Urban ecology has quickly become established as a central part of ecological thinking. As cities continue to grow in size and number, two questions serve to unify this broad and multidisciplinary research landscape: (1) how can urban ecology contribute to the science of ecology, and (2) how can urban ecology be applied to make cities more livable and sustainable? In spite of the advances made thus far, there are many unexplored ways of integrating the science and application of urban ecology. Although scientists assess and make predictions regarding the connections between environmental and socioeconomic processes, practitioners involved in real-world application deal with urban planning and with designing ecosystem services to improve living conditions for all urban inhabitants and to make cities more sustainable. Research in urban ecosystems can be developed from many different perspectives, and we suggest that each perspective has something to offer both society and the science of ecology. We present several research perspectives and describe how these can integrate conceptual and applied aspects to bridge the figurative gaps between trees, buildings, and people.

In proposing the ecosystem as an organizational framework, Tansley (1935) explicitly included the effects of humans. When asking, “Is man part of ‘nature’ or not?” Tansley concluded that “human activity finds its proper place in ecology”. Nowhere is the human–nature interface more unmistakable than in urban ecosystems, and urban ecology has quickly become established within the discipline of ecology (Grimm et al. 2013). This rapid development was fueled by a need for multidisciplinary approaches when studying the extraordinary rate of urbanization and the complex connections among sociological and environmental factors (Brennan 1999; Young 2009). Now, for the first time in recorded history, the majority of people live in cities; moreover, with the characteristics of cities foreshadowing those of the planet, urban ecology is playing an increasingly important role within ecology (Grimm et al. 2008a). Furthermore, urban ecosystems will be on the “front lines” of environmental and sociological change, providing urban ecologists with new and exciting possibilities that combine research with implementing urban design and planning, as well as advocating policy.

Across the biological sciences, efforts to understand the mechanisms that underlie patterns have found both inspiration and a worthy challenge in the city (Grimm et al. 2008b). Human amplification of ecological processes in urban areas tightens the links among these processes at different biological, temporal, and spatial scales. For example, disease spread through co-occurring populations of wild animals and household pets depends on the behavior, evolution, and immunological responses of both the human and the domesticated animals; local regulations; pet owner behavior; and the habitat configuration, nutrient availability, and climate of the broader ecosystem (Adler and Tanner 2013). Ecologists have developed principles to help understand such processes, but considering them within an urban framework demands a more integrative way of thinking (Grimm et al. 2000; Forman 2008a).

Pickett et al. (2008) characterized the challenges urban ecologists face: “urban ecosystems are complex, dynamic biological–physical–social entities, in which spatial heterogeneity and spatially localized feedbacks play a large role”. Addressing such challenges requires interdisciplinary thinking and, depending on the goals of a project,
perhaps also an interdisciplinary team (Collins et al. 2000; Cid and Pouyat 2013; McHale et al. 2013). Indeed, an urban ecology study might require a team composed of ecologists, economists, sociologists, meteorologists, hydrologists, health-care professionals, landscape designers, planners, and politicians (Bettencourt and West 2010). Such broad, multifaceted collaborations have made remarkable progress in understanding the holistic social–biophysical–ecological processes of urbanization over the past several decades (Pickett et al. 2008; Collins et al. 2011; Grimm et al. 2013).

Although our understanding of urban ecosystems is expanding rapidly, how to use this growing body of knowledge to the benefit of society is much less well established (Brennan 1999; Leach et al. 2010; Cote and Nightingale 2012).

As scientists continue to learn more about the intended and unintended consequences of engineering built environments, they are in a position to begin asking what urban ecology can do for the science of ecology (eg Collins et al. 2000) as well as for society (eg Young and Wolf 2006; Pataki et al. 2011; Douglas 2012). Specifically, how can urban ecologists promote ecological investigation and work with planners and politicians to make cities more livable and sustainable? Such questions can be asked from many different perspectives (eg Grimm et al. 2008b; Bearley 2010; Cook and Swyngedouw 2012; Pincetl 2012; Wheeler 2013; Childers et al. 2014), so maintaining a diversity of approaches will allow the field of urban ecology to continue to develop as a science while simultaneously providing benefits to people living in cities (Young and Wolf 2006).

However, a diverse combination of disciplines, goals, and stakeholders can also make integrating and advancing science more difficult. Finding ways to integrate research, planning, and citizen involvement is therefore also vital for urban ecologists. We present five different research perspectives on urban ecosystems (Figure 1), show how each opens a potential new path forward for the interested ecologist, and discuss how these perspectives can improve our ecological understanding as well as the livability of cities.

We argue that the success of urban ecology will be measured by the ability of urban ecologists to continue advancing the science while simultaneously providing tangible benefits to society. Future success therefore depends on ecologists’ ability to include elements that are unfamiliar to their discipline and often to science in general. Ecologists – whether focused on behavior, communities, evolution, physiology, or ecosystems – are well positioned to address these challenges, given their training in system approaches that can be directed to both the basic and applied aspects of urban systems (Pickett and Cadenasso 2006).

### Five perspectives of urban ecology research

#### The ecology and evolution of, and in, cities

The multitude of interactions between humans and urban ecosystem function has been studied from many angles. From an ecological perspective, the types and degrees of disturbances associated with urban ecosystems challenge scientists to develop principles to trace complex feedbacks between human actions and their effects on ecosystems and organisms. Two emerging ideas are broadening the scope of this approach.

First, urban environments are not created de novo, but are developed within the context of their region. As global change accelerates, this context plays an important role in the challenges associated with accelerated urbanization (De Sherbinin et al. 2007), creating a situation in which urban areas could begin to face place-based vulnerabilities to climate hazards that lie outside even recent urban experience (Kunkel et al. 2010). Furthermore, not all cities grow and develop in the same way (McHale et al. 2013). As products of human planning within the context of broader regional scales, urban
Figure 2. As aging urban infrastructure degrades, many ecological, social, and economic problems, as well as opportunities, may arise. Urban ecologists will be called on to help develop science and policy to maximize the opportunities for urban inhabitants equitably and in sustainable ways.

areas are likely to change and respond to challenges in different ways. These responses not only apply stress to human infrastructure but also move ecosystems into new and unfamiliar states. The science of urban ecology will be well served by including these states as they are created by human-induced changes at many scales. Therefore, in addition to developing principles that help to generalize urban ecosystems, it is equally important for urban ecologists to investigate and predict the ways in which cities differ globally.

Second, as they become larger, older, and more interconnected, cities have the potential to act as hotspots of microevolution; examples include rapid evolution in response to antagonistic selective pressures (eg antimicrobials, pesticides, and hunting), pollution, and fragmentation (Vandergast et al. 2007; Cheptou et al. 2008; Whitehead et al. 2010). From the perspective of ecological communities, the complex effects of fragmentation can reshape intraspecific competition and interspecific interactions, which in turn cause changes in dispersal, competitive behavior, and social behavior. These hotspots could provide ideal opportunities to observe and understand evolution in the “new wild”, including the eco-evolutionary feedbacks between urban organisms and their environments. In addition, as with predicting how cities will differentially respond to global change, predicting evolutionary responses on a local scale will help planners and designers more effectively manage future climate hazards and less-desirable urban organisms.

The ecology of urban infrastructure

The study of ecology in cities has often focused on non-human organisms and remnant habitats, and how they respond to human-induced changes around them. However, the built environment itself is an important part of the urban ecosystem. Understanding this “gray infrastructure” (ie man-made components of urban ecosystems) on its own terms is an emerging frontier for ecologists, and one that is tied to questions of design and engineering.

Under a shifting climate regime, infrastructure will be increasingly stressed not only by altered nutrient, material, and water flows, but also by the effects of invasive species. Understanding how urban ecosystems respond to stress requires the inclusion of all infrastructure, including the built environment. Aging and degradation of urban infrastructure comes with ecological and economic costs, as well as with design and planning opportunities (Figure 2; Kaushal and Belt 2012). Although creating infrastructure has traditionally been the purview of engineers and designers, evaluating how biophysical and socioeconomic environments interact with design must become part of the broader science of urban ecology (Grimm et al. 2008b). For instance, urban ecologists will be called on to evaluate how different combinations of gray and green (ie biologically derived components of urban ecosystems) infrastructure affect stormwater runoff to control flooding and erosion, maintain nutrient retention and cycling, and provide other services such as recreation (Collins et al. 2011; Pincetl 2012). Evaluation of the functioning of the built environment can capitalize on “designed experiments”, wherein scientists work with landscape designers to give urban ecologists avenues to simultaneously create and evaluate designs in a controlled manner (Felson et al. 2013; Ahern et al. 2014). These types of experiments will further an understanding of complex ecological concepts and provide applied solutions.

In addition to shifting biogeophysical contexts, processes within the urban ecosystem can change with city size. From this perspective, research on the size of habitat patches, which has played a key role in ecological thinking, can be applied to cities. Larger cities may provide a greater range of public goods (eg services, parks, roads, and airports) with lower per capita infrastructure needs, but also bring public ills (eg congestion, pollution, disease, and crime; Bettencourt 2013). The expansion of cities is generally associated with an increase in social quantities (eg wages and innovation), as well as economic inequality and segregation among urban inhabitants, emphasizing the importance of understanding how heterogeneous characteristics of a city scale with size. Including ecological and sociological theory and applied ecology within urban ecosystems will lead to system components, from the buildings and pipes in the urban core to the exurban fringe, being treated as part of the whole (Forman 2008b).
The science of nature within cities

Just as urban ecosystem science brings the built environment into the purview of ecological thinking, it recognizes human well-being as a focal point of urban planning and design, and acknowledges that issues such as health, happiness, comfort, safety, and security are inextricably tied to humans’ connections with the natural world. As cities continue to grow and transition from the sanitary ideal of the past century to a sustainable mix of various colored infrastructures (eg gray man-made components, green vegetation, brown soils, and blue water), a new understanding of the role that nature plays in urban society will need to be developed (Pincetl 2012; Grimm et al. 2013). Just as urban ecosystems result from the interaction between human design and a larger regional context, so cities themselves can be thought of as “reconstructed nature” (Pincetl 2012), with both shared and unique characteristics (Figure 3). In fact, cities offer urban inhabitants multiple ways of being engaged with nature according to their preferences and social, cultural, and environmental conditions (Standish et al. 2013).

Although interactions between humans and their surrounding flora have been assumed to be important, the actual geographical relationships between humans and plants are still surprisingly vague (Head and Atchison 2009). There is increasing evidence of physiologically and psychologically important interactions between humans, their socioeconomic status, and their surrounding environment (Heynen et al. 2006; Wolch et al. 2014). Excessive heat and poor air quality have negative consequences for human health, and a lack of trees in the environment, often associated with low socioeconomic status, translates into sociological, physiological, and psychological costs (Figure 4; reviewed in Wolch et al. 2014). Furthermore, there are potential human physical and psychological benefits to having access to green space with high biodiversity (Fuller et al. 2007), although the benefits of actual diversity versus perceived diversity are still unclear (Dallimer et al. 2012). In addition to the direct health benefits associated with green space, stewardship of urban green space resulting from an interest in health and recovery can be associated with social, natural, and economic capital (Burls 2007). In this way, urban green space simultaneously provides both individual and common goods. However, not all urban human–flora interactions are positive. For instance, urban parks may be associated with personal safety issues (reviewed in McCormack et al. 2010), and pollen from urban plants can cause respiratory problems (Lyytimäki et al. 2008). By gaining a better understanding of the relationship between nature and city residents, urban ecologists can help design cities that optimize both infrastructure and ecosystem services.

The importance of an intersection between the city and the natural world for urban inhabitants (eg gardens and parks) is a central theme of “middle nature”, which conceptually describes turning nature into culture and providing access to all by merging the natural world and the built environment (Cosgrove 1993). Middle nature therefore is a way of considering the many roles of cultivated nature in the city. Some of these roles involve the benefits that nature provides to humans within the built environment (ie ecosystem services). But how these services are measured is open to interpretation (Reyers et al. 2013) and further depends on how such services are defined as well as on humans’ experience with the natural world (Krasny et al. 2014). The way in which people inhabit this world in turn shapes the broader phenomena of urban culture, economics, and governance, each of which varies dramatically at global and local scales. Yet scientists know surprisingly little about how these feedbacks filter from the urban ecosystem back into human experience, let alone society. Surveys have shown that individuals are happier in the short term when they have higher financial incomes; but at larger temporal and spatial scales, individuals may feel less secure, satisfied, or safe (Head and Atchison 2009; Heynen et al. 2006; Lyytimäki et al. 2008; Wolch et al. 2014).
tial scales, human life satisfaction is more strongly correlated with social capital (i.e., social cohesion and personal investment in the community) and access to quality outdoor recreation (Vemuri et al. 2011; Hager et al. 2013). How satisfaction with the environment feeds back to modify society remains to be seen.

The behavior and evolutionary ecology of urban humans

The social, political, and economic structure of urban societies largely determines the way in which humans create the urban environment. But what do ecologists have to offer in terms of understanding phenomena that have long been the subjects of history, economics, and political science? Below, we spell out two of the reasons that ecological thinking does indeed have a place in analyzing the dynamics of urban humans.

First, many ecologists work comfortably with complex feedbacks among processes that occur at different organizational levels, from physiology to climate. For example, the urban heat island effect involves processes ranging from the physics of surfaces, sunlight, and water, to the physiology of plants and the behavior of humans – and each of these processes can be decoupled temporally and spatially. Understanding the consequences of urban heat islands for plants and animals requires an understanding of their behavioral, physiological, and possibly evolutionary responses, including a positive feedback from reduced evapotranspiration and increased air conditioning, back to increased temperatures. Placing humans within a socioecological context requires an understanding of these types of feedbacks. The physiological stresses of urban heat islands are accentuated in lower-income areas, which typically have reduced tree cover (reviewed in Wilson 2011 and Wolch et al. 2014). Behavioral responses are more limited in these areas because poverty reduces opportunities for active or passive cooling, for example through the use of swimming pools (Harlan et al. 2007). Urban heat islands are thus embedded in a succession of feedbacks involving human society, with poorer areas becoming trapped in a local warming cycle. These feedbacks, with their ties to nature within cities, exemplify the difficulties that ecologists face when including political and socioeconomic issues in their analyses (Wolch et al. 2014). In a given city, how do ecologists effectively persuade elected municipal officials that more trees need to be planted in response to voters demanding a higher standard of living? Furthermore, what types of trees should be planted, how many, and where? Or rather how should urban areas be designed to optimize the human–environment relationship (Pataki et al. 2011)? Only by making known the explicit connections between the natural environment and quality of life will ecologists be able to help in the design of urban areas most affected by this relationship.

Second, ecology, like all of biology, is unified through evolutionary thinking. From an evolutionary perspective, early humans generally used group living strategies to deal with the selective pressures of finding resources, gaining knowledge, and obtaining protection; humans have
therefore evolved a wide range of psychological mechanisms to collectively solve these challenges (Van Vugt and Kameda 2013). As the ancestors of modern humans developed new technologies, leading to intensification (eg agriculture), the effects of niche construction and social structure on group cohesion, information sharing, and workforce specialization were key components of their success (Johnson and Earle 2000). In principle, modern humans evolved from ancestors that used social cohesion to solve problems relating to uncertainty in their environment (Larson and Christensen 1993; VAN VUGT and KAMEDA 2013). As social cohesion in urban areas disintegrates, largely due to a combination of socioeconomic and environmental pressures, cities are becoming increasingly prone to crime (Kuo and Sullivan 2001, reviewed in Brennan 1999), again linking nature and health with human behavior. In many areas, governmental intervention plans overlook these underlying determinants (Jütersonke et al. 2009), thereby complicating the integration of science and policy. Before discussing this issue, however, we must first address how groups of individuals living in proximity agree on a set of common goals (Levin 1999). Urban ecologists are positioned to use research and principles from voting theory and collective decision making, as well as from behavioral and evolutionary ecology, to understand governance in cities where humans and non-human animals share common environmental and economic resources (Ehrlich and Levin 2005).

*Citizen and stakeholder science*

Many successful ecologists think about their study systems from the perspectives of the organisms or ecosystems that they study (eg “thinking like a mountain”; Leopold 1949). As humans become more integrated into ecological studies as both agents and subjects, ecologists find themselves in the unusual position of needing to think about the urban environment as would non-scientists. Paradoxically, thinking like a typical urban human might be more difficult for an urban ecologist than thinking like a deer in a forest. Every urban resident brings a unique objective, perspective, history, and set of needs – determining the identity and location of the stakeholders most in need of science and policy integration is a daunting but essential part of urban ecological studies.

Involving these stakeholders as partners in research, particularly with regard to sustainability and access to ecosystem services, generates useful questions and interactions (Groffman et al. 2010). The model of “civic ecology” – where scientists work with urban residents to develop questions and methods, collect and interpret data, and ultimately translate these data into policy recommendations – can be far more effective than the more traditional one-way dissemination of knowledge from scientists to the general public (Krasny and Tidball 2012). This comparison between information sharing and information flow is critical to integrating science and policy in urban ecosystems. If obtaining funding, performing research, and publishing results are not having an effect “on the ground”, then collaborating with stakeholders could provide a mechanism to do so.

Even for general science questions that do not directly involve people, urban ecology is an ideal setting for new collaborations and teaching opportunities. For instance, exclosure experiments, residential development, and the evolution of urban organisms all provide opportunities for involving stakeholders, including students and citizen scientists (Dickinson et al. 2012). As working with stakeholders becomes more “normal” for urban ecology, problem solving by integrating science and policy will be one of the primary advances.

**Conclusions**

The term “ecology” was coined by Ernst Haeckel to mean “the study of the house or habitation”, whereas “economics” has the related but more directed meaning of “the art of managing a household”. For most people, the city is now their “house”. Just as architects cannot design buildings without considering the people who inhabit them, policy makers cannot manage cities without a holistic understanding of how urbanization affects both human and non-human residents. Furthermore, as urban populations grow and infrastructure ages, studies that can best determine how to provide cost-effective services to the urban inhabitants most in need will be in high demand. Ecology encompasses a broad spectrum of disciplines; with their diverse set of skills and interests, ecologists will be able to provide links between the natural and built environments. To ensure this outcome, urban ecologists must find ways of continuing to promote the science of ecology while also becoming more involved with planners and policy makers. As demonstrated here, although the research perspectives of urban ecology can be extremely varied, they share a common, inclusive theme of promoting science and benefiting society. The difficulties of integrating science and policy can be amplified when, as is often the case, stakeholders have differing agendas. For example, how do we balance the need for managing the “global commons” with the need for addressing the increasingly imperative “brown issues” of pollution and land degradation (Brennan 1999)? And how can we promote the protection of endangered species in an area while ignoring the health and environmental problems faced by the people living there (Hartoy and Satterthwaite 1991)? Such questions are further complicated when the associated costs and benefits vary with temporal and spatial scales. Environmentalists are occasionally accused of caring more about trees than people; perhaps when we fail to include people as part of our studies, this may appear equally true of ecologists. By approaching urban ecosystems with a more inclusive perspective, which seeks to integrate both conceptual and
applied aspects, urban ecologists will be better prepared to help bridge the gaps between trees, buildings, and people.

The German writer Goethe (1749–1832) supposedly said, “A poem is just as much a part of nature as a tree”. The built environment, nature in its many forms, and humans all share a complex network of interdependent connections that provide both academic and applied challenges. To advance the science of ecology, as well as promote benefits to society, urban ecologists must approach their discipline in a similarly inclusive manner, ready to incorporate unfamiliar areas ranging from economics to politics. But such roles can be challenging. For example, how will advocating policy affect scientists’ ability (real or perceived) to remain objective? For now we can only say, “let your conscience be your guide”, and suggest this as another area where collaborative research would be useful. Although making these links is challenging, Goethe’s observation highlights a key element of modern urban ecology and suggests that interfacing with unfamiliar disciplines will help us to understand and more effectively manage the urban ecosystems that are coming to dominate our planet.

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