community similarity (e.g., β-diversity) is used as the dependent variable to compare how species composition changes with environmental and spatial distance (e.g., heterogeneity or dissimilarity) between patches (Fig. 2). These techniques are also commonly paired with variation partitioning on a community matrix (a table of species occurrence or abundance across sites) to abstract the spatial and environmental effects on biodiversity (Borcard et al. 1992; Legendre 2008) and distinguish between deterministic versus stochastic processes (Smith and Lundholm 2010). When local, deterministic processes, or environmental heterogeneity, structure communities, we can expect a positive relationship between β-diversity and environmental dissimilarity between patches, irrespective of spatial distance (Fig. 2a, b). However, if spatial effects are important due to stochastic processes or dispersal limitation, then spatial distance between patches will likely have a strong, positive relationship with community dissimilarity (Fig. 2b–d).

In addition to testing the relationship between spatial distance and environmental dissimilarity with β-diversity, our conceptual model also encompasses urban ecosystems by integrating the concept of *social factors*. To empirically test social factors within a metacommunity framework, multivariate social

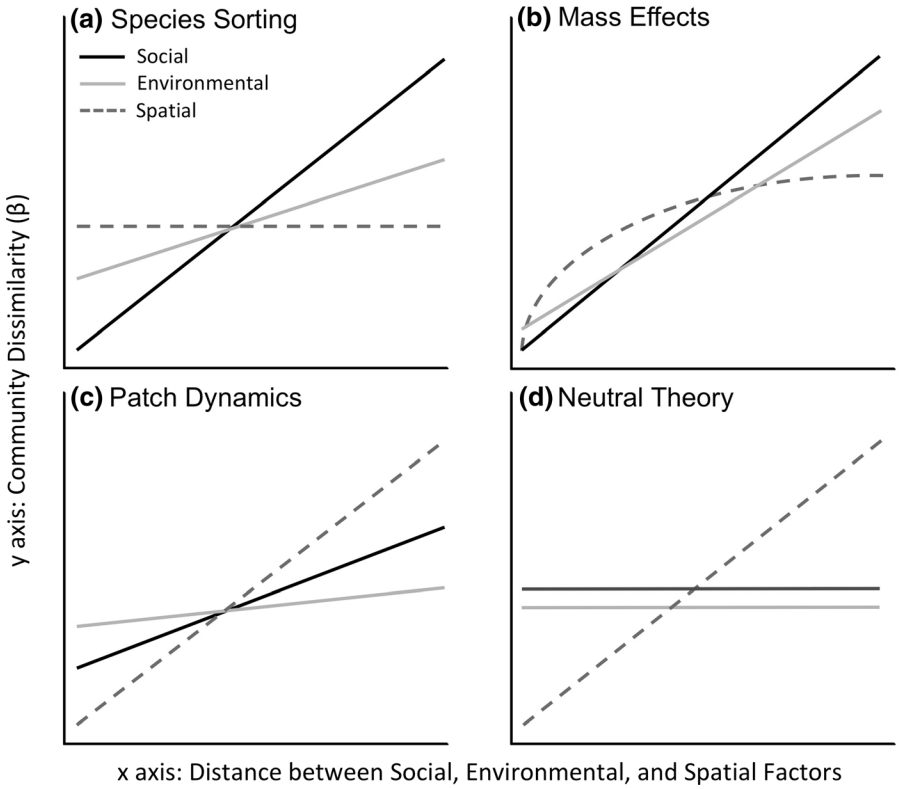

Fig. 2 Predictions of how urban biodiversity (measured as β-diversity or community dissimilarity) will vary between sites that differ in social, environmental, and spatial factors under **a** species sorting, **b** mass effects, **c** patch dynamics, and **d** neutral theory metacommunity models. Each metacommunity model places assumptions on the relative influence of environmental and spatial factors. We include predictions based on social factors from our conceptual framework. The x-axis represents the variation (or pairwise distance) in social, spatial, and environmental factors between patches. The y-axis represents the dissimilarity in the species composition between patches (β-diversity). Modified from Leibold and Chase (2017c)

distances (or dissimilarities) can be calculated as the magnitude of differences between multiple social variables in the same way we evaluate environmental or spatial distance. For example, a low-income neighborhood would be socioeconomically distinct from a high-income neighborhood, so we would expect to see a difference in ecological community composition between these neighborhoods if local socioeconomic factors were an important in structuring ecological communities for the system (Grove et al. 2006; Leong et al. 2018). Overall, our framework, which includes social factors, better encompasses the dynamics of urban ecosystems and can be applied to more effectively predict ecological communities because it considers people as an active component of the ecosystem.

Summarizing social, environmental, and spatial factors

Based on the extant social-ecological literature in light of the metacommunity perspective, we predict that all four metacommunity models have utility in urban ecosystems. Under the species sorting model, we expect local social and environmental factors, despite spatial configuration, to influence metacommunity structure (Fig. 2a). In patches with a large degree of human investment and decision making based on preferences, we expect that social factors will be the most strongly related to biodiversity. However, in unmanaged patches (such as preserved open space or vacant lots), local environmental factors driving deterministic processes may be more important than social factors. In support of the mass effects model, urban ecological assemblages are primarily related to

a combination of social and environmental factors (Lerman and Warren 2011; Lerman et al. 2012b, 2018; Cook et al. 2012; Belaire et al. 2014; Warren et al. 2019), with the extent of available habitat often being the delimiting factor that determines urban biodiversity (Beninde et al. 2015).

Environmental factors are further reinforced by the social norms or formal regulations (informal and formal institutions) that spatially structure management decisions that influence biodiversity (Nassauer et al. 2009; Minor et al. 2016; Sisser et al. 2016; Goddard et al. 2017; Gallo et al. 2017; Locke et al. 2018). In contrast to deterministic models, patch dynamics emphasizes the importance of spatial configuration. Here, social factors would share variation with spatial factors because urban landscapes are often structured along social boundaries such as neighborhoods and municipalities (Fig. 2c). The patch dynamics model also uniquely explains the high spatial and temporal turnover in cities through processes such as ecological disturbance (Lepczyk et al. 2008; Ripplinger et al. 2016; Grimm et al. 2017). Lastly, neutral theory (Fig. 2d) captures the stochasticity characterizing novel communities in urban landscapes (Sattler et al. 2010), which highlights the key roles of dispersal limitation and evolution in urban landscapes (Rosindell et al. 2011; Alberti et al. 2020).

Conclusion

Land use and land management decisions influence the assembly of ecological communities and the resulting biodiversity in cities. However, there is a lack of consensus on the processes that structure the assembly of novel ecological communities, or how to incorporate human dimensions into our understanding of community ecology across scales. The field of landscape ecology is well-positioned to connect social-ecological dynamics in cities by linking the multi-scalar concepts of the metacommunity perspective and social factors at various levels that determine land management decisions (Wu and Hobbs 2007). Here we link the concepts of spatial and environmental heterogeneity with social (human) factors to explain the processes by which novel ecological communities assemble in urban ecosystems though land management decisions. Overall, our conceptual model contributes to current theory of urban ecology and, more specifically, how human–environment interactions mediate metacommunity structure and thus biodiversity in cities. We suggest future research directions test our multi-scalar model with data, including metacommunities from different taxonomic and functional groups across diverse metropolitan areas. Continued work to increase the interdisciplinary understanding of complex interactions between people and biodiversity in cities can further improve efforts to better predict and manage urban and other ecosystems driven by social-ecological dynamics.

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