Meta-analyses

Editor's Choice OIKOS

Oikos 125: 761–768, 2016
doi: 10.1111/oik.02883

Subject Editor: Christopher Lortie. Editor-in-Chief: Dustin Marshall. Accepted 27 August 2015

The biodiversity–ecosystem service relationship in urban areas: a quantitative review

Carly Ziter

C. Ziter (ziter@wisc.edu), Dept of Zoology, Univ. of Wisconsin, Madison, WI 53706, USA.

By 2050, up to 75% of people globally will live in cities. Despite the potential ramifications of this urbanization for ecosystem services (ES), and the importance of locally produced ES for the health and wellbeing of urban residents, syntheses addressing the underlying ecology of ES provision rarely include urban areas. Here, I conduct a quantitative review of urban ES studies in the ecological literature, synthesizing trends across the discipline. I also quantify the extent to which this work considers the organisms and ecosystem components responsible for ES provision using two approaches: assessment of biodiversity–ES relationships, and an adaptation of the service provider concept. The majority of urban ES studies were conducted in western, developed countries, and typically assessed a single service in a single city – largely ignoring ES synergies and tradeoffs, and cross-city comparisons. While several different ES are studied in urban ecosystems, the field is dominated by weather and climate-related regulating services, with assessments of cultural services particularly lacking. Most studies described a habitat type as the service provider; however, studies that considered the biodiversity–ES relationship were more likely to identify a specific functional group, community, or population as the key provider of an ES. The biodiversity–ES relationship itself was most frequently characterized as dependent on the composition of species, functional traits, or structures, rather than correlated with the magnitude of any specific biodiversity metric. While the study of ES in urban ecosystems is increasing, there exists considerable room for further research. Future studies would benefit by expanding the number and categories of ES assessed within and across cities, as well as broadening the geographical scope of urban ES research. Biodiversity–ES assessments in urban ecosystems would also benefit from an expansion of the biodiversity types considered, particularly regarding non-species based approaches, and consideration of non-native and invasive species.

Synthesis

Urban ecosystem services (ES) affect the health and wellbeing of over 3.5 billion people who live in cities. However, syntheses addressing ES provision rarely include urban areas. I conducted the first quantitative review focused explicitly on the ecology of urban ES, including the role of biodiversity in service provision. I found that studies typically measure only a single service in one city, precluding assessment of ES synergies, tradeoffs, and cross-city comparisons. I also found that while most studies attribute ES provision to a habitat or land-use type, studies that consider biodiversity-ES relationships are more likely to recognize a specific functional group, community, or population as the key provider of an ES.

Globally, 50% of people live in cities, with up to 75% expected to live in urban areas by 2050 (UN 2012). This increasing urbanization not only has a large environmental impact – urban areas account for the majority of global energy use and greenhouse gas (GHG) emissions, for example (Grimm et al. 2008) – but can also act as a key macroscale driver of local ecology, sometimes overriding natural climatic and ecological factors (Groffman et al. 2014). Thus, the increased prevalence of urban areas has ramifications for ecosystem structure and function, and consequently ecosystem services (ES), defined as the benefits people receive from ecosystems (MA 2005).

Existing at the nexus of high population density and high consumption, urban areas are typically thought of in the context of reducing resource demand rather than producing ecosystem services (ES). However, components within urban ecosystems can be significant ES providers, particularly as cities grow to encompass broader spatial areas (Gaston et al. 2013, Haase et al. 2014). For example, some cities have been estimated to store the equivalent carbon per unit area as tropical forests (Churkina et al. 2010). Additionally, as centers of human populations, urban areas are key players in the transfer of ES to beneficiaries. Natural spaces and green infrastructure within urban areas provide citizens with places to recreate, and increase aesthetics, for example, while urban agriculture provides residents with local food. This local provision of ES to urban occupants is an important factor in how functional and enjoyable a city is to live in (Gaston et al. 2013). In addition to increasing the 'livability' of a city, however, urban ES can also have direct health and safety benefits – e.g. moderation of heat island effects that could otherwise contribute to a rise in mortality (Patz et al. 2005) – and serve to increase the long-term sustainability of urban areas (Wu 2014).

While ES assessments in urban areas are becoming increasingly common (Haase et al. 2014), the extent to which we understand the ecology of urban ES provision remains unclear. Quantification of ES can be difficult in areas containing complex land-cover mosaics, and that often represent "novel ecosystems" in terms of their composition (Wu 2014). Particularly, our understanding of which organisms, communities, or habitat characteristics are most important for ES provision (the service provider concept, Luck et al. 2009) is limited. This includes a lack of consensus as to the nature of the biodiversity–ecosystem service (BES) relationship; whether, and how, biodiversity influences ES provision. While our desire to manage landscapes for both biodiversity conservation and ES provision has led to a proliferation of studies investigating the BES relationship, recent syntheses have largely ignored urban areas (Balvanera et al. 2006, Cardinale et al. 2012). Due to differences in community composition and spatial patterning of urban ecosystems compared to their non-urban counterparts, we might expect aspects of the urban BES relationship to be unique, with implications for policy and management recommendations.

Through a review of the peer-reviewed literature, I identify ecological studies of urban ES, synthesizing trends across the discipline. Next, I quantify the extent to which urban ES assessments incorporate the underlying ecology using two approaches: quantification of BES relationships, and adaption of Luck et al.'s (2009) service provider concept. Developed specifically to account for the ecological underpinnings of ES provision, the service provider concept delineates the ecological units required to generate a given ES, allowing for a more concrete link between ecosystems and ecosystem functions and the services that they provide. A particular strength of this concept is its application across levels of ecological organization, allowing for synthesis of studies that not only analyze different services, but also occur at different scales and in different habitats.

Specifically, I ask: 1) which ES, and categories of ES, are most commonly measured in urban ecosystems? 2) to what extent is urban ES provision associated with some measure – e.g. species, functional, community – of biodiversity, and what is the nature of these BES relationships? 3) which levels of organization are most often attributed as service providers, and to what extent are native vs. non-native species recognized as service providers in urban areas?

Material and methods

My review is based on peer-reviewed publications indexed in ISI Web of Science that included the topic terms "urban" and "ecosystem service*" up to 1 March 2015; ISI "topic terms" search the title, abstract, keywords, and ISI's "keywords plus" field. While use of the term "ecosystem services" certainly excludes some studies, I intended to capture studies that self-identify as part of the ES literature, compared to those that may measure a service, per se, but do not place their work in an ES context. Only English-language primary research articles were included. My initial search identified 1161 studies, the titles and abstracts of which I screened to retain only those that actually measured at least one ES within an urban area.

Specifically, studies were required to be primarily focused on an urban setting (rather than include urban areas as one land-use type of many), and investigate ES provision within urban areas, rather than impacts of urbanization on provision of ES in non-urban systems. Additionally, I only considered studies that included a strong ecological component – studies focused primarily on economics or social sciences were excluded. For example, a study that included both an ecological assessment of a service as well as economic valuation would be included, whereas a study focused solely on economic valuation of, or societal perception of, a service would be excluded. I included studies focused on the description of new conceptual frameworks or methodology only if an applicable urban ES case study was included.

I compiled data from the 77 resultant studies (Supplementary material Appendix 1) into a database, including: 1) bibliographic information; 2) the ES measured – including number, category, and specific service(s); 3) the geographic region and habitat type(s) focused on; 4) the spatial extent of the study; 5) whether specific policy or management recommendations were made; 6) the service provider; 7) the type of biodiversity measured (if applicable); 8) the nature of the BES relationship, and; 9) the role of native/non-native species in service provision (Supplementary material Appendix 2). Specific categories for multi-level criteria are described in Table 1.

Results

Urban ecosystem service assessments

With the exception of one 1996 study (Freedman et al. 1996), no studies in the database were published prior to 2005, after which publication levels were relatively low until 2010. From 2010 onwards, however, the urban ES field has grown rapidly (Fig. 1). Approximately 80% of studies were conducted in either North America or Europe (31 studies each – one of which spanned both continents), a trend that has been relatively stable through time. The remaining 20% of studies occurred in Asia, Oceania and Africa (8, 6 and 2 studies, respectively).

Studies typically assessed only a single ES (77%), and very rarely included three or more ES (Fig. 2A). However, the number of ES assessed in a single study ranged from 1 to 13 across all papers, resulting in 133 unique ES assessments from the 77 studies. The majority of studies occurred at the spatial extent of an urban landscape, with ES measured in a mix of land-use/land-cover types across one contiguous urban area – typically a municipality or metropolitan area (Fig. 2B). The remaining studies were fairly evenly split between those occurring within a portion of one urban area (at the patch or multi-patch scale), and regional to multi-regional scale studies that include multiple urban areas (Fig. 2B). The majority of the 133 ES assessments were conducted in terrestrial habitats, with aquatic habitats included less than 25% of the time (Fig. 2C). Of the nine studies

Table 1. Categories used to quantify attributes of urban ecosystem service studies related to spatial extent, ecosystem services, biodiversity type, and service providers. Ecosystem service categories are adapted from TEEB classifications (TEEB 2011), with the exception of "local climate and air quality", which was split into two ES ("local climate" and "air quality") in accordance with how these ES are typically assessed in the urban ES literature. Biodiversity type (modified from Feld et al. 2009) indicates the type(s) of biodiversity the authors measured (regardless of how it was ultimately found to influence ES provision), while the service provider category (modified from Luck et al. 2009) indicates the level of organization identified by the authors as the dominant, or most important, provider of the service.

Criteria	Categories and description
Spatial extent	*Patch:* a patch of a single land-use type *Multi-patch:* single patches of more than one land-use type *Urban landscape:* mix of land-use types across a single contiguous urban area *Region:* multiple urban areas within the same broad geographical area *Multi-regional:* multiple urban areas in different geographical regions
Ecosystem services	*Provisioning:* food; raw materials; fresh water; medicinal resources *Regulating:* local climate; air quality; carbon sequestration and storage; moderation of extreme events; waste-water treatment; erosion prevention and maintenance of soil fertility; pollination; biological control *Cultural:* recreation and mental and physical health; tourism; aesthetic appreciation and inspiration for culture, art, and design; spiritual experience and sense of place *Habitat or supporting:* habitat for species; maintenance of genetic diversity
Biodiversity type	*Genetic:* measures that address single genes or alleles *Species:* measures that address taxonomic composition, or identify keystone/ indicator species (often related to a limited group, compared to community diversity) *Community:* measures that address the composition of species within or across sites, account for relative importance/abundance *Functional:* measures that address the diversity of ecosystem functions performed, e.g. functional traits of vegetation, or guilds of species *Structural:* measures that address spatial or temporal structure, e.g. growth forms of different vegetation *Habitat:* measures that address the diversity of habitat types present
Service provider	*Population:* service is best provided by a particular species *Functional group:* service is best provided by organisms with a specific functional trait, or set of functional traits (e.g. vegetation with hairy leaves) *Community:* service is best provided by a particular composition of species (e.g. a specific forest type, or an aquatic vegetation community) *Structural component:* service is best provided by a particular structural component of an ecosystem, regardless of species or traits (e.g. street trees) *Habitat type:* service is best provided by a particular habitat type (e.g. green space) *Abiotic:* service is most influenced by an abiotic component (e.g. sunlight, tidal movement)

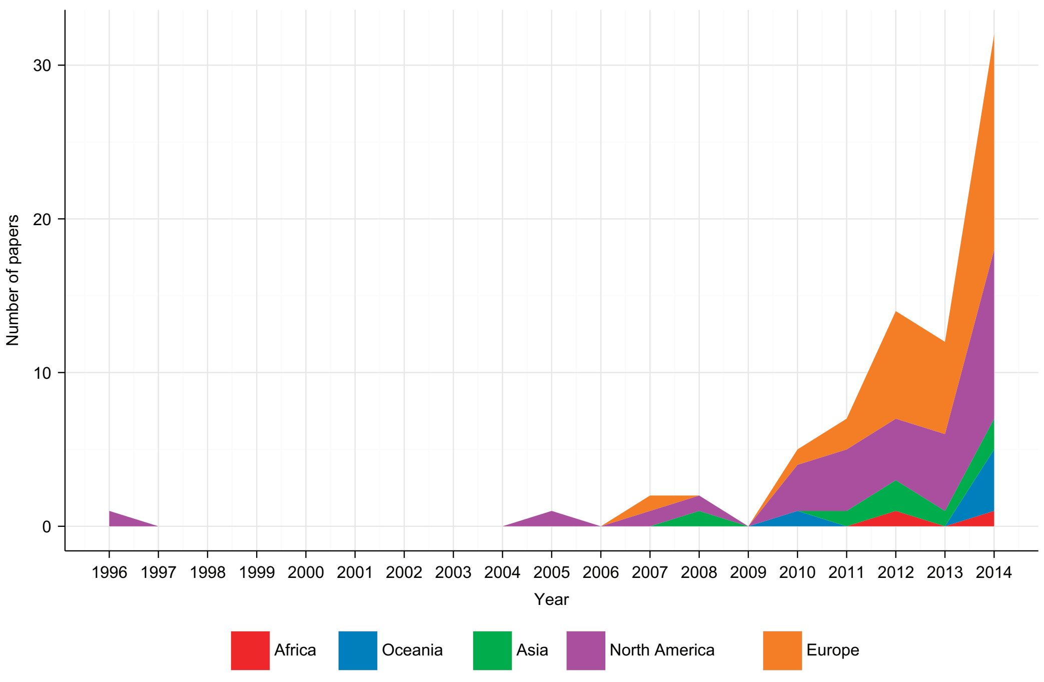

Figure 1. Number of urban ecosystem service publications and their continent of focus. A total of 77 publications identified in ISI Web of Science were analyzed. Two studies published in 2015 are not pictured here, occurring in Asia and Oceania. While European and North American focused studies dominate the literature, studies have occurred on all (inhabited) continents except South America.

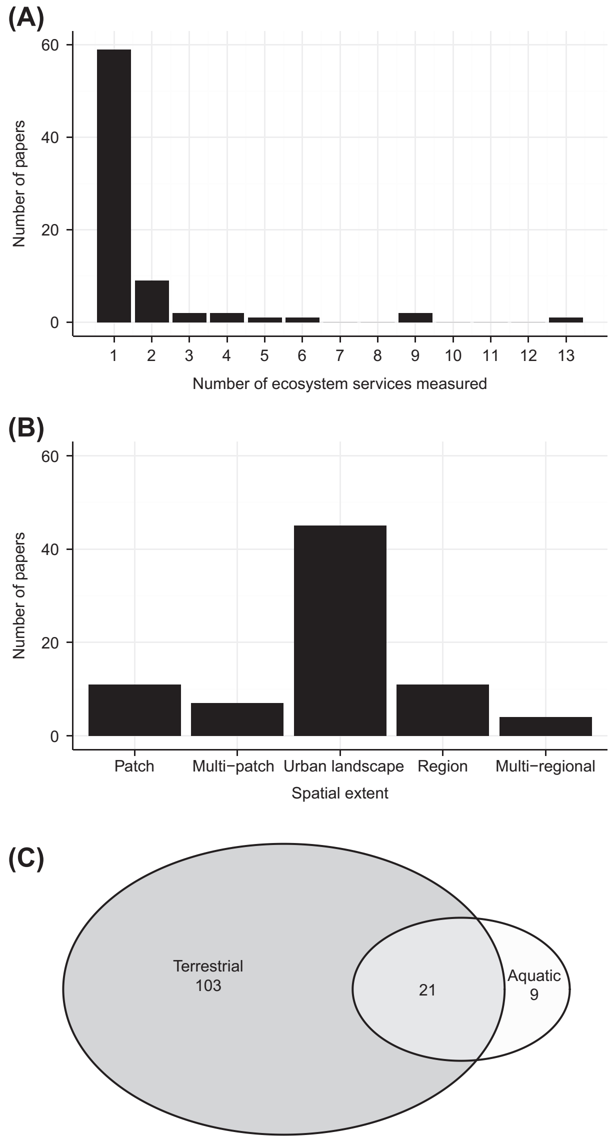

Figure 2. General trends across urban ecosystem service assessments. A total of 77 publications identified in ISI Web of Science were analyzed, representing 133 unique ecosystem service assessments. (A) Represents the number of ecosystem services assessed per publication. (B) Represents the spatial extent at which the study took place. Only a single study occurred at 2 scales, and thus appears in two categories. (C) The habitat(s) in which the ecosystem service was assessed. Area of the ellipses is proportional to the number of unique ecosystem service assessments, also represented numerically.

that focused solely on aquatic habitats, four focused on wetlands, four on streams/rivers, and only one on an urban lake. Just under a third of studies (21 of 77) contained a socio-ecological component, while 48 made explicit policy and/or management recommendations.

Ecosystem services and service categories

Seventeen of the 18 ecosystem services classified by The Economics of Ecosystems and Biodiversity (TEEB) (Table 1; TEEB 2011) were represented in the database (Fig. 3), along with three 'other' ES that did not fit within the existing TEEB classes: climate change adaptation, refuse consumption, and noise regulation. Regulating ES were most common, comprising slightly less than 75% of ES assessments (97 of 133). Cultural and provisioning ES were roughly equally represented at just over 10% of assessments each (16 and 14, respectively), with the remaining 6 assessments comprised of habitat or supporting ES (Fig. 3). Services related to climate and/or weather made up the majority of assessments, with carbon sequestration and storage, local climate (e.g. temperature regulation, or moderation of urban heat islands), and moderation of extreme events (typically flooding or storms) the top three assessed ES. Together, assessments of these three ES comprised almost half the total. Recreation and mental and physical health – classified as a single service under TEEB – was the most common cultural ES, and food the most frequently assessed provisioning service.

Biodiversity and ecosystem services

Of the 133 unique ES assessments, a component of biodiversity was concomitantly measured in just under half (63 assessments). However, only 47 assessments actually considered the relationship between biodiversity and the ES in question (hereafter 'BES link') – with the remainder typically including biodiversity as a habitat descriptor, or as a model component, for example in the case of allometry-based carbon assessments. The percentage of assessments that considered a BES link varied greatly between individual ES (Fig. 3 shaded bars). Assessments of some ES were almost ubiquitous in their incorporation of biodiversity (e.g. biological control, spiritual experiences and sense of place), whereas others rarely assessed biodiversity of any type (e.g. moderation of extreme events, food). Studies of habitat or supporting services were most likely to consider BES links, and provisioning ES least likely.

Biodiversity was most often assessed at the species level. Of the 47 relevant assessments, 38 measured some aspect of species diversity (e.g. richness, identity of common species) – albeit sometimes in conjunction with another biodiversity type. Functional and community diversity were each measured approximately one-third as frequently as species (in 13 and 12 assessments, respectively), followed by structural diversity (nine assessments). Habitat and genetic diversity were measured in only four and two assessments, respectively; in both cases, genetic diversity took the form of a gene-based community index in aquatic systems, rather than intra-specific diversity. In addition to being most common overall, species diversity was also the most common biodiversity type measured within each of the four ES categories, and was considered in at least one assessment for each specific ES. Functional diversity, contrastingly, was only measured for regulating services, despite being the second most commonly measured type of biodiversity overall (Supplementary material Appendix 3 Table A1).

In the majority of assessments the nature of the BES link was non-correlative in nature, with less than a quarter reporting that increased biodiversity either positively (nine assessments) or negatively (two assessments) affected ES provision (Fig. 4). Rather, the BES link was most often characterized as dependent on the composition of species,

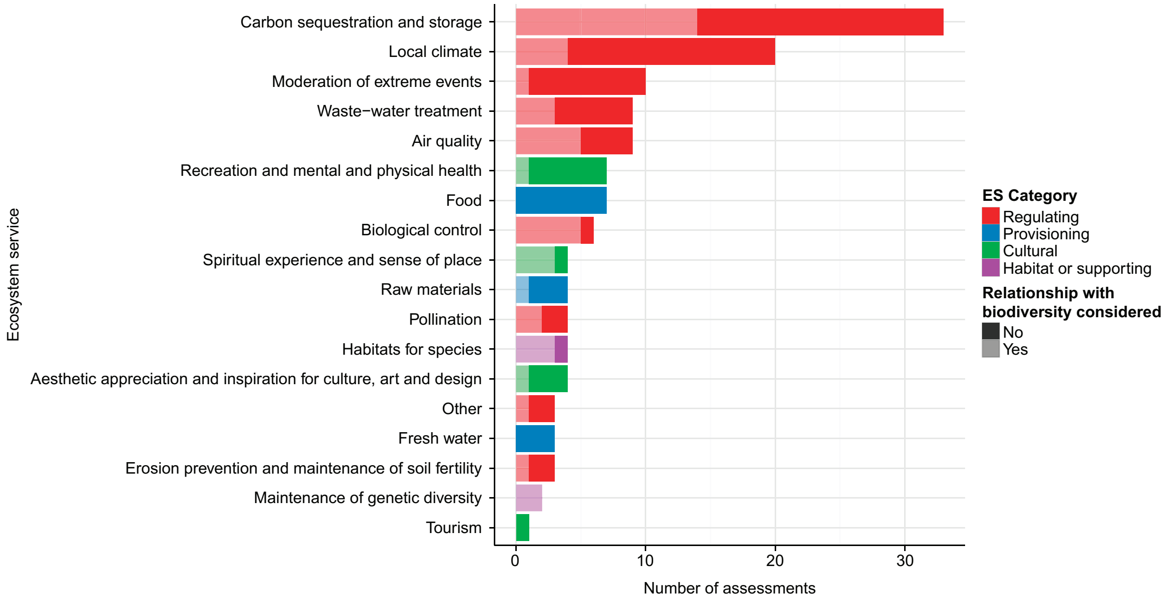

Figure 3. Total number of urban ecosystem service assessments corresponding to each ecosystem service. Colours represent the ecosystem service category, while shading represents the number of studies that do, or do not, consider the relationship between biodiversity and the ecosystem service in question. A total of 77 publications identified in ISI Web of Science were analyzed, representing 133 unique ecosystem service assessments. Services are classified according to TEEB (TEEB 2011), with the exception of "local climate and air quality", which has been split into 2 separate services. Of the TEEB ecosystem services, only the provisioning service of medicinal resources is absent here. Services classified under "other" include climate change adaptation, noise regulation, and refuse consumption.

functional traits, or structures (24 assessments), rather than on the magnitude of a given biodiversity metric. In the remainder of cases, biodiversity either had no reported effect on ES provision, or was used as an indicator of ES provision itself. The latter case – biodiversity as an indicator – was the dominant type of BES relationship for both cultural and habitat or supporting services (Fig. 4).

Service providers and ecosystem services

The service provider was identified and categorized for 127 of the 133 ES assessments (Supplementary material Appendix 3 Table A2). In the remaining six, a mix of components was described as providing the ES, with no indication as to their relative importance. Habitat type – often "urban green space", "permeable surfaces" or "tree cover" – was described as the service provider three times more frequently than any other category (62 assessments, Fig. 5); reflecting the use of land-cover classes as the unit of comparison for many urban ES assessments. Functional groups and communities were the next most common (20 assessments each), followed by structural components – typically street trees – and then populations. A small minority of studies reported abiotic variables as more important for ES provision than biotic components. Ecosystem service assessments that considered the role of biodiversity were relatively less likely to describe a service provider at the level of a habitat type or structural component, instead describing populations, functional groups, or communities as the most important providers of a given ES (Fig. 5 – shaded bars).

The relative role of native versus non-native or invasive species in ES provision was infrequently discussed, with only 28 of 133 assessments mentioning native or non-native status of any species in the study area, and only 10 explicitly discussing a relationship between these species and ES provision. The majority (7 of 10) identified non-native or invasive species as contributing positively to ES provision, with three specifically identifying these species as key ES providers.

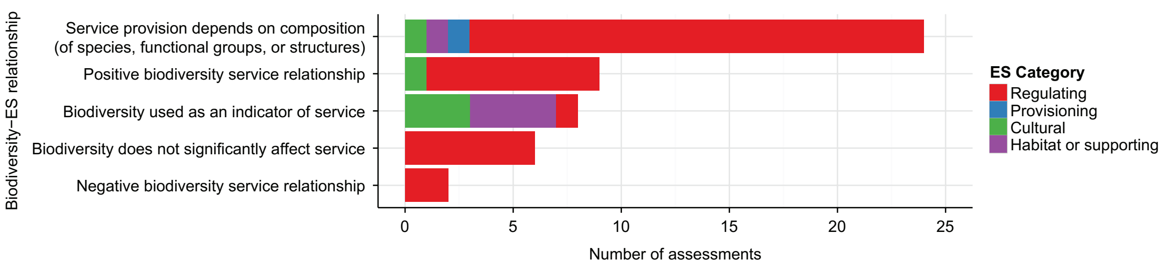

Figure 4. The nature of the biodiversity–ecosystem service relationship for 47 urban ecosystem service assessments that considered a link between biodiversity and a given ecosystem service. Colours represent the ecosystem service category (TEEB 2011). A total of 77 publications identified in ISI Web of Science were analyzed, representing 133 unique ecosystem service assessments.

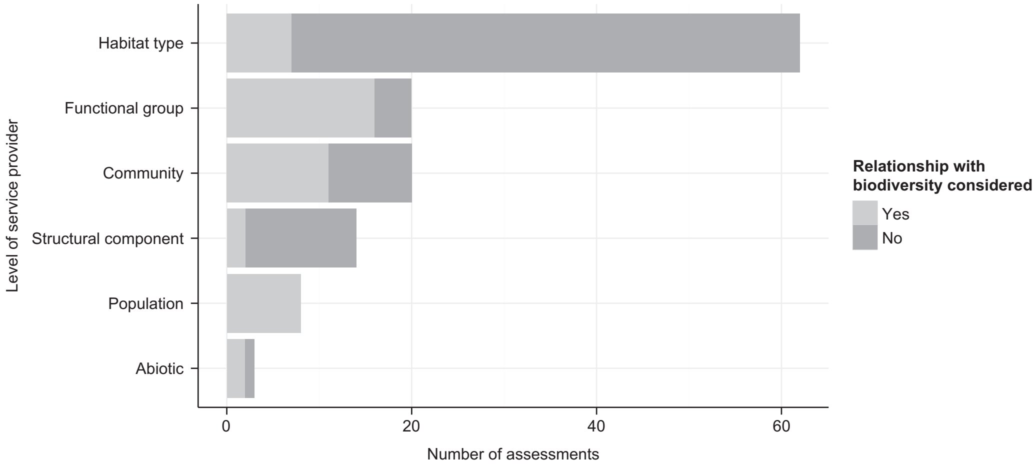

Figure 5. Total number of urban ecosystem service assessments corresponding to each category of service provider – the level of organization identified by the authors as the dominant, or most important provider of the service (modified from Luck et al. 2009). Shading represents the number of studies that do, or do not, consider the biodiversity–ecosystem service relationship. A total of 77 publications identified in ISI Web of Science were analyzed, representing 133 unique ecosystem service assessments.

Discussion

In this review, I have synthesized urban ecosystem services research in the ecological literature, quantifying the extent to which this work addresses the specific organisms and ecosystem components responsible for ES provision in urban areas. While recent reviews have addressed both the broader field of urban ES (Haase et al. 2014), and the BES relationship in non-urban ecosystems (Cardinale et al. 2012, Balvanera et al. 2014) this is the first review to my knowledge that focuses explicitly on the underlying ecology of urban ecosystem services. Furthering our understanding of the ecological components that underpin urban ecosystem service provision is an important step in improving urban sustainability.

Consistent with previous work (Haase et al. 2014), I find that the majority of urban ES research occurs in western, developed countries (Fig. 1). Studies typically assess only a single service in a single city, only rarely comparing cities across different regions (Fig. 2A–B). This predominantly single-city, single-service focus precludes the study of ES synergies and tradeoffs in urban areas (although see Dobbs et al. 2014, Lauf et al. 2014), as well as cross-city comparisons. Given the relevance of urban ecosystem services research to urban planning and sustainability (Andersson et al. 2014, Wu 2014), addressing the relationships between multiple ES as well as how they are affected by shared drivers and management decisions should be a priority of future work. Cross-city comparisons could also be particularly interesting given recent attention to the homogenizing effects of urbanization (Groffman et al. 2014). Indeed, in one of the few multi-regional scale studies analyzed here, Larondelle et al. (2014) found similar patterns in urban structure classes and temperature regulation between New York City and Berlin.

Ecosystem services in urban ecosystems

Regulating services comprised the majority of ES assessments, with climate and weather-related services measured most frequently (Fig. 3). While the Millennium Ecosystem Assessment (MA 2005) identified a lack of research on regulating ES compared to provisioning, their dominance in the urban ES literature is perhaps unsurprising, given: 1) the policy relevance and straightforward assessment of the regulating ES of carbon sequestration and storage, which comprises a quarter of the analyzed assessments – many of which were done using available models such as iTree (<www.itreetools.org>) and; 2) that production systems, and the provisioning services they yield, are generally spatially separated from urban centres, while regulating services can often only be delivered in situ, and are difficult to replace (O'Farrell et al. 2012). For example, food and raw materials can easily be grown or harvested in rural or natural areas outside of a given city, and transported – often over great distances – to those who benefit from them. Services such as the reduction of storm water runoff or the moderation of urban heat island effects, however, are delivered largely in place, relying much more heavily on the characteristics of the local environment. This prevalence of specific ES and ES categories is largely in line with the results of Haase et al. (2014), although I find that regulating ES dominate the literature to an even greater extent, with cultural and supporting ES in particular less common. This mismatch in the frequency of both cultural and supporting ES is likely due in part to methodological constraints. My exclusion of economic and social science based studies may bias against cultural ES, which are frequently assessed via methods such as contingent valuation, market price approaches, or choice experiments, rather than ecological methods (Milcu et al. 2013). Thus, while urban green space is frequently acknowledged as important for the enjoyment and health of residents (Tzoulas et al. 2007), my results indicate that the underlying ecology of cultural ES provision remains understudied in urban ecosystems. This is particularly true regarding the underlying mechanisms by which biodiversity may influence cultural services. A more detailed consideration of cultural service provision should be an important goal for future urban ecological research. Habitat or supporting ES, on the other hand, likely form only a small percentage of the current database due to their frequent classification in recent work as ecosystem functions, or natural capital, rather than explicitly as ecosystem services.

Despite the dominance of a few specific ES, nearly the full range of TEEB services were assessed in at least one study, representing the wide variety of ES measured in urban ecosystems. Interestingly, some of the ES among the most likely to be exclusively measured in urban centres – for example noise regulation (Radford and James 2013), or refuse consumption (Youngsteadt et al. 2014) – did not fit within existing TEEB classifications. Similarly, although categorized separately here, air quality services such as oxygen production and pollutant removal, and the local climate service of temperature regulation are considered one service under TEEB, despite their distinct usage as different ES provided by urban ecosystems. Thus, while the current database precludes a comparison to non-urban ecosystems, urban ES studies appear in at least some cases to focus on services that are rare in the broader ES literature.

The underlying ecology of urban ecosystem service assessments

I used two approaches to quantify the extent to which urban ES assessments incorporated underlying ecological components: an assessment of the BES relationship, and an adaptation of the service provider concept (Luck et al. 2009). The relationship between biodiversity and ES was considered in only 47 of 133 ES assessments. Biodiversity was most often measured as some aspect of species diversity, consistent with trends in the broader ES literature (Feld et al. 2009, Balvanera et al. 2014). While habitat or supporting services were most likely to be linked to biodiversity, this is primarily due to biodiversity being considered an ES indicator itself in many of these assessments (Fig. 4), as well as the small number of habitat or supporting assessments analyzed overall. Indeed, given the low number of assessments for most individual ES (Fig. 3; Supplementary material Appendix 3 Table A1), limited conclusions can be drawn regarding relationships between specific ES and biodiversity. However, given the ubiquity of species-related biodiversity measures, it is intuitive that a service like biological control – which by its nature requires specific organisms or types of organisms – would almost universally incorporate biodiversity, whereas ES that tend to rely less on particular species than on entire habitats or communities, for example services involving the regulation of water (Harrison et al. 2014), rarely incorporate biodiversity. My results support that studies that consider a broader range of biodiversity types are needed to more fully quantify the BES relationship for specific services, particularly for ES that may rely on less commonly measured aspects of biodiversity such as structural or functional diversity, rather than species. In addition to the study of multiple ES, studies incorporating multiple measures of biodiversity would further improve our understanding of how to best manage for ES provision in urban ecosystems.

Consistent with the broader BES literature, I find that although both positive and negative relationships exist, biodiversity was more likely to be positively related to ES than negatively (Harrison et al. 2014). However, unlike the focus of much of the broader BES literature on quantifying correlations between biodiversity and service provision, I find that the urban BES relationship is most often described in a non-correlative way – with specific species, functional traits, or structures contributing to ES provision, rather than a numeric metric of biodiversity (Fig. 4). Thus, maximizing biodiversity will not necessarily increase ES provision in urban areas. Rather, in order to manage urban landscapes for ecosystem service provision, future work should focus on further developing our understanding of which underlying ecological components contribute to provision of specific ES. Additionally, the positive role of specific species was not limited to native species, with non-native or invasive species found to contribute to high ES provision in multiple studies (Escobedo et al. 2010, Timilsina et al. 2014, Youngsteadt et al. 2014). Given the high prevalence of non-native species, as well as generalist or synanthropic species, in urban ecosystems, it is perhaps to be expected that non-native species were found to contribute to urban ecosystem service provision. Overall, however, very few urban ES studies (or indeed, non-urban ES studies, Eviner et al. 2012, McLaughlan et al. 2014) explicitly address the impact of non-native or invasive species on ES provision, representing an important gap in the literature.

While there are similarities across the categories of biodiversity type and service provider, the two concepts provide different information about the relationship between ES and underlying ecological components. Unlike biodiversity type, which simply indicates the particular elements of biodiversity measured in a study, the service provider indicates the level of organization considered most important for ES provision – regardless of whether biodiversity is quantified at all. Thus, the service provider often reflects two situations: 1) several measures of biodiversity or other ecological factors may have been investigated, with the service provider the level of organization found most important, or; 2) the service provider may simply indicate the level at which comparisons were conducted, with no more detailed ecological assessments done (that is, the framing of the study influences the results). The latter situation partially explains why habitat types and structural components are so commonly attributed as the service provider, particularly in studies that do not assess biodiversity (Fig. 5). Many studies compare the level of ES across different habitats types, and thus a particular habitat type a priori becomes the service provider. The fact that assessments that did investigate biodiversity were also more likely to identify specific communities, functional groups, or populations as the service provider implies that more detailed study of the ecological underpinnings of urban ES provision is often warranted. For some services, by limiting observations to the level of habitat, we may be missing the influence of a particular species, functional group, or community type that would lend itself to more detailed planning and management for urban ES provision.

Conclusion

By 2050, up to 75% of people globally will live in cities. Despite the potential ramifications of this increased urbanization for ecosystem services, and the importance of locally produced ES for urban residents, studies that address the underlying ecology of ES provision rarely consider urban ecosystems. Here, I find that although a wide variety of ES have been studied in urban areas, there exists considerable room for further research. The field is dominated by assessments of climate and weather-based regulating services, with cultural services in particular less common than one might expect based on the broader literature. The majority of these urban ES studies measure only a single service, across a single North American or European city – limiting our ability to compare the effects of management strategies on multiple services, or to assess synergies and tradeoffs, as well as impeding cross-city comparisons. Future research should focus on expanding the number and categories of ES studied within and across cities, as well as broadening the geographical coverage of urban ES work. I also find that while most assessments describe service provision as occurring at the level of a habitat or land-use type, assessments that take into account the underlying relationship between an ES and biodiversity are more likely to recognize a specific functional group, community, or population as the key provider of an ES. A focus on non-species aspects of biodiversity in future studies will continue to expand our knowledge of the biological underpinnings of urban ES provision, particularly for services that have been found to infrequently consider biodiversity-ecosystem service links.

Acknowledgements – I thank Stephen R. Carpenter and the Winter 2015 "Ecosystem Concepts" class at the Univ. of Wisconsin-Madison for valuable feedback throughout the development of this work. I also thank Monica G. Turner and Eric Pedersen for helpful comments on a version of the manuscript. I am supported by a Natural Science and Engineering Research Council of Canada doctoral fellowship, as well as by the Water Sustainability and Climate Program of the National Science Foundation (DEB-1038759).

References

Andersson, E. et al. 2014. Reconnecting cities to the biosphere: stewardship of green infrastructure and urban ecosystem services. – AMBIO 43: 445–453.

Balvanera, P. et al. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. – Ecol. Lett. 9: 1146–1156.

Balvanera, P. et al. 2014. Linking biodiversity and ecosystem services: current uncertainties and the necessary next steps. – BioScience 64: 49–57.

Cardinale, B. J. et al. 2012. Biodiversity loss and its impact on humanity. – Nature 486: 59–67.

Churkina, G. et al. 2010. Carbon stored in human settlements: the conterminous United States. – Global Change Biol. 16: 135–143.

Dobbs, C. et al. 2014. Multiple ecosystem services and disservices of the urban forest establishing their connections with landscape structure and sociodemographics. – Ecol. Indic. 43: 44–55.

Escobedo, F. et al. 2010. Analyzing the efficacy of subtropical urban forests in offsetting carbon emissions from cities. – Environ. Sci. Policy 13: 362–372.

Supplementary material (available online as Appendix oik-02883 at <www.oikosjournal.org/appendix/oik-02883>) Appendix 1–3.

Eviner, V. T. et al. 2012. Measuring the effects of invasive plants on ecosystem services: challenges and prospects. – Invas. Plant Sci. Manage. 5: 125–136.

Feld, C. K. et al. 2009. Indicators of biodiversity and ecosystem services: a synthesis across ecosystems and spatial scales. – Oikos 118: 1862–1871.

Freedman, B. et al. 1996. Tree species composition, structure, and carbon storage in stands of urban forest of varying character in Halifax, Nova Scotia. – Can. Field Nat. 110: 675–682.

Gaston, K. J. et al. 2013. Managing urban ecosystems for goods and services. – J. Appl. Ecol. 50: 830–840.

Grimm, N. B. et al. 2008. Global change and the ecology of cities. – Science 319: 756–760.

Groffman, P. M. et al. 2014. Ecological homogenization of urban USA. – Front. Ecol. Environ. 12: 74–81.

Haase, D. et al. 2014. A quantitative review of urban ecosystem service assessments: concepts, models and implementation. – AMBIO 43: 413–433.

Harrison, P. A. et al. 2014. Linkages between biodiversity attributes and ecosystem services: a systematic review. – Ecosyst. Services 9: 191–203.

Larondelle, N. et al. 2014. Applying a novel urban structure classification to compare the relationships of urban structure and surface temperature in Berlin and New York City. – Appl. Geogr. 53: 427–437.

Lauf, S. et al. 2014. Linkages between ecosystem services provisioning, urban growth and shrinkage – a modeling approach assessing ecosystem service tradeoffs. – Ecol. Indic. 42: 73–94.

Luck, G. W. et al. 2009. Quantifying the contribution of organisms to the provision of ecosystem services. – BioScience 59: 223–235.

MA (Millennium Ecosystem Assessment) 2005. Ecosystems and human well-being: synthesis. – Island Press, Washington DC.

McLaughlan, C. et al. 2014. How complete is our knowledge of the ecosystem services impacts of Europe's top 10 invasive species? – Acta Oecol. 54: 119–130.

Milcu, A. I. et al. 2013. Cultural ecosystem services: a literature review and prospects for future research. – Ecol. Soc. 18: art44.

O'Farrell, P. J. et al. 2012. Insights and opportunities offered by a rapid ecosystem service assessment in promoting a conservation agenda in an urban biodiversity hotspot. – Ecol. Soc. 17: art27.

Patz, J. A. et al. 2005. Impact of regional climate change on human health. – Nature 438: 310–317.

Radford, K. G. and James, P. 2013. Changes in the value of ecosystem services along a rural–urban gradient: a case study of Greater Manchester, UK. – Landscape Urban Plan. 109: 117–127.

TEEB - The Economics of Ecosystems and Biodiversity 2011. TEEB manual for cities: ecosystem services in urban management. – <www.teebweb.org >.

Timilsina, N. et al. 2014. Analyzing the causal factors of carbon stores in a subtropical urban forest. – Ecol. Complex. 20: 23–32.

Tzoulas, K. et al. 2007. Promoting ecosystem and human health in urban areas using green infrastructure: a literature review. – Landscape Urban Plan. 81: 167–178.

UN (United Nations) 2012. World urbanization prospects. – UN, New York.

Wu, J. 2014. Urban ecology and sustainability: the state-of-the-science and future directions. – Landscape Urban Plan. 125: 209–221.

Youngsteadt, E. et al. 2014. Habitat and species identity, not diversity, predict the extent of refuse consumption by urban arthropods. – Glob. Change Biol. 21: 1103–1115.