The future of urban biodiversity research: Moving beyond the 'low-hanging fruit'

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“If cities create environmental problems, they also contain the solutions. The potential benefits of urbanization far outweigh the disadvantages: The challenge is in learning how to exploit its possibilities.”

*UNFPA State of World Population 2007.
Unleashing the Potential of Urban Growth*

Role of cities in conserving biodiversity

In the one hundred years since the emergence of the discipline of ecology, the world's human population has grown from 2 billion people, with 14% living in urban areas, to now being 7 billion people, over half of which are living in urban areas. The increase in size and number of cities and towns around the world has rapidly accelerated in order to accommodate this population growth. Over a ten year period from 1990 to 2000 in the USA alone, more than 1.4 million hectares of land adjacent to cities (e.g., agriculture, forest, wetland and grassland/shrublands) was lost to urban development (McDonald et al. 2010).

Urban areas are highly modified landscapes, and are one of the systems that have been most affected by human-accelerated environmental change (Likens 1992). The ecological consequences of this expansion of urban areas include changes in the distribution, abundance and composition of the plant and animal species, the local extinction of native plant and animal species, and the introduction of new plant and animal species into urban ecosystems. The lack of plants and animals in urban environments can have measurable impacts on the human inhabitants of cities, leading to a growing disconnect between people and nature. There is also a growing

body of evidence that the amount of vegetation and open space in cities can have an effect on human health and well-being (Louv 2005, Townsend 2006, Rose et al. 2008). By taking a more active approach to urban biodiversity management and enhancement, it is possible to reverse these trends and create healthy, resilient cities and towns for both people and biodiversity.

Cities and towns also support a significant proportion of the world's biodiversity (Miller and Hobbs 2002, McDonald et al. 2008, Müller 2011, Secretariat of the Convention on Biological Diversity 2012), and have a critical role to play in global conservation efforts (Secretariat of the Convention on Biological Diversity 2012). Cities are often built in highly productive and biodiverse landscapes, contain important indigenous plant communities and many rare or threatened species. Thus, cities can also play an increasingly important role in global conservation efforts through local actions. There are many organization, municipalities and programs around the world such as Local Governments for Sustainability (ICLEI), ICLEI's Local Action for Biodiversity Programme, UN-Habitat for A Better Urban Future, URBIO-International Network Urban Biodiversity & Design and the Stockholm Resilience Centre all recognize the importance of urban areas for biodiversity conservation at both the local and global scale. Actively managing biodiversity within urban areas can deliver strong outcomes for regional biodiversity conservation, as well as increasing the quality of life for the city's human inhabitants. There are enormous opportunities to engage and educate a large number of people within a relatively small geographic area and create support for global biodiversity initiatives through consumer behavior, activism and individual behaviors. Thus, there is a tremendous opportunity for urban ecologists to participate in creating biodiversity-rich and sustainable cities for the future.

Translating practitioner questions into actionable science

If cities are to successfully conserve biodiversity at local scales, the impacts of urbanization on the biodiversity and ecology of urban areas needs to be understood. This understanding must then be incorporated into the design, construction and management of our cities and towns to improve urban biodiversity outcomes. As ecologists, we need to make sure that we not only study the ecology of urban areas

(i.e., basic science), but we must also work collaboratively to ensure this information is used to make meaningful contributions to the decisions being made by local governments, built environment professionals (e.g., architects, planners, engineers, landscape architects, etc), land managers and other decision-makers. Through this contribution, our science can play a vital role in enhancing urban biodiversity and ecology outcomes, and not merely observing or documenting species decline. This is similar to the call in the 1920s/30s for the discipline of ecology to take a more active role in conservation and management of natural resources, rather than focusing only on basic science questions (Hagen 2008).

Around the world, the movement for sustainable and resilient urban areas has been accompanied by a growing call for locally relevant ecological information and principles to guide urban development and management (Thompson and Steiner 1997; Steiner 2002; Cadenasso and Pickett. 2008, Nassauer and Opdam 2008, Pickett et al. 2013). Unfortunately, there is currently a disconnect between the questions planners, designers and decision-makers are asking urban ecologists, and the questions urban ecologists must ask to contribute to improving urban systems. Planners, designers, managers are asking questions that are relevant to their day-to-day decision making: How much green space is necessary to maintain biodiversity? How small can habitats be that still support biodiversity? How much connectivity is required in an urban landscape to support diverse plant and animal populations and communities? However, these are not the questions that urban ecologists need to be asking in order to contribute to enhancing urban ecosystems.

As urban ecologists, we need to be translating questions from the practitioners into strong, ecologically relevant questions that, once addressed, will provide information back to practitioners to help them improve biodiversity conservation outcomes. For example, to answer the question 'how much green space is necessary to support biodiversity?' ecologists should be asking questions such as 'What are the ecological processes determining population viability and what are the attributes of green spaces that drive these processes?' This would allow urban ecologists to provide advice to planners about minimum levels of green space, and advice to designers and managers on the appropriate features to include in order to achieve the desired biodiversity outcomes. As another example, to rigorously answer the question 'How much connectivity is required in an urban landscape to support diverse plant and

animal populations and communities?', we first need to ask the basic science question 'How are the populations of plants and animals influenced by the configuration of habitat across the urban landscape?' In this question the focus is on the population dynamics of plants and animals, but the final result can inform the design of cities by providing an understanding of what level of landscape connectivity is required, and what landscape configurations contain optimum levels of connectivity required to support a diversity of plants and animals.

To summarize, in order to address pressing questions from urban practitioners and decision-makers regarding the preservation, management and enhancement of urban biodiversity, urban ecologists first need to translate their questions into ecologically relevant questions that can be addressed by basic science, and then use the scientific outputs to provide explicit advice back to practitioners so they can achieve their desired outcomes.

Move beyond the 'low-hanging fruit'

Over the past 25 years or so urban ecologists have primarily focused on describing the patterns of biodiversity in cities and towns (McDonnell and Haas 2008). Speaking metaphorically this represents the 'low-hanging fruit' of urban biodiversity research. Recently, there has been a growing call to develop a more mechanistic understanding of the processes that underlie the observed patterns which represent the 'high-hanging fruit' (Shochat et al. 2006; McDonnell et al. 2012). In this paper we will address the need for urban ecologists to reach for the 'higher-hanging fruit' and to ask robust, ecologically relevant, basic ecological questions. To achieve this goal we will examine three essential strategies for improving the actionable science outcomes of our research.

First, we need to continue to ensure that all urban ecology studies contextualize the temporal, spatial, physical and demographic window or frame during which the study took place, so that it can be evaluated in a broader global context (McDonnell and Haas 2009; Apostolopoulou and Paloniemi 2012). Second, we need to refine the questions we are asking in order to get a more detailed understanding of the drivers and mechanisms contributing to observed ecological outcomes. Refined questions explicitly examine the causal mechanisms underlying the distribution and abundance

of urban biodiversity. Finally, we need to test for confirmed generalizations using comparative studies that consider multiple cities, regions, climatic zones, cultural and social contexts. The following sections will address each of these three elements in more detail.

Provide an explicit statement of context

All good historians explicitly state the temporal, spatial and cultural context (i.e., window) in which their historical research is being undertaken (Cronon 2004). This not only involves stating the time period being investigated, but also requires the historian to explicitly state which lens they are using to interpret the events, as not all historical analysis is conducted from the current state of cultural norms and biases. Over the last decade, numerous authors have stated the importance of defining the urban context in which the research is being undertaken (McIntyre et al. 2000, Theobald 2004, Hahs and McDonnell 2006, McDonnell and Hahs 2008, 2009). Where this urban context has been quantified, the authors have usually used a broad, aggregate measure of urbanization, as they are often the measures that are most readily available. These aggregated measures include human population size, land-use, and land-cover such as percent impervious surface, or extent of urban development.

McDonnell and Hahs (2008) use the analogy of cities as mountain ranges (Fig. 1), where the level of urbanization is analogous to altitude. Some cities are broad flat plateaus (e.g., Los Angeles), some are high steep peaks (e.g., Hong Kong), and all cities can be placed somewhere into this framework. In reality, most cities are more accurately depicted as mountain ranges that appear as a cluster of peaks of different heights (see Fig. 2 in McDonnell and Hahs 2008). Broad, aggregated measures of urbanization allow us to define the current development state of a city or study, and place it into a broader global context. This is important as social and ecological dynamics vary in cities at different points along a development trajectory (i.e., along gradients within and between cities; Boone et al. 2012). The ecology of mountains is as complex as cities; however ecologists studying them can categorize life zones simply based on their height above sea level and distance to the equator which allows them to place the distribution of montane plants and animals in a broader global context (Körner 2003). Developing a similar understanding for urban systems

will allow us to begin making similar progress in describing trends within a broader global context.

[Insert Fig. 1]

In the 1980s, the science of ecology made a significant leap forward with the explicit recognition and incorporation of hierarchical spatial scales into ecological theory, practice and management (Allen and Starr 1982; O'Neill et al. 1986). For ecologists studying urban ecosystems it is critical that we understand and utilize a hierarchical approach to both our basic and applied research activities. Clergeau et al. (2006) emphasized the need to explicitly state the spatial scale that the urban ecological research is addressing in order to avoid false generalizations that may be true for one spatial scale such as the entire city, but not true for an alternative spatial scale such as specific site locations within an urban area. Therefore, when we are defining the 'window' for our research, we also need to explicitly state what spatial scale is being examined.

Finally, we would like to echo the words of William Cronon from his essay on the use of environmental history in which he states that 'neither nature nor culture is static' (Cronon 1993, pg 13). Urbanization is commonly depicted as a wave with urban expansion advancing from an established urban area out into a more sparsely populated and undeveloped peri-urban region. Different spatial positions along the wave exhibit different resources and dynamics that affect the survival of plants and animals. The crest of the wave represents the area currently experiencing the most rapid urban transformation. Further back from the crest, there are smaller wavelets of change such as infilling, gentrification, or revitalization. Conversely, cities may also experience population loss and infrastructure decay due to economic downturns, political events, climate change and catastrophic events (Steiner 2011). Therefore, it is imperative that we continue to provide an explicit statement of the 'window' of the city's developmental history that we are studying. The use of broad, aggregated measures are critical here, as they are easily accessible, and therefore can provide a common reference point for comparing between studies.

Ask more precise questions

As we mentioned in the previous section on “translating practitioner questions”, much of the research that has been done to date is falling short of providing the information that is required to provide solid advice to address the pressing questions from built environment professionals working to preserve, manage and enhance urban biodiversity. More precise, basic ecological research is required to begin addressing this knowledge gap. There are two simple options for addressing this challenge: 1) improve our understanding of the specific elements of urban ecosystems that directly impact upon biodiversity through the use of more refined predictor variables; 2) developing a stronger understanding of the mechanisms affecting biodiversity outcomes through the use of more refined ecological response variables.

Refine predictor variables to identify drivers

During the formative years of urban ecology in the early 1990s, many of the technologies and datasets that are now available for characterizing urban environments were not widely available. Therefore, many urban ecology studies relied upon the broader aggregate measures of urbanization (e.g., distance to center of business district (CBD), land-use, etc.) as surrogate variables to indicate the altered environmental conditions within their study sites, not unlike the use of elevation in the study of mountains (McDonnell et al. 1993, 2012). This approach was also useful as there was very little information about the ecological trends and patterns present in urban areas, and the broad measures of urbanization allowed the field to develop a basic understanding relatively quickly (i.e., ‘low-hanging fruit’). After the last 25 years of growth in the field, we now have a very large body of studies from around the world that provide some intriguing insights into how urbanization may be affecting ecological patterns and processes.

However, these studies are limited when they are being called upon to address the pressing questions from practitioners for two basic reasons. First, these studies have primarily been funded and undertaken to advance the basic science of urban ecology rather than address applied research questions. To bridge the gap between basic and applied urban ecology research we want to encourage researchers to refocus their efforts and address the fundamental knowledge gaps that practitioners have identified. The second reason is that much of the urban ecology research to

date has relied upon broad aggregated predictor variables, which are only able to indicate signals or trends that are too general to be effectively used to inform management and conservation decisions. To improve our science, we would encourage urban ecology researchers to build upon the large body of previous research, and search for ways to refine their predictor variables (within both basic and applied research questions) to deliver higher quality information back to the practitioner.

Examples of question-driven specific measures include vegetation structure, availability of resources such as water, nutrients, nest sites, as well as food availability, noise levels, night-lighting levels, trampling intensity and predator abundance to name a few. They also include components of the social realm such as human values, preferences and behaviors and their interaction with demographic and economic factors (e.g., Alberti, 2008, Grimm et al., 2000, Pickett et al., 1997, Pickett et al., 2011). Question-driven variables can better define urban conditions while providing more detailed understandings of the resources or conditions that directly influence the patterns of distribution and abundance of the plants and animals as well as the flow of water, nutrients and energy. For example, evidence from Melbourne suggests that the recently established permanent grey-headed flying-fox (*Pteropus poliocephalus*) camp in the city, that was over 400 km east of the nearest historic camp, has been facilitated by an increase of available food resources due to the trend of planting trees from more northern states as street trees in the 1970s, along with a reduction in the number of frost events due to the heat island effect which created a more favorable climatic envelope for this species (van der Ree et al. 2005, Williams et al. 2006). Another example of question-specific measures is the call by urban ecologists studying biogeochemical cycles to include engineering, urban demographic trends and household-scale actions in order to improve the quality of their science (Kaye et al. 2006).

There are a number of disadvantages with the use of these more specific predictors. While technological improvements allow researchers to obtain more site specific information, there is an associated cost with collecting and processing that information when it has not been previously available. Site specific information is not always available for non-study areas, so extrapolating the outcomes of model predictions across space can be difficult. The methods collecting question-specific

variables is even less standardized than for broad measures of urbanization, which will be a barrier to comparative studies across cities to develop confirmed generalizations (Mac Nally 2000). Those disadvantages can be partially countered by including studies that look at how aggregate measures of urbanization may be influencing the presence or configuration of more question-specific measures (Grace et al. 2010). For example, levels of artificial night lighting could be strongly related to human population density or road density; which might allow these surrogate variables to be used in predicting ecological responses over broader areas. The difference is that the aggregate measures are not drivers in themselves; they are simply correlated with them. The benefits that arise from investing in the collection of question-specific measures are the increased understanding of urban systems that would not otherwise be possible, and in the long run this improved understanding deliver better outcomes for biodiversity in urban landscapes.

Refine response variables to identify mechanisms

The development of a more mechanistic understanding of how environmental conditions in urban areas influence biodiversity patterns and processes is an important strategy (see Shochat et al. 2006) that has been adopted by a handful of urban ecologist (e.g., Marzluff et al. 2001, Jerzak 2001, Gering and Blair 1999, Gregg et al. 2003, Pouyat and Carriero 2003, Gaston et al. 2005). Developing this mechanistic understanding requires refining response variables from quite broad, aggregated measures, generally related to patterns such as species richness or abundance, to measures that are more closely related to ecological processes such as guilds or functional traits. The use of these approaches provides information that points to potential mechanisms behind the observed response. These can be monitored directly by investigating physiological conditions (e.g. Shochat et al. 2004) or population processes such as recruitment success (Stout et al. 2007). Trophic dynamics in urban areas may differ from non-urban systems, and this may indicate how species composition and resource availability are influencing population processes (Faeth et al. 2005). For example, the loss of plant species with a reliance on specialized mammal or bird pollinators indicates that the loss of pollinators from urban areas is responsible for the subsequent loss of other species that were dependent on them. Once these potential mechanisms have been identified, they

can then be tested to determine the degree of support both within the system and between systems.

While refined measures of ecological response can be studied using aggregate predictor variables, a more detailed understanding of mechanisms and drivers will obviously emerge more quickly if we refine our quantification of the potential drivers (predictor variables) at the same time. The recent urban ecology literature has some excellent examples of how research questions using refined predictor and response variables has delivered a more detailed understanding of ecological patterns and processes in urban landscapes (e.g., Becker et al. 2013, Bonnington et al. 2013, Williams and Winfree 2013). As more of this detailed research emerges, urban ecology will be better placed to answer some of the pressing questions from urban practitioners.

We also need to broaden the set of predictor variables and include social science and human response variables within urban ecology research in order to improve our understanding of social drivers of ecology in urban landscapes (e.g., links between human preferences and the presence of particular plant traits, Kendal et al. 2012); and our understanding of how the biodiversity components of urban landscapes affect human health and wellbeing (e.g., the diversity of flowering shrubs in residential gardens improves immunological health, Hanski et al. 2012). By improving our understandings of the interplay between the social and ecological systems, we will also be able to provide more targeted solutions to questions related to the construction and management of biodiversity-rich, green healthy cities and towns.

Testing for confirmed generalizations

Our knowledge base regarding the ecology of cities and towns has been growing in leaps and bounds over the past 25 years but much of this research has been predominantly place-based and focused on one or two cities or urbanization gradients centered on a single metropolitan area (McDonnell and Hahs 2009). The number of similar studies that investigated the distribution and abundance of organisms conducted over a range of cities is very small and thus the science of urban ecology has few if any confirmed generalizations or principles that will motivate basic research while also informing practitioners who design, build and

manage cities and towns (McDonnell and Hahs 2009). In order for the science of urban ecology to contribute to the development of biodiversity-rich cities and towns, our research needs to move beyond place-based research to identify generalities or principles regarding the distribution and abundance of plants and animals in urban environments. For example, our discipline could develop general ecological principles regarding the ability of organisms, guilds and communities to persist in cities, or identifying the major ecological causes of the demise of organisms, guilds and communities in cities beyond habitat loss.

Using the tools of our science and working with planners, designers, engineers and managers, it would be extremely valuable to explore how to alter the structure, composition and dynamics of cities to maintain viable populations and communities of plants and animals. One of the most efficient ways of developing these generalizations or principles would be to develop well designed comparative studies ranging from local to regional scales and global scales (McDonnell et al. 2009). Indeed, Ward (2010) suggests that in the fields of geography and planning there has been a recent revival of the comparative approach in the study of cities. Well designed comparative studies have been effectively used by ecologists for decades to investigate patterns, identify ecological signals, and explore generalities in patterns.

At present, there are few if any confirmed generalizations regarding biodiversity in the urban ecology literature. The work of Niemelä et al. (2002) and the other Globenet researchers have provided a strong foundation for identifying generalizations about the effect of cities and towns on Carabid beetle populations. There is a growing concurrence of information that indicates light pollution in cities has a significant and measurable negative impact on night flying insects (Longcore and Rich 2004, Rich and Longcore 2006, Gaston et al. 2012) and there are a handful of studies that indicate urban noise pollution can negatively influence bird, amphibian and mammal populations (Barber et al. 2010, Francis et al. 2012). Over the last decade, there has been an effort by urban ecology researchers to identify and confirm generalizations regarding phenomena such as the relationship between human population density and biodiversity (Luck 2007), biotic homogenization in cities (Schwartz et al. 2006, McKinney 2006, Clergeau et al. 2006) or the phylogenetic structure and traits of urban floras (Ricotta et al. 2009, Knapp et al.

2009, Duncan et al. 2011), but additional planned continental and global comparisons are required to create a broader and more robust set of urban ecology generalizations.

Reaching for the ‘higher fruits’

As cities and towns continue to be created and grow there is an increasing call from the public and urban professionals to maintain and even increase urban biodiversity (Müller and Werner 2010). Unfortunately, many pressing questions regarding the conservation of urban biodiversity from urban practitioners and decision-makers have gone unanswered due to the lack of appropriate social and ecological data. Urban ecologists need to seriously consider these questions and translate them into ecologically relevant questions that can be addressed by basic science, and then use the scientific outputs to answer the practitioner’s initial question.

To date, the majority of urban ecology research has involved collecting the ‘low-hanging fruit’. Due to the large knowledge gap surrounding ecological patterns and processes in urban areas as the modern discipline of urban ecology emerged in the 1970s, the most obvious place to start addressing this gap was to collect basic ecological information about patterns and to look for signals that could be used to create new hypotheses and direct future research (McDonnell 2011). Our subsequent knowledge base was primarily built on broad, aggregate predictor variables (e.g., distance to CBD, land-use, percent cover of impermeable surfaces and vegetation, etc.) as this was the information most readily available at the time. In order to move our science forward we need to progress beyond documenting patterns of biodiversity in cities and towns and investigate the underlying mechanisms that influence these patterns. After 25 years of research, we now have a large collection of ‘low-hanging fruit’ which allows us to begin looking for strategies to reach for the ‘fruit’ higher up the tree.

Urban ecologists can continue with our current ad hoc approach of describing and comparing the distribution and abundance of organisms in different cities and towns around the world while also increasing the number of mechanistic studies driven by more refined predictor and response variables. This approach will, in due time, allow us to reach our ultimate goal of identifying confirmed generalizations on the

mechanisms through which urbanization affects biodiversity. But if urban ecologists are strategic, we can reach a superior outcome more quickly than would be possible if we continue with our current uncoordinated approach. So what options do we have for creating a more coordinated approach? One possible strategy enlisted by researchers in other fields is to develop a standard research methodology focused on a specific mutually agreed upon critical research question and apply it to as many cities and towns around the world as possible. Adler et al. (2011) used this approach to examine an important ecological question regarding the relationship between productivity and species richness in non-urban environments.

There have been relatively few experimental studies conducted in urban environments (but see Gering and Blair 1999, Pouyat and Carriero 2003, Gregg et al. 2003, Gaston et al. 2005, Shochat et al. 2004, 2006). In order to reach the 'higher fruit' we encourage the initiation of more small and large scale experiments both within a city and between cities. Recently, Felson and Pickett (2005) have called for more ecological experimentation to be incorporated into urban design. Although it would be very challenging for urban ecologists to attempt large scale management experiments similar to those proposed by Walters and Hollings (1990), the effort could provide significantly new levels of understanding of the underlying mechanisms that influence the distribution and abundance of organisms in urban environments.

There are also a growing number of funding opportunities available, such as the Research Coordination Networks (RCN) funded by the US NSF and Europe's ALTER-Net program, for groups of researchers with a common research interest in synthesizing existing data and analysing it in new ways that can extract greater value from the information than would be possible from individual studies on their own (Duncan et al. 2011, McDonald et al. 2011). The coordination of research groups focused on these 'higher fruit' questions could accelerate progress in the development of our ecological and social knowledge of the structure and function of urban ecosystems.

If urban ecology is going to provide strong knowledge to inform actions, we need to strengthen the focus on refining our understanding and work towards the development of confirmed generalizations regarding the relationship between the structure and function of urban ecosystems and biodiversity. Refined understanding

can be achieved through the three methodological considerations described above: 1) defining the study window to place the study into a broader context, 2) collecting and using more explicit question-driven measures of the urban condition in order to improve our understating of urban ecological drivers as well as recording more detailed ecological responses to provide insights into the ecological mechanisms underlying an observed response, and 3) expanding studies to include multiple cities, regions and countries. Ultimately, we want to be able to deliver important ecological understanding to inform decisions made about cities and towns in the future, and by asking the right questions we can get there more quickly.

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Figure caption

Fig. 1. A diagrammatic representation of cities as mountains (a). The taller the mountain the greater intensity of urban. Cities exhibit a diversity of forms so b) illustrates a high steep mountain analogous to Hong Kong while c) represents a low flat city such as Los Angeles. Key: CBD = Central Business District.

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