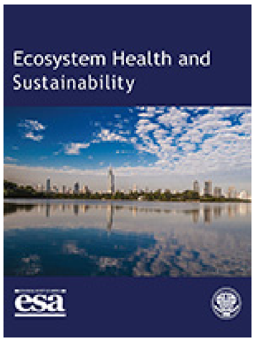

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Evolution and future of urban ecological science: ecology *in*, *of*, and *for* the city

Steward T. A. Pickett,[1,6] Mary L. Cadenasso,[2] Daniel L. Childers,[3] Mark J. McDonnell,[4] and Weiqi Zhou[5]

[1]Cary Institute of Ecosystem Studies, Millbrook, New York 12545 USA
[2]Department of Plant Sciences, University of California, Davis, 1 Shields Avenue, Davis, California 95616 USA
[3]School of Sustainability, Arizona State University, Wrigley Hall, PO Box 875402, Tempe, Arizona 85287 USA
[4]Australian Research Centre for Urban Ecology, Royal Botanic Gardens Victoria c/o School of BioSciences, University of Melbourne, Victoria 3010 Australia
[5]Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, 18 Shuangqing Road, Haidian District, Beijing 100085 China

Abstract. The contrast between ecology *in* cities and ecology *of* cities has emphasized the increasing scope of urban ecosystem research. Ecology *in* focuses on terrestrial and aquatic patches within cities, suburbs, and exurbs as analogs of non-urban habitats. Urban fabric outside analog patches is considered to be inhospitable matrix. Ecology *of* the city differs from ecology *in* by treating entire urban mosaics as social–ecological systems. Ecology *of* urban ecosystems incorporates biological, social, and built components. Originally posed as a metaphor to visualize disciplinary evolution, this paper suggests that the contrast has conceptual, empirical, and methodological contents. That is, the contrast constitutes a disciplinary or "local" paradigm shift. The paradigm change between ecology *in* and ecology *of* represents increased complexity, moving from focus on biotic communities to holistic social–ecological systems. A third paradigm, ecology *for* the city, has emerged due to concern for urban sustainability. While ecology *for* includes the knowledge generated by both ecology *in* and ecology *of*, it considers researchers as a part of the system, and acknowledges that they may help envision and advance the social goals of urban sustainability. Using urban heterogeneity as a key urban feature, the three paradigms are shown to contrast in five important ways: disciplinary focus, the relevant theory of spatial heterogeneity, the technology for representing spatial structure, the resulting classification of urban mosaics, and the nature of application to sustainability. Ecology *for* the city encourages ecologists to engage with other specialists and urban dwellers to shape a more sustainable urban future.

Key words: *city; complexity; framework; interdisciplinary; paradigm; social–ecological system; spatial heterogeneity; Special Feature: An Ecology in, of, and for the City; sustainability; urban ecology.*

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Introduction

Modern urban ecological science is a relatively new discipline (Collins et al. 2000, McDonnell 2011, Wu 2014). Although there are venerable and important precedents, ecology as a whole seemed to awaken to urban areas as a legitimate habitat for study in the late 1990s (Grimm et al. 2000). In part, this shift was driven by an increasing understanding that humans and their actions were components of virtually all ecosystems, regardless of the distance of those places from dense human settlements (McDonnell and Pickett 1993). The shift was also based on an understanding of urbanization as one of four main global transformations of the biosphere (Vitousek 1997). Furthermore, the shift followed the transition of the Earth's human population from predominantly rural to majority urban in the first decade of the 21st century (United Nations 2012). Finally, two cultural shifts facilitated the growth and evolution of urban ecological science: the increasing reach and rates of economic and cultural globalization (O'Brien 2012) and the growing concern of sustainability in cities and towns (Birch and Wachter 2008).

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[6] **E-mail:** picketts@caryinstitute.org

The change in urban ecological science from a marginal interest to a widely pursued and theoretically motivated ecological field can be framed as a shift or expansion in paradigms. This paper defines paradigm for the purposes of analyzing the evolution of urban ecology, and lays out the three main paradigms that expose the change in the science since the middle of the 20th century. Those paradigms are labeled ecology *in*, ecology *of*, and ecology *for* the city, where city is shorthand for any urban or urban-influenced settlement. These three paradigms can be compared along three axes: chronology, model approach, and complexity. That is, they differ in the period during which each matured, the growth from biological through transdisciplinary models, and the nature of temporal and spatial complexity they highlight. The specific differences among the *in, of,* and *for* paradigms are characterized in terms of (1) their disciplinary foci, (2) the theory and research approaches employed, (3) the modeling techniques applied, (4) the nature of classifications within urban regions that they suggest, and finally (5) how they can be applied to the concerns of sustainability. We identify important research frontiers within each of the three paradigms.

What is a Paradigm in Urban Ecology?

The concept of paradigm in science is an extraordinarily broad and complex one (Kuhn 1970). A paradigm can apply to a large inclusive area of science or to a particular specialty within a discipline (Simberloff 2014). In other words, a paradigm shift within a discipline can constitute a refinement to the concept beyond the founding definition (Devlin and Bokulich 2015). In all cases, a paradigm has four components: (1) a collection of often unrecognized or unexamined fundamental assumptions that operate in the background of everyday science; (2) an array of modeling and representation strategies; (3) a way in which different research processes, including experimentation, comparison, observation, and modeling are deployed and related to each other; and (4) large conceptual and theoretical frameworks supporting and summarizing research in the field (McDonnell et al. 1993, Pickett et al. 2007). The term "paradigm" can refer broadly or "globally" to all these four aspects of a science, or it can focus more narrowly or "locally" on the exemplars employed by a science (Devlin and Bokulich 2015). Articulating these two scales of paradigms opens the way for examining more local paradigms within a discipline (Pickett et al. 2007) and acknowledges that paradigms might expand within a science. That is, different local paradigms can coexist and complement each other. In this paper, we focus on the "local" paradigms of urban ecological science to understand the evolution of the discipline.

Urban ecology can be said to have three paradigms (Cadenasso and Pickett 2013, Childers et al. 2014). One is the ecology *in* the city; a second is the ecology *of* the city (Pickett et al. 1997*a*, Grimm et al. 2000), and the third is the ecology *for* the city (Childers et al. 2015). We describe these in more detail below, developing key contrasts along the way (Fig. 1).

Ecology in the city

In this paradigm, biologically oriented ecologists take their toolkit into cities, suburbs, and towns to study habitat or ecosystem types that are familiar to them but which are embedded in an urban or urbanizing matrix. This approach was pioneered in Europe and Asia, with notable contributions appearing after World War II (Numata 1977, Goode 1989, Wang and Lu 1994, Sukopp 2008, McDonnell 2011, Wu 2014). The habitat types chosen for ecological study in cities were often close structural analogs to those outside of cities and included forest patches, parks, cemeteries, meadows, vacant lots, wastelands, streams, and wetlands. The context and drivers affecting those patches could be assumed to be the built environments and human populations outside of the habitat of interest. Descriptive variables in patch context under the ecology *in* cities paradigm might include impervious cover, roads, buildings, human population density, or economic activity. Urban wildlife ecology was also an early and important contributor to understanding the ecology *in* the city (Adams 2005). Research questions focused on such things as biodiversity, community succession, exotic species performance and spread, adaptation of organisms to urban disturbances and stresses, food web structure, constraints on biotic community assembly, and the biological and physical structure of urban waterbodies. Adaptation and adaptedness of urban animals has been an important question and is an expanding research frontier (McDonnell and Hahs 2015).

Comparison of analog urban and suburban patches of a particular type with those beyond the urban fringe brought ecology *in* the city to a regional scale. Such

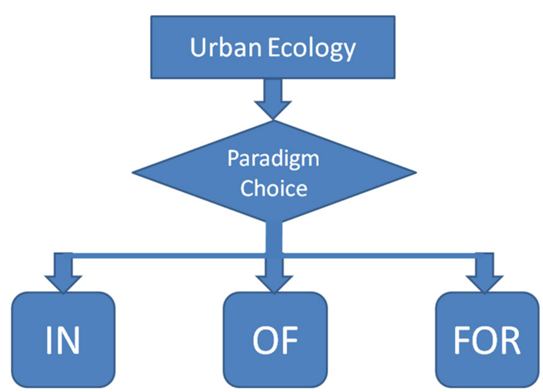

Fig. 1. Urban ecology as a science is represented by three paradigms. The paradigms are "local" and exist within the discipline of urban ecological science.

comparisons were often made through transect studies, and the comparisons were achieved by constructing environmental contrasts as conceptual gradients. This approach is the now familiar urban–rural gradient strategy (McDonnell and Hahs 2008). Ecological research *in* the city has been motivated by desires to enhance urban planning, such as providing access by residents to nature (Nilon 2011, Goode 2014) and improving human health through mitigation of pollution (Baro et al. 2015). Traditionally, these goals have been satisfied through focus on specific green and blue spaces within the urban fabric, with examples ranging as widely as greenways, parks, and streams, but now boosted by such infrastructure as green walls and green roofs (Birch and Wachter 2008). In general, the results of research on ecology *in* the city have informed many activities including biotic conservation, urban planning, park design and management, and urban gardening.

The ecology *in* the city paradigm has been widely applied. We provide three examples. The first shows how biodiversity has changed in an urban park in Boston (Drayton and Primack 1996). Between 1894 and 1993, a total of 155 plant species were lost from Middlesex Fells, a 400-ha wooded park. There were 422 plant species present in 1894. Sixty-four new species, mostly exotics, had appeared by 1993. While native species accounted for 83% of the species in 1894, they only represented 74% of the flora 100 yr later. Many of the remaining native plant species existed as only one or a few small populations in 1993. Mesic woodland species were disproportionately lost from the Fells. Management to reduce human disturbance in this isolated park was suggested.

A second example is of the abundance of birds in small greenspaces in Baltimore, Maryland (Rega et al. 2015). The role of small patches dominated by vegetation in cities, although appropriate to the study of ecology *in* cities, has been largely neglected. The coverage of vacant lots, small parks, and residential yards within a 200-m radius of bird census points was calculated. The abundance of two native bird species, American robin (*Turdus migratorius*) and northern cardinal (*Cardinalis cardinalis*), and that of two introduced species, house sparrow (*Passer domesticus*) and European starling (*Sturnus vulgaris*), were modeled to determine which land-cover types best explained the distribution and abundance of the species across the city. American robin abundance was positively associated with small parks and negatively associated with vacant land, indicating a requirement for greenspace management. European starlings were negatively associated with small parks, but had the greatest likelihood of occurrence in the "concrete canyons" of the commercial core. This study of ecology *in* the city, again, provides information useful for management.

Because ecology *in* the city has so often been concerned with urban forests, our final example concerns the dynamics and configuration of urban forest patches in Baltimore (Zhou et al. 2011). The patterns of forest cover from 1914 to 2004 in metropolitan Baltimore were analyzed through historic maps and aerial photographs. Imagery and maps were available to assess forest patches in 1914, 1938, 1957, 1971, 1999, and 2004. Surprisingly, the total forest area remained virtually constant over time, but creation and disappearance of specific patches of forest was substantial. While the total forest area was stable, forest patches became increasingly fragmented as the number, size, shape, and spatial distribution of forests within the watershed were altered. Over the 90-yr period, the location of high rates of forest cover change shifted from close to the urban core to more distant suburban locations, which coincides with the spatial shift of new urban development. That is, forest cover tended to be more stable in the core city; however, forest cover changed more in areas where suburban development was still going on. The spatial array of forest patches as significant contributors to the ecology *in* the city are an important topic for sustainability planning and understanding urban amenities.

Ecology *of* the City

A second paradigm, the ecology *of* the city, was identified in the late 1990s (Pickett et al. 1997*a*, Grimm et al. 2000; Fig. 1). Ecology *of* the city moves beyond the analog patches of the ecology *in* the city. In doing so, it requires two things. First, it requires rigorous characterization of patches and habitats that are not dominated by non-human organisms. Second, it requires sophisticated understanding of how the social and socially determined human processes affect and suffuse even the analog patches ecologists had traditionally been studying. These additions to the ecology *in* the city approach necessitated interaction with a variety of social sciences, geography, economics, and urban design, for example. Further explorations with engineers, complexity scientists, and science and technology studies broaden the scope of urban ecology (McPhearson et al. 2016). Under the ecology *of* the city approach, there is no "outside" of analog biological patches as there had been under the ecology *in* the city. All patches, their interactions, changes in individual patches, and the entire mosaic need to be considered in this broadly holistic paradigm.

To facilitate the study of the ecology *of* the city, a number of integrative frameworks have been proposed (Machlis et al. 1997, Pickett et al. 1997*b*, Redman et al. 2004, Collins et al. 2011, Pickett and Zhou 2015). Although they differ in detail, they all agree that the interactions between social and biogeophysical structures and processes are pervasive, reciprocal, and intertwined (McPhearson et al. 2016). Feedbacks between them are common, and the causes of urban structure and change reside at that interface. The complexity of social systems has required ecologists to think differently than traditional ecologists (McIntyre et al. 2000). For example, the relatively simple characterizations of population embodied in the decadal U.S. census have had to be complemented by the characterizations of human institutions, social norms, organizational networks, and power relations (Dow 2000, Ostrom 2012). Adding to this complexity of social organization is the fact that all of these components change over time and have different spatial extents (Machlis et al. 1997, Cadenasso et al. 2006, Grove et al. 2015).

Land-cover change reflects the complexity addressed by the ecology *of* cities paradigm. One outcome of the coupled social–biophysical nature of urban systems has been the development of a new conceptualization of urban heterogeneity codified in a classification scheme that characterizes urban land cover. The classification system, called HERCULES (Cadenasso et al. 2007, Zhou et al. 2014), identifies and classifies all patches within an urban system based on the type and the proportion of vegetation, of buildings and other built structures, and of ground surface cover. Thus, it accommodates features that have both biological and social origins without conflating land use and land cover. In many applications, this approach has proven more powerful than standard urban land-use/land-cover schemes (Cadenasso et al. 2007, Zhou et al. 2008).

Some examples of the ecology *of* the city approach existed as early as the 1970s. The multidisciplinary exploration by Stearns and Montag (1974) stands out. Social and biological researchers, spurred perhaps by the environmental concerns that were becoming widespread starting in the 1970s (e.g., the U.S. Clean Water Act and the establishment of Earth Day), called the attention of scholars to the needs and opportunities for integrated urban research. Meanwhile, the Australian ecologist Stephen Boyden brought together an interdisciplinary team to study Hong Kong (Boyden et al. 1981) with four stated project goals. The Hong Kong urban study sought to understand (1) the relationships between environment and people, especially as they affected health and well-being; (2) Hong Kong as an ecosystem, especially the flow of materials and energy; (3) the urban ecosystem as a whole as it relates to health and well-being; and (4) cultural adaptation to adverse environmental conditions (Boyden 1976). Recognizing the skepticism of many ecologists and the novelty of their questions, Boyden et al. (1981) constructed an integrated conceptual framework and a novel approach that focused on, in their terms, energy flow, air pollution and artificial heat production, nutrient flow, water resources and water pollution, mortality patterns, fertility patterns, noise levels and their effects, home medicine, and the relationship between environment and child growth.

While the holistic goal of the Hong Kong human ecology program and its component foci may sound very familiar to contemporary ecology *of* the city researchers, there are some important differences. Perhaps most significant is the difference between the ecosystem ecology of the 1960s and 1970s compared to that of today. In that pioneering era of ecosystem ecology, a more aggregated approach to whole system dynamics held sway, as exemplified by the International Biological Program (Coleman 2010). In contrast, the holism of contemporary ecosystem science is more hierarchical, allowing the disaggregation of high-level processes into their component structures and processes (Allen and Starr 1982). Furthermore, contemporary ecosystem science deals much more explicitly with the role of species identity and biodiversity, the role of spatial heterogeneity, and the role of disturbance and temporal complexity than the predominant ecosystem science in the 1960s and 1970s (Pickett and White 1985, Jones and Lawton 1995, Lovett et al. 2005). Contemporary ecosystem ecology also focuses more on processes rather than on stable outcomes of material and energy transformation processes. Importantly, contemporary social sciences exhibit a parallel increase in interest in spatial processes of resource control and allocation, power relationships, and institutional deployment (Gottdiener 1985). The parallels between contemporary social sciences and contemporary ecosystem science facilitate the social–ecological integration of the ecology of the city. Incorporating political processes in the understanding of urban functioning also enlivens the ecology of the city. Political processes including discourse about environmental benefits and hazards, the role of social power, or the influence of visionary political leaders can play important roles in applying the ecology of the city (Goode 2014, Grove et al. 2015).

The foresight, creativity, rigor, and inclusiveness of the ecology *of* the city approach embodied in the Hong Kong human ecology project are impressive. While it should arguably have been transformative of ecology in the urban realm, it was rarely used as a foundation for comparison by ecologists at the time. The gap may have been due to the long-standing biases of many ecologists against studying settled systems (e.g., Kingsland 2005), along with their blindness to the richness and reach of human agency as portrayed, for example, in the human ecosystem framework of Machlis et al. (1997).

Regional and international comparisons among cities are frequently called for (Hahs et al. 2009, McDonnell and Hahs 2013). An ecology *of* cities approach can help achieve this goal. Because the most inclusive comparisons of urban areas will span cultures, economies, political systems, and socio-demographic differences (McHale et al. 2015), it will be important to include these dimensions in framing such comparisons. For example, a global comparison of urban biodiversity (Aronson et al. 2014) notes that loss in species density was best explained by anthropogenic features such as land cover and city age. These features of urban areas suggest an inclusive, ecology *of* cities framing to promote the comparisons.

Relationship of ecology *in* with ecology *of*

The ecology *of* the city label was introduced to alert ecological scientists to the value of thinking about cities, suburbs, and exurbs as ecosystems. Clearly indicating the existence of bioecological processes and

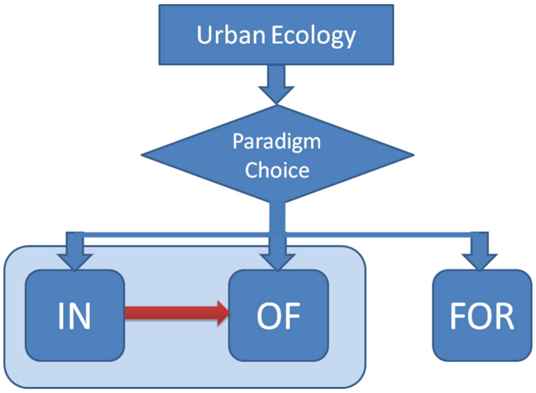

Fig. 2. The paradigm of ecology *of* the city has emerged from and complements the ecology *in* the city paradigm.

structures, both obvious and inconspicuous, in urban systems was a goal of the distinction between ecology *of* versus the ecology *in*. Furthermore, the contemporary, process-oriented view of ecosystem ecology was explicitly adopted by the ecology *of* the city perspective (Grimm et al. 2000). Bringing together the understanding of spatial and temporal complexity introduced by landscape ecology (Turner et al. 2007) and the understanding of episodic events codified by the study of natural disturbance (Dale et al. 1998) were important advances from the 1980s that were incorporated into ecology *of* the city.

Although the two paradigms of ecology *in* and ecology *of* the city have been presented as contrasting sets, in fact research and practice pursued under the ecology *of* the city paradigm includes ecology *in* (Fig. 2). Hence, the evolution of the field has been *via* an expansion of paradigm, not by a revolutionary overthrow as Kuhn's (1970) global perspective would expect. Much important research on analog patches, biotic communities, and the processes locally driven by microbes, plants, and animals is still required. Focusing on the evident open space components of cities, suburbs, towns, and exurbs continues to yield novel insights and information that are useful to planners, designers, managers, and citizens (Pickett et al. 2013a). The ecology *of* the city paradigm recognizes the value of such spatially focused research and practice, but goes beyond that to put it in an integrated context (Childers et al. 2015). Furthermore, it recognizes focal patches and their complex matrix as interacting components of the integrated urban ecosystem.

Ecology *for* the city

This paradigm evolved from the first two, but in a context of linking ecological science with civic processes (Fig. 3; Krasny and Tidball 2012, Cadenasso and Pickett 2013). Concerns with human well-being, urban livability, and the biological richness of cities have been motivations of urban ecological science since its inception. For some, these motivations have been paramount. For others, the pure joy of understanding an underinvestigated ecosystem has been the motivation. Both are sound reasons to pursue research about city, town, suburban, and exurban systems. The paradigm of ecology *for* the city recognizes the legitimacy of both pure and use-inspired research (Grove et al. 2015). But it also acknowledges that for ecological research to be of greatest use, the integration achieved by ecology *of* the city must extend well beyond scholarly and research disciplines (Childers et al. 2014, 2015).

Ecology *for* the city as a paradigm adopts a philosophy of stewardship, or "knowledge to action" (Childers et al. 2014). That is, it takes the urban ecosystem as a social–ecological system in which scientific knowledge is integrated with decision-making dialogs and processes of all sorts (Chapin et al. 2011). Notably, one root of the term "steward" describes a member of a household or other institution who is responsible for the well-being and functioning of that household. It adds an ethical component to scientific understanding (Rozzi et al. 2014). Stewardship identifies some research and synthesis activities as valuable because of their utility to managing, restoring, or sustaining (Musacchio 2008) urban ecosystems.

Ecology *for* the city may also be seen as an extension of the land ethic of Aldo Leopold (Meine 1988) to the urban realm (Grove et al. 2015). To accomplish this ethical openness, ecology *for* the city includes dialog with citizens, groups, agencies, technical staff, and decision-makers to identify research goals, analyze existing data, and thus jointly and collaboratively produce useful and relevant knowledge. However, stewardship also highlights the need to improve basic understanding of urban ecosystems by those same constituencies. Ecology *for* the city emerges out of ecology *in* and ecology *of* the city, but filters those concerns through the explicit needs of sustainability. It does not replace the need for understanding

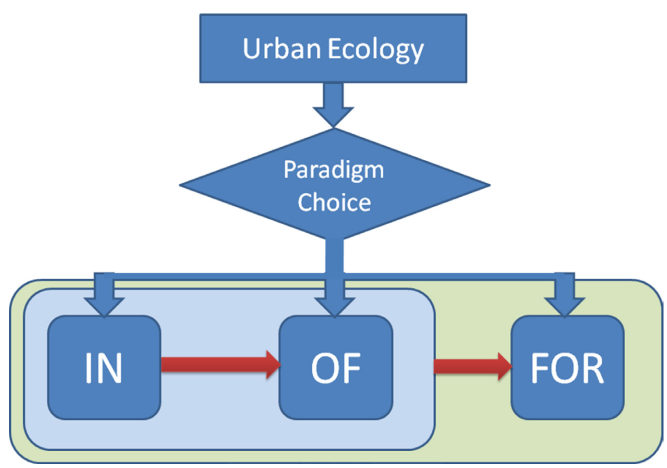

Fig. 3. The ecology *for* the city paradigm employs insights from the other two paradigms, but engages scientists and scientific knowledge in dialog and practice for action toward the sustainable city.

ecology *in* or ecology *of* the city (Fig. 3). Rather, it links those kinds of understanding and knowledge with the normative goals of environmental integrity, social equity, and economic viability in framing the questions and solutions it pursues (Rozzi et al. 2014).

Of course, the fundamental scientific requirement to be true to the data remains paramount. But so is respect for local knowledge, the concerns of citizens possessing different degrees of power and wealth, and modes of communication that are effective in different venues and communities (Pickett et al. 2011, Boone and Fragkias 2012). While ecology *for* the city embeds the research process and at least some cadre of researchers in interaction with urban institutions, it does not shirk its responsibility to the data. Admittedly, what questions are posed jointly by researchers and various social actors and what data are relevant to the dialog can guide the research that is coproduced (McPhearson et al. 2016). Once the investigation has begun, data generated by and the criticism emerging from a diverse, connected scientific community should guide the validity of the conclusions reached. Power, politics, and wealth should not shape the scientific conclusions, even though these contexts may affect the original questions and the way that the scientific knowledge is used.

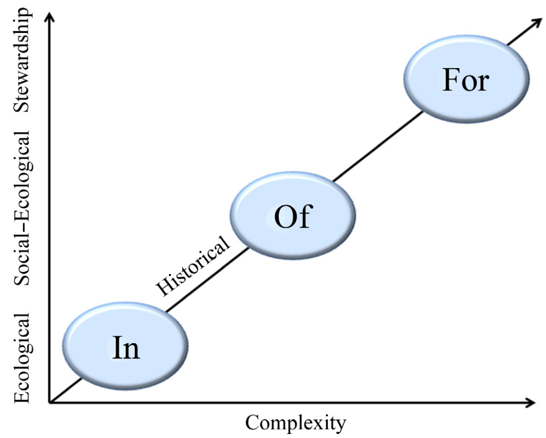

Fig. 4. The three paradigms can be ordered along three continuua: The *z*-axis represents the chronology or history of their consolidation; the *y*-axis represents the inclusiveness of their modeling approaches; and the *x*-axis shows the complexity of the system studied or influenced. The chronological axis represents the mid-20th-century conception of ecology *in* the city near the origin, the introduction of the ecology *of* paradigm in the 1970s with its consolidation in the 1990s, and the emergence of the ecology *for* the city paradigm in the 1990s. The model approach moves from a predominantly biotic community focus near the origin, through a social–ecological approach, and culminates in a stewardship approach. Complexity is relatively low near the origin with the focus on primarily a biological level of organization, through an ecosystem approach with the addition of the physical environment and interactions between the biota and the physical environment, and ends with a complex, spatially differentiated mosaic of social–biophysical interactions that have ethical implications. The three paradigms trace out an idealized trajectory in this conceptual space.

Characterizing the Paradigmatic Contrasts

The three paradigms embody contrasting concerns and approaches. We orient these contrasts along three main dimensions or continua that we present as simplifying ideals rather than detailed trajectories (Fig. 4). These continua summarize the key relationships among the paradigms *in, of,* and *for.*

Chronological continuum of research

From the perspective of connection to mainstream ecology, the three paradigms arose and were consolidated along a historical sequence (Fig. 4). Ecology *in* the city was active and well represented as early as the 1950s in Asia and Europe (Numata 1977, Sukopp and Weiler 1988, Wang and Lu 1994). Although the ecology *of* the city was very effectively introduced in the Hong Kong study conducted in the 1970s, and was clearly framed in the concepts and concerns presented by Stearns and Montag (1974), this paradigm only became integrated into mainstream ecology in the 1990s (Collins et al. 2000). Ecology *for* the city is the most recently promulgated paradigm (Childers et al. 2015). Of course, individual researchers and even entire projects, as in the case of the Hong Kong program, have been motivated by improving the quality of life and environment in and around cities for a long time (Goode 1989, Platt et al. 1994). An ecology *for* cities reflects a maturation of the field as a whole from a narrow disciplinary and spatially focused research perspective, to a multidisciplinary and spatially extensive research perspective, and then to a perspective that engages scholarly disciplines and civic society in a reciprocal interaction aimed at envisioning and shaping the sustainable city.

A continuum of system models

The ecology *in* cities paradigm employs a biological and bio-ecological approach. It focuses on conspicuously vegetated areas, surface waters, or non-human organisms within the urban fabric. Ecology *of* the city in contrast adopts a holistic and social–ecological systems approach. We note that the use of the entire word "social" implies equity between the social and the biophysical realms of urban settlements and does not subordinate social as a modifier of ecology, as might the phrase "socio-ecological." We believe that this more equitable phrasing is significant in representing the evolution of thinking and practice along the continuum (Fig. 4). Notably, the social includes technology, economy, and power relations, for example (McPhearson et al. 2016). Finally, the newer paradigm of ecology *for* the city involves researchers in shared stewardship relationships. Stewardship was defined as an accepting of responsibility for the biosphere as a household. Stewardship has found a formal home in ecological science as an aspect of the Earth Stewardship Initiative of the Ecological Society of America (Chapin et al. 2011, Sayre et al. 2013). The model types on this continuum thus move from bio-ecological, through social–ecological systems, to Earth stewardship (Fig. 4).

A continuum of complexity

A continuum of complexity exists with an increase in the types of interactions and with more opportunities for the involvement of human motivations and actions. The simple end of the continuum focuses on biotic patches and takes human artifacts and decision-making as simplified contextual conditions. Moving to ecology *of* the city adds the complexity of human institutions, decisions, and designed structures as dynamic and sometimes nonlinear parts of the system. Finally, at the most complex end of the continuum, stewardship adds the responsibility of science to the ethical realm (Rozzi et al. 2014). Sustainability thinking embodies normative values and shared goal setting. Sustainability also extends the focus of ecology *for* the city into the future, given its ethical requirement established by the "Brundtland Commission" (World Commission on Environment and Development 1987) not to disadvantage future generations. The consolidation of sustainability thinking since the era of the Brundtland Commission suggests that we should consider ecological research to be embedded in society and social processes (Walker et al. 2004, Platt 2006). The urban ecologist has thus moved from an observer of a part of the system, to a seeker of understanding of the entire ecosystem in its spatial breadth, to a responsible and self-critical participant in the system and its future (Felson 2013).

Implications of the Paradigms

Paradigms in science are a rich source of insight. We employ the Kuhnian local approach to paradigms (Devlin and Bokulich 2015) as ideal poles of contrast in order to delimit the conceptual space in which urban ecological research has developed. The paradigms have several specific implications. Their initial use was to suggest the novelty of the fledgling urban Long-Term Ecological Research (LTER) programs funded by the US National Science Foundation (NSF) in 1997 in Baltimore and Phoenix. The phrase "ecology *of* the city" was used to suggest the new things that these two urban LTER programs had to add to ecological theories and approaches to understand cities as spatially complex and extensive social–ecological systems. In part, this was required to overcome the skepticism about the value of research in urban areas that was common among American ecologists at the time. In spite of the arguments of Stearns and Montag (1974), the example of Boyden et al. (1981), and the explorations of the urban–rural gradient in the New York metropolitan area (McDonnell et al. 1997, McDonnell and Hahs 2008, Pouyat et al. 2009), many ecological colleagues working outside of urban areas doubted the feasibility or significance of urban ecology to the science as a whole. The founding proposals for the NSF-funded urban LTER programs sought to link with mainstream ecological ideas in order to overcome such skepticism. In the case of Baltimore, an ecology *of* the cities paradigm was operationalized by testing the applicability of the watershed approach to a metropolitan area. The watershed concept had proven to be a powerful approach in non-urban systems (Groffman et al. 2003), and the scope of watersheds was easily adapted to inclusive social–ecological research. Since that time, the ecology *of* the city has become a standard way to describe the range of urban ecological research (Gaston 2010, Adler and Tanner 2013, Tanner et al. 2014, Douglas and James 2015). For example, when the NSF and the USDA Forest Service jointly funded exploratory Urban Long-Term Research Areas (ULTRA-Ex), an ecology *of* the city approach was clear in the request for proposals.

The paradigmatic contrast is also methodological in its implications. For example, while ecology *in* the city tends to focus on isolated patch types, ecology *of* the city usually includes broader spatial scales, many patch types, and large distances. Another methodological implication of the ecology *of* cities paradigm is the need for greater sophistication in how the human dimensions of urban ecosystems are expressed (Dow 2000). For example, an early exploration of human causality along the urban–rural transect in the New York metropolitan region (McDonnell and Hahs 2008, Pouyat et al. 2010) explored human population density and road density in sample blocks surrounding study forests from the Bronx in New York City to exurban western Connecticut (Medley et al. 1995). The ecology *of* cities perspective might also examine hypotheses about such things as the economics of subdivision-type development, lifestyle choices, and investment in green and gray infrastructures, among others. For example, the ecology of prestige is a hypothesis that emerged from an ecology *of* cities. It seeks to understand whether and how neighborhood social cohesion and social group identity affect environmental structures and functions (Grove et al. 2014).

The contrast in paradigms has also been useful as a metaphor for communicating research knowledge to the public and decision-makers. It is a useful rhetorical opening for explaining that urban ecology does not just study parks or nature reserves, but rather examines the entirety of the urban fabric. It also helps explain that social structures and interactions along with biological and physical phenomena are crucial parts of models describing urban structure and change. For example, understanding "natural" disasters in urban systems as combinations of biophysical forces, built infrastructure, and human responses is a feature of the ecology *of* the city (Pickett and Cadenasso 2008).

Next, we summarize the contrasts and application of the three paradigms along five dimensions, chosen to represent the spatial heterogeneity as a fundamental component of urban systems. Any paradigm can be described in terms of what discipline(s) it encompasses, what theory applies to the topic area, what kinds of models are appropriate to the topic, what kinds of typologies or classifications support comparison and generalization in the area, and how the paradigm relates to stated social goals (Pickett et al. 2007). The dimensions as they apply to the three paradigms of urban ecology can be summarized as (1) disciplinary focus; (2) relevant theory of heterogeneity; (3) modeling strategies for representing and mapping heterogeneity; (4) the nature of the classifications that result from those theories and strategies; and (5) application of the paradigm to sustainability (W. Zhou et al., *unpublished manuscript*). Although some supporting details have been mentioned earlier in the paper, our purpose here is to extend and synthesize the insights into the *in*, *of*, and *for* urban ecological paradigms.

Disciplinary focus

Ecology *in* the city focuses on the disciplines of biology and ecology. Wildlife inventories (Adams 2005) and botanical surveys (Sukopp 2008), successional studies in woodlands and parks (Bornkamm 2007), composition and functioning of wetlands (Ehrenfeld 2004) and forest patches (McDonnell and Hahs 2008) are examples of the biotic focus of ecology *in* the city. The study of pest or disease organisms harbored in those patches is also relevant.

In contrast, ecology *of* the city has a more integrated disciplinary focus, a social–ecological systems approach. It therefore examines organisms that are not confined to vegetated ("green") or aquatic ("blue") patches. In fact, ecology *of* the city extends analysis to built and infrastructural patches along with the obviously biotically dominated patches. For example, the ecology *of* the city addresses streams not only as free-flowing, aboveground features, but as a network that incorporates downspouts, gutters, culverts, storm drains, and stormwater drainage networks. A further example is addressing lawns having different degrees of management, as well as vegetable gardens, vacant lots, and waste places. Holism in the ecology *of* cities paradigm includes the interactions between social and biophysical processes in congruent or overlapping locations. For example, the discovery of an unexpected negative relationship of tree canopy with violent crime in Baltimore neighborhoods reflects the integration across disciplines (Troy et al. 2012). Notably, the practical work of restoration, boosting or integrating the effects of biological amenities in cities, has operated in this multidisciplinary space for decades (Goode 2014). Our aim here is to make this integration an explicit part of the theory of urban ecological science.

Ecology *for* the city is *trans*disciplinary in the sense that it involves urban scientists representing many research disciplines, along with local communities, associations, agencies, designers, and decision-makers in the planning, design, and use of jointly produced research and solutions (Childers et al. 2015). This is where urban ecology moves into "knowledge to action" while at the same time a wide range of decision-makers in cities become more informed about how their urban ecosystem functions. This knowledge-to-action stewardship often involves participatory approaches to urban ecological research, design, and management. In effect, ecology *for* cities is about integrating knowledge of the urban ecosystem among all of the human players in that system. Because the ecology *for* paradigm relies on the nature of information produced by the ecology *in* and ecology *of* paradigms, we contrast those two as sources supporting the ecology *for* the city paradigm. As we noted above, the space of action has been explored by urban designers, restorationists, and community activists for many years (Burch 2003, Krasny and Tidball 2012, Goode 2014). We wish to highlight the theoretical power of this integration with social and civic processes.

Theory of heterogeneity

Heterogeneity is one of the most conspicuous features of urban systems (Lynch 1960, Jacobs 1961, Shane 2005). However, the three paradigms deal with heterogeneity in different ways. The ecology *in* the city paradigm in its pure form uses a binary representation of heterogeneity, built versus non-built. Although some applications do parse the built environment to varying degrees (Fischer et al. 2013, Lehmann et al. 2014), the idealization helps to define the conceptual space in which urban ecological science is evolving. Thus, the relevant idealized theory of heterogeneity in the ecology *in* cities paradigm can be called the "patch/matrix" theory. Following such biological precedents as island biogeography theory, the two components in a binary landscape are a hospitable non-built one, comprising patches and corridors, embedded in a hostile or uninhabitable built matrix (Cadenasso et al. 2013). The biotic patches are, as mentioned earlier, often analogs of those that ecologists have traditionally studied outside of urban areas. Admittedly, some of the biologically valuable habitats are novel ones (Bradshaw 1981, Goode 2014). In contrast to the biotically dominated patches, the built component captures everything else. Typically, the "everything else" includes buildings in commercial, industrial, or residential neighborhoods, roads, water supply, and sanitary infrastructure, for example. Often called the "gray" component of cities, the non-biotic patch phase has often been taken as a uniform or aggregated "other" in the ecology *in* cities paradigm. Often missed in this approach are small vegetated components associated with gray infrastructure and buildings, and the intersection of buried infrastructure with the conspicuous biotic component.

A different theory of heterogeneity applies to the ecology *of* the city paradigm as a contrasting conceptual position. The ecology *of* the city paradigm sees urban systems as internally complex and dynamic. Furthermore, it sees all elements of heterogeneity as potentially consequential to social–ecological relationships. In other words, it theorizes urban systems as spatially complex mosaics of patch types. Under this theory, the types (i.e., content), numbers, frequencies, boundaries, changes in, and interactions among patches are all drivers of system structure and function.

A key feature of the complexity of patchiness in the ecology *of* cities paradigm is that the patches themselves may be hybrids of both biotic and human-derived elements. Thus, buildings, infrastructure, and surfaces become elements of hybrid patches and not necessarily always patch types in themselves. Research under the ecology *of* the city paradigm is advanced by theorizing patches as hybrids of a wide variety of structural components, including trees and shrubs, grass or crops, bare soil, pavement, water, and buildings. Patches may be hybrids of these components to varying degrees and proportions (Cadenasso et al. 2007). Different patches in the mosaic may be differentially hostile or supportive of various organisms (Lehmann et al. 2014), including humans, and different biophysical and social processes. The features determining support or constraint may change internally or may be influenced by the interaction among patches. Hence, the theory can be summarized as a functional form of patch dynamics and is thus called dynamic heterogeneity (Pickett et al. 2016). The ecology *for* the city paradigm continues to employ the mosaic theory of heterogeneity.

Mapping technology

Each paradigm translates the relevant theory of heterogeneity through an ideally suited mapping approach. In the simple patch/matrix theory of the ecology *in* the city paradigm, a coarse spatial and coarse conceptual mapping technology is adequate. The well-known and long-available LANDSAT satellite platform, with 900-m^2 pixels, is adequate to capture large "green" patches and has typically been used to locate larger intact "natural" areas to preserve or restore (Qian et al. 2015). The availability of false color infrared imagery or of multispectral imagery with higher spatial resolution from space-based platforms has permitted the refinement of mapping based on binary categories. But the emphasis has still been on green, blue, or gray structures, with pixels as the standard unit, each of which is mapped as a single and distinct cover type.

The theory of heterogeneity appropriate for the ecology *of* the city paradigm requires a different mapping approach than for the ecology *in* the city. First, because all spatial patch types of the urban system are of interest, a two-phase technology is inappropriate. Second, because many patches will be hybrids of biotically and socially derived structures, maps must incorporate mixed patch types. Fortunately, finer spatial resolution data are available to identify various green, blue, and gray components of the patches that constitute cities, suburbs, and exurbs. These various elements of spatial cover can now be readily detected from many remote sensing platforms. These elements can form the basis for object-oriented mapping approaches as opposed to the conceptually coarse, pixel-based approaches available in the past (Zhou and Troy 2008, Zhou et al. 2014).

But greater spatial resolution in and of itself is not adequate to represent complete urban mosaics (Cadenasso et al. 2007, 2013, Zhou et al. 2014). For example, standard land-use/land-cover classes of commercial, industrial, low–medium–high-density residential, transportation, water, and bare soil are inadequate to expose many environmental drivers (Pickett 1993). Residential areas of any given housing density may have vastly different amounts of tree and grass cover, with different effects on water flow, energy budgets, and human perceptions and use. Therefore, both high spatial resolution and the refined conceptual discrimination of patch elements are required for the ecology *of* cities paradigm.

The mapping of specific social features that an ecology *of* cities approach requires is based on different sources. Social data are often attained *via* the administrative records, such as the U.S. decennial census, or from surveys and interviews, or from commercial data on personal or housing transactions. These data are amenable to mapping and to comparison with biophysical structures and functions in space. To achieve the integrated mapping required to do ecology *for* cities, the demographic and social data types just mentioned must be complemented with variables such as concentrations of power, the often incongruent distribution of different modes of governance, and maps of the flows of information and influence among formal and informal institutions. Contrasting aesthetic values and landscape psychologies (Hofmann et al. 2012, Nassauer 2013) can also be mapped across hybrid patch mosaics.

How boundaries between patches are represented also can differ between the ecology *in* versus ecology *of* the city paradigms. Object-oriented, high-resolution discrimination of various cover elements means that the patch boundaries can be chosen to highlight different and particular relationships. Integration is not restricted to congruence within pixels, or to the scale of coarse pixels. Rather, boundaries can be chosen at various scales so as to combine social and biophysical cover elements relevant to different research questions or policy analyses.

Not all comparisons need to be of existing conditions. Comparison can also focus on alternative futures, or follow

Fig. 5. The green and gray spaces of Berlin as an example of the focus on biotopes in binary urban classification. (Image from NASA Goddard. In the public domain.)

the implications through time of different climate and other change-adaptation strategies. This flexibility allows scenario generation and comparison, which is a key feature of the ecology *for* the city approach (Childers et al. 2015).

Classification strategy

The differences in disciplinary focus, the theory of heterogeneity used, and the mapping technology applied under the contrasting paradigms suggest different strategies for patch classification. The ecology *in* the city classification separates green and blue components from the gray or built environment. Classifications may recognize different types or property regimes of green/blue infrastructure, for example, different kinds of parks, or stream versus wetland. However, the traditional intent has been to identify and map the "ecotopes" of the city. Coarse-scale boundaries are usually portrayed in such binary classifications (Fig. 5). The space beyond these ecotopes is often left undifferentiated, as it is of little interest to a traditional ecology *in* cities approach.

Under the ecology *of* the city paradigm, the entire urban mosaic is relevant, important, and thus classified. Green, blue, and gray are all divided into more finely differentiated elements, and the classifications allow individual patches to contain elements that represent hybrids of biophysical, built, and social processes. The HERCULES classification (Cadenasso et al. 2007, Zhou et al. 2014) is a prime example of this sort of cover classification (Fig. 6).

Ecology *for* the city requires multiple classifications that may be related to key aspects of sustainability. This can be accommodated by a layered approach, such as that employed in GIS. No single classification can address all the system features relevant to sustainability. Sustainability is a process, not an outcome (Childers et al. 2014), and includes a normative, socially determined set of goals. Additional features in urban classification that relate to these goals might include social group identity, measures of environmental vulnerability, environmental decision-making equity, differentiation in social capital, governance structures, and economic capital. The contrasting aesthetics, landscape preferences, or perceived risks associated with different patches can also play a role in the dialogs for planning sustainable interventions (Ahern 2011, Nassauer 2013). For example, different social groups may prefer or avoid trees: Some may accept water-conserving plantings, while others

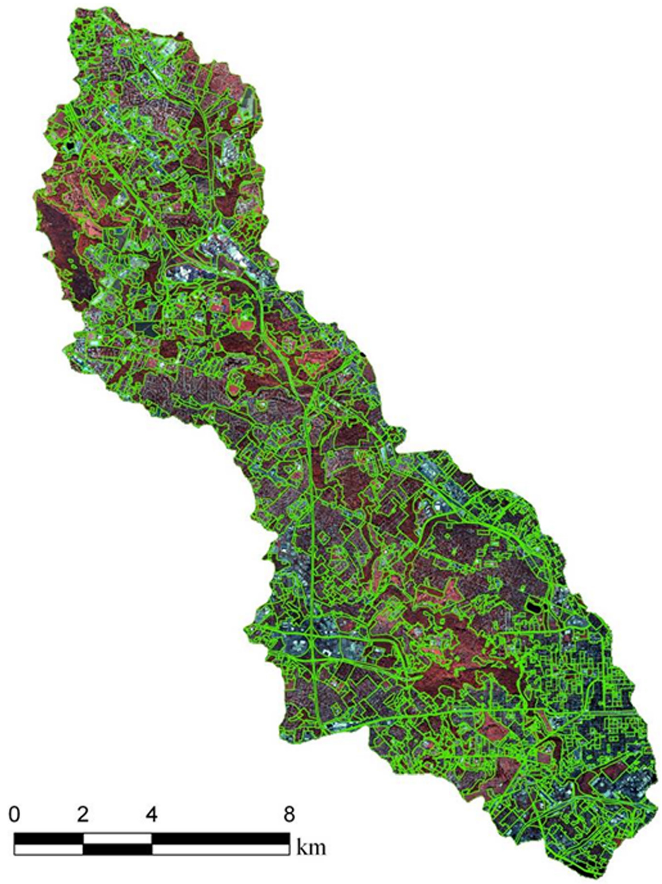

Fig. 6. A comprehensive classification of the Gwynns Falls watershed, Baltimore, Maryland, following the HERCULES system of Cadenasso et al. (2007).

demand yards filled with mesic species even in arid landscapes (Buckley et al. 2013, Larson et al. 2013). Such social, economic, and governance features often relate to key inertias that work to keep an urban system in its current state or on its current path (Childers et al. 2014). These systemic inertias may potentially hinder sustainable solutions, or they may provide opportunities for achieving sustainable urban trajectories.

Application to sustainability

Sustainability is supported by three pillars: environmental integrity, social equity, and economic viability (World Commission on Environment and Development 1987, Redman et al. 2004). The ecology *in* cities paradigm addresses the environmental pillar by identifying, characterizing, and locating areas in urban systems that have conspicuously biologically determined structures. Such areas are then assumed to generate ecosystem services and may be evaluated in terms of their ability to generate those services. Although the ecosystem service approach does connect ecotopes and green or blue patches to human well-being, the initial focus is on the biological components of cities, suburbs, and exurbs. The focus on ecotopes and spatially explicit ecosystem services places this application at the same coarse scale used by urban or regional planners.

The ecology *of* cities paradigm addresses all three pillars of sustainability (Cadenasso and Pickett 2016). Because it employs hybrid patches, and multidimensional, object-oriented classifications of these patches, ecology *of* cities approaches are especially applicable to the comprehensive concept of sustainability. This application operates at a design scale and considers the functions of designs in their specific patches, but also their contribution to the functionality, and hence the sustainability, of entire urban patch mosaics.

Ecology *for* the city identifies resilience (Holling 1996, Folke et al. 2012) as a goal for solutions that promote sustainability, and hence elevates urban resilience to be a major planning goal (Musacchio 2009). In addition, ecology *for* the city acknowledges that local design and adaptive management must be paired. It further requires the engagement of all three pillars of sustainability in the civic dialog, and places transdisciplinary interactions in the service of comprehensive sustainability planning and using resilience mechanisms toward the normative benefits of sustainable decisions and solutions (Pickett et al. 2014).

We summarize the contrasts among the three paradigms across dimensions of disciplinary focus, applicable theory, mapping technology, classification system, and application to sustainability theory (Fig. 7).

Conclusions

The contrast between the ecology *in* and the ecology *of* cities was introduced in a short editorial in 1997 in the first issue of the journal *Urban Ecosystems* (Pickett et al. 1997*a*). That brief piece aimed to indicate the expansion of urban ecological science beyond its familiar biotic foundations, and to help explain to mainstream ecologists the interdisciplinary opportunities associated with the two urban long-term ecological research projects established that year. Shortly thereafter, the integrative contrast between the two paradigms was explored at greater depth (Grimm et al. 2000). Since that time, the contrast between ecology *in* and ecology *of* cities has proven to be a useful organizing lens for the continued growth and maturation of urban ecological science. For example, the contrast has become familiar enough that it is now used in textbooks as a framing device (Gaston 2010, Adler and Tanner 2013, Douglas and James 2015). In this introductory and framing role, the paradigmatic contrast primarily stands as a metaphor, an image of the changing shapes of an evolving field.

This paper has added the insight that the paradigmatic contrast between ecology *in* and the ecology *of* cities has implications beyond metaphor. In fact, the contrast has empirical and methodological contents. Furthermore, the contrast has practical connections, with attempts

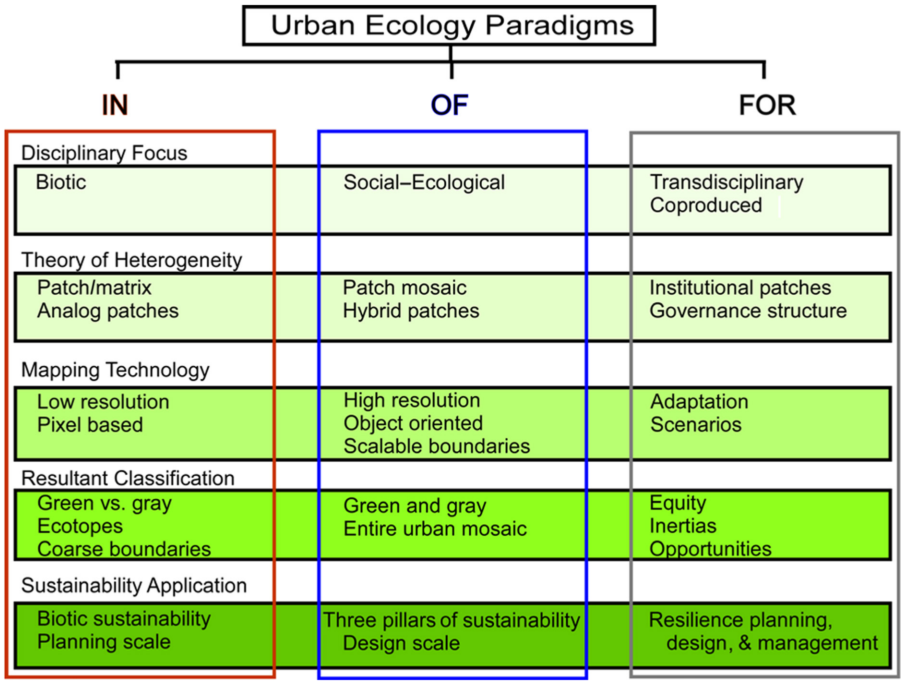

Fig. 7. The three paradigms of urban ecology characterized by contrasts along five dimensions of scope, theory, method, classification, and application.

to integrate ecological integrity into neighborhoods and cities, thus stimulating conceptual change. Like all paradigms, each of these two urban ecological approaches embodies background assumptions that have rarely been articulated. Likewise, as a paradigm, each one comprises major conceptual and theoretical structures having their own frameworks. Both paradigms also involve specific methodologies, which we have illustrated by the ways that spatial heterogeneity is conceived, measured, and mapped. Other research foci are also likely to differ between the paradigms, but for the sake of focus, we have addressed the issue of spatial heterogeneity as the guiding principle. Heterogeneity is one of the fundamental and persistent concerns of urbanists (Lynch 1960, Jacobs 1961, Shane 2005), and of mainstream ecology alike (Scheiner and Willig 2011). Thus, it serves as a useful boundary object for exposing the interdisciplinary nature of contemporary urban ecological science.

It is important not to see these two paradigms as loser and winner, as they are sometimes portrayed. It is true that the ecology *in* the city paradigm matured and was widely used long before the ecology *of* cities paradigm took shape and was commonly followed. Ecology *of* the city has not supplanted ecology *in* the city; in fact, in many ways the ecology *of* adds to ecology *in* the city. Research that can be described as concerned with ecology *in* the city is still answering important questions and providing salient information about cities, suburbs, exurbs, and the relationships among them and other ecosystem types. Ecology *in* and ecology *of* cities are in fact complementary research and modeling approaches that are both needed for full understanding of urban social–ecological systems. Although it is beyond our scope here, the two paradigms may well have implications and connections with still other urban theories, such as those of ecological footprints (Toth and Szigeti 2016), industrial ecology (Chertow 2000), power laws of urban size (Bettencourt and West 2010), political ecology (Bennett 2010), the megaregion (Marull et al. 2013), the metacity (McGrath and Shane 2012), and the continuum of urbanity (Boone et al. 2014).

The ecology *for* the city paradigm is one of ecological stewardship, involvement of science in civic discourse, and engagement with the processes of shaping urban systems and their components. It is a transdisciplinary paradigm in that it brings researchers, professional practitioners, decision-makers, and urban residents into dialog about ecological knowledge and its implications. These implications can address biophysical restoration, social revitalization, economic vitality, and environmental justice as important processes contributing to urban sustainability. Ecologists and environmental scientists have for a long time joined many others in desiring the integration of ecological knowledge into the designs, plans, and processes of urban systems. The ecology *for* the city paradigm thus unifies the other two and accepts the ethical challenge of scientific engagement in the quest for sustainable cities and a better future.

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