Ecosystem service supply in an urban landscape: roles of landscape structure, historical land-use, and biodiversity

By

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Abstract

Ecosystem service supply in an urban landscape: roles of landscape structure, historical land-use, and biodiversity

Carly D. Ziter
Under the supervision of Professor Monica G. Turner
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Unprecedented urban growth has markedly changed ecosystem structure, function, and biodiversity, and consequently the ecosystem services our health and wellbeing depend on. To improve urban sustainability, it is important to identify opportunities to manage cities for increased ecosystem service provision. This requires understanding urban areas as spatially heterogeneous and temporally dynamic ecosystems. This dissertation combines synthesis, observational, and experimental approaches to ask how landscape structure, historical land-use, and biodiversity impact multiple ecosystem services in urban landscapes. In chapter 1, I conducted a global meta-analysis focused explicitly on the underlying ecology of urban ecosystem services, centered on the role of biodiversity in service provision. The remaining chapters focus on Madison, WI, and consider how landscape context (Chapter 2, 4) and biological invasion (Chapter 3) may influence ecosystem services in a temperate, mid-size city.

Through meta-analysis, I showed that urban biodiversity-ecosystem service research would benefit from increasing the number and types of services assessed, broadening its geographical scope, and expanding types of biodiversity measured – including consideration of non-native species. Using empirical data, I assessed the effect of spatial and temporal context on ecosystem services in Madison, a historically agricultural urban landscape. By measuring biophysical indicators of three services (carbon storage, water quality regulation, runoff regulation), I showed that considering the full mosaic of urban greenspace and its history is needed to estimate the kinds and magnitude of ecosystem services in cities, and to augment regional assessments that may underestimate urban ecosystem service supply. Using a bicycle-mounted temperature sensor, I showed that impervious surfaces and canopy cover interact to affect summer air temperature, and that urban forest management provides a powerful lever to increase temperature regulation services. Understanding invasion-ecosystem service linkages is also important in urban ecosystems – where non-native species are common. I conducted reciprocal field experiments to test whether an incipient urban invader, the Asian jumping worm, might interact with an established invasive, common buckthorn, with consequences for ecosystem services. Contrary to the "invasional meltdown" hypothesis, I found no evidence of co-facilitation, with positive conservation implications. Overall, this research has implications for using urban landscape management to enhance ecosystem service provision.

Introduction

Ecosystem Services, the benefits people derive from ecosystems, are an increasingly prominent topic in ecological research and conservation decision-making. While explicit study of "ecosystem services" is relatively new, the underlying concept that natural systems perform services fundamental to human wellbeing did not arise recently, but has been present in environmental and ecological discourse for over a century (Mooney and Ehrlich 1997). As early as 1864, George Perkins Marsh's Man and Nature referenced the ways in which people relied on natural systems. This was followed by Vogt's pioneering work on natural capital (1948), Osborn's decree that ecological systems "make possible not only our life but, to a large degree, the industrial economy upon which civilization rests" (1948), and Aldo Leopold's poetic recognition of the irreplaceability of nature's benefits to society (1949). The field as we currently recognize it has also grown from a rich intellectual legacy across several disciplines. Decades of research on ecosystem ecology and ecosystem function inform the biological underpinning of service provision (Tansley 1935, Lindeman 1942, Odum 1953, Golley 1993), and many parallels can be drawn between modern ecosystem services research and the multiple-use paradigm in forestry and ecosystem management (Kessler et al. 1992; Christensen et al. 1996).

While the term *ecosystem services* dates back to 1981 (Ehrlich and Ehrlich 1981), contemporary ecosystem service research is widely acknowledged to have gained mainstream prominence only after the publication of Gretchen Daily's (1997) book, and particularly following the 2005 Millennium Ecosystem Assessment – which brought awareness to the simultaneous increase in demand for, and decline in supply of, many ecosystem services globally (MA 2005). Highlighting the need to map, model, and measure ecosystem services to inform decision-making and improve human wellbeing (Bennett et al. 2005, Carpenter et al. 2006), the

MA catalyzed a vast body of literature on ecosystem services that continues to grow (Seppelt et al. 2012, Bennett 2017). In the past decade, considerable advances have been made towards understanding synergies and tradeoffs among multiple services (Bennett et al. 2009, Nelson et al. 2009), spatial (Raudsepp-Hearne et al. 2010, Qiu and Turner 2013, Lamy et al. 2016) and temporal (Sutherland et al. 2016, Tomscha and Gergel 2016, Graves et al. 2017) patterns of ecosystem service provision, and the relationship between ecosystem services and biodiversity (Haines-Young et al. 2010, Mace et al. 2012, Balvanera et al. 2014, Harrison et al. 2014). However, much of this work has focused on production landscapes – i.e., agricultural or forested systems – with ecosystem services research only much more recently gaining prominence in urban areas (Ziter 2016, Schwarz et al. 2017).

An improved understanding of urban ecosystems, and the services they provide, is critical in today's world. Up to 75% of the global population is expected to live in cities by 2050 (United Nations 2012), with urban areas expanding twice as fast as population growth (Seto et al. 2012). This increasing urbanization not only has a large environmental impact – urban areas account for the majority of global energy use and 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 drivers (Groffman et al. 2014). Urban ecosystems are temporally dynamic and spatially heterogeneous, have distinct climates, and often differ greatly in their biodiversity compared to surrounding rural or natural ecosystems (Cadenasso et al 2007, Forman 2014, Groffman et al. 2016, Lepczyk et al. 2017, Pickett et al. 2017). By virtue of these changes to ecosystem function and structure, urban expansion includes both obstacles to, and opportunities for, ecosystem services.

Existing at the nexus of high population density and high consumption, cities are often thought of as areas of ecosystem service demand or consumption, rather than supply – and consequently are often absent from major ecosystem service syntheses (e.g. Seppelt et al. 2011, Balvanera et al. 2014). An increasing body of research shows that urban ecosystems can also be significant providers of services to local residents, however, particularly as cities grow to encompass broader spatial areas (Gaston et al. 2013, Haase et al. 2014). Urban green spaces improve aesthetics, give residents places to recreate (Andersson et al. 2015), and provide access to local food (Lin et al. 2015). Local provision of ecosystem services not only increases the 'livability' of a city, but also provides health and safety benefits, for example moderation of heat island effects that engender a host of serious health issues (Patz et al. 2005, Jenerette et al. 2015), and improvement of mental health and wellbeing (Soga and Gaston 2016, Cox et al. 2017). Urban ecosystems can provide benefits beyond city borders, as well; some cities can store as much carbon per unit area as tropical forests, including an estimated 10% of total US carbon storage (Churkina et al. 2010), and may provide a refuge for species of conservation concern such as insect pollinators (Kaluza et al. 2016, Hall et al. 2017).

Despite this recent growth in urban ecosystem service research, there remain considerable gaps in our understanding of ecosystem services in urban areas compared to production or natural systems (Gaston et al. 2013, McPhearson et al. 2016). For example, most urban studies consider only one service (Haase et al. 2014, Ziter 2016), precluding consideration of synergies and tradeoffs, as well as discussion of how shared drivers or management decisions may affect multiple services within a city. To increase sustainability of cities, researchers and decision-makers need a better understanding of how to manage urban areas for multiple ecosystem services (Wu 2014). Additionally, many studies rely on land cover or habitat based proxies to map ecosystem services (Zhao and Sander 2018), often using relationships derived in non-urban systems. Such proxies may be poor surrogates for service provision (Eigenbrod et al. 2010); likely particularly so in urban ecosystems, where land use and management intensity change frequently over time, and within-land-cover variability is typically high (Cadenasso et al. 2007, Pickett et al. 2017). Recent work outside of urban landscapes shows both spatial patterns (Qiu and Turner 2013, Mitchell et al. 2013, Lamy et al. 2016), and temporal dynamics (Renard et al. 2015, Tomscha and Gergel 2016, Graves et al. 2017) are important drivers of ecosystem services and their interactions. Given the fine spatial heterogeneity and complex land use history that characterize most urban areas, cities are powerful – and under-utilized – systems for exploring the influence of current landscape structure and land use legacies on service provision.

The relationship between biodiversity and ecosystem services is also ripe for consideration in urban areas, which have been largely absent from biodiversity-ecosystem service syntheses (Cardinale et al. 2012, Balvanera et al. 2014). Understanding this relationship at scales relevant to decision-making is a priority of ecology research (Mace et al. 2012). There is little consensus, however, regarding which aspects of biodiversity – e.g. number of species or functional groups vs. specific species or their interactions – are most important for providing ES. Urban ecosystems are often characterized as low diversity, with just a few highly abundant species (Shochat et al. 2006); however, the influence of urban land use on biodiversity is much more nuanced (McKinney 2008). While loss and simplification of habitat in urban areas does lead to declines in many species, urban ecosystems also promote increased biodiversity via high habitat heterogeneity, high supplemental food sources, and high dispersal rates into urban areas due to accidental and deliberate importation (McKinney 2006, 2008, Avolio et al. 2018). These mechanisms often disproportionately favour non-native (and often invasive) species, which are both more likely than native species to be imported into cities, and to thrive there (McKinney

2006). Yet despite this pivotal role of non-native and invasive species in shaping urban biodiversity, their effects on ecosystem services remains a key question in urban ecology (McPhearson et al. 2016).

Compounding these challenges is a research bias towards a relatively small number of large cities. Although half the world's urban population lives in cities under 500,000 inhabitants (Brunn et al. 2011), a disproportionate number of urban ecosystem service studies focus on large centers – e.g., New York, Baltimore, Phoenix, Beijing, Berlin – rather than their small or midsize counterparts. A more complete understanding of urban ecosystem services must include not only large urban centers, but also smaller cities representative of those that many people live in.

This dissertation combines synthesis, observational, and experimental approaches to ask how landscape structure, historical land-use, and biodiversity impact multiple ecosystem services in urban landscapes. First, I conducted a global meta-analysis of urban ecosystem services (Chapter 1), focusing on the extent to which studies consider the organisms and ecosystem components responsible for service provision using two approaches: assessment of biodiversity-ecosystem service relationships, and an adaptation of Luck et al.'s (2009) service provider concept. The remaining chapters focus on empirical study of Madison, Wisconsin, a midsized North American city. Chapters 2 and 4 focus on landscape context, and advance our understanding of the spatial and temporal dynamics of ecosystem service supply. I first measured biophysical indicators of three ecosystem services (carbon storage, water quality regulation, runoff regulation) to ask how land-cover, land-use history, and within-land-cover variability influence ecosystem services in this historically agricultural urban landscape (Chapter 2). I then used a custom bicycle-based temperature sensor to characterize the intra-urban heat island – focusing on the potential of urban trees to provide temperature regulation services (Chapter 4).

Chapter 3 circles back to biodiversity, focusing specifically on invasion-ecosystem service linkages. I conducted reciprocal field experiments to ask how an incipient urban invader, the Asian jumping worm, might interact with an established invasive shrub, common buckthorn, with potential consequences for ecosystem services in urban/peri-urban landscapes.

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Chapter 1 – The biodiversity-ecosystem service relationship in urban areas: a quantitative review

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Abstract

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 [*Editor's Choice*]

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.

Introduction

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 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 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 (e.g. 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?

Materials 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 March 1st 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: (i) bibliographic information; (ii) the ES measured – including number, category, and specific service(s); (iii) the geographic region and habitat type(s) focused on; (iv) the spatial extent of the study; (v) whether specific policy or management recommendations were made; (vi) the service provider; (vii) the type of biodiversity measured (if applicable); (viii) the nature of the BES relationship, and; (ix) 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 3 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 9 studies that focused solely on aquatic habitats, 4 focused on wetlands, 4 on streams/rivers, and only 1 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

3 “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 3 assessed ES. Together, assessments of these 3 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 (9 assessments). Habitat and genetic diversity were measured in only 4 and 2 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 4 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 (9 assessments) or negatively (2 assessments) affected ES provision (Fig. 4). Rather, the BES link was most often characterized as dependent on the composition of species, 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 6, 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 3 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 3 specifically identifying these species as key ES providers.

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 Millenium Ecosystem Assessment (2005) identified a lack of research on regulating ES compared to provisioning, their dominance in the urban ES literature is perhaps unsurprising, given: a) 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; b) 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.

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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 Legends

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.

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.

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.

Figure 1

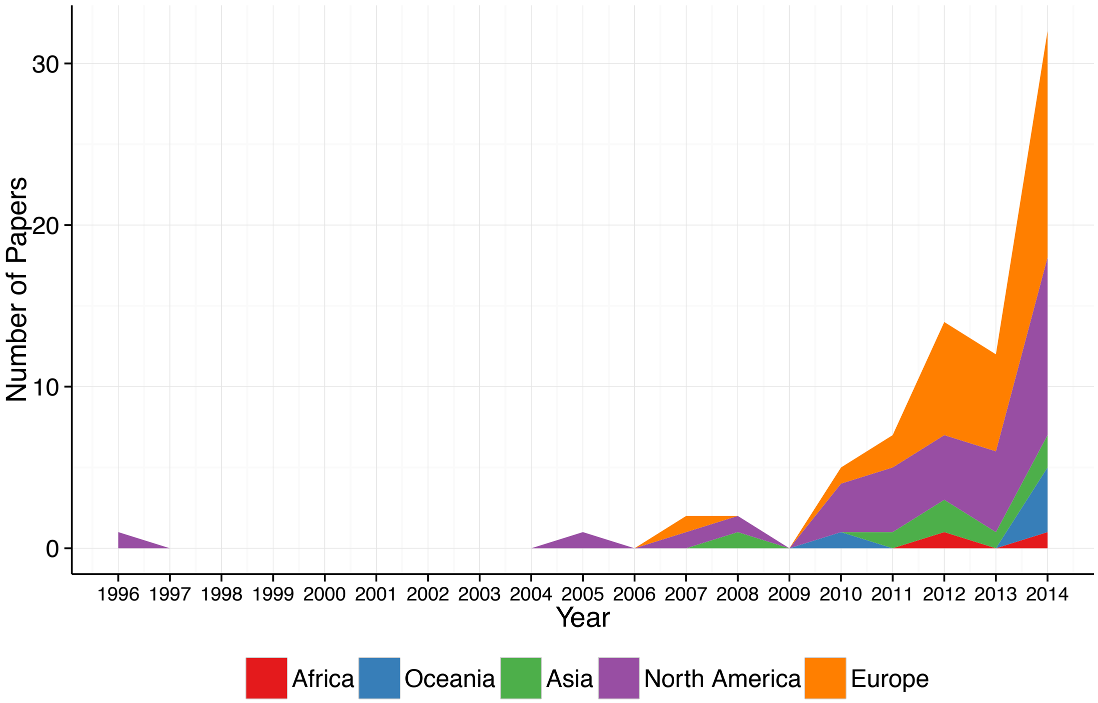
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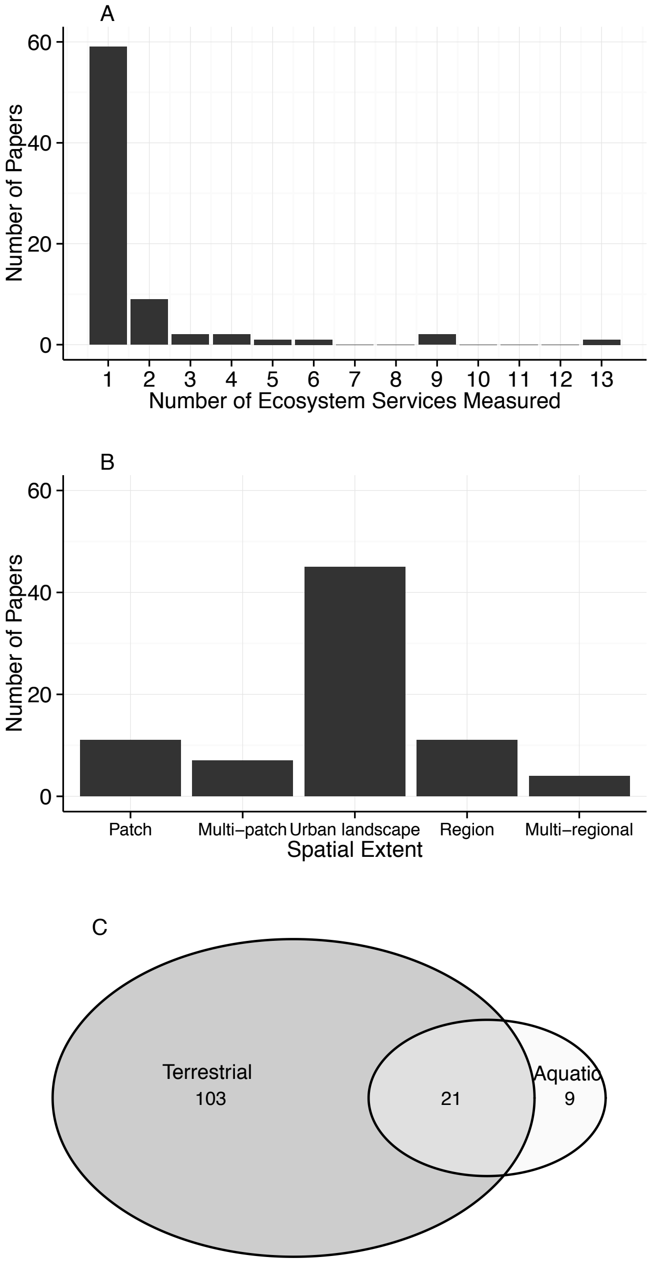
Figure 2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Aquatic
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Figure 3

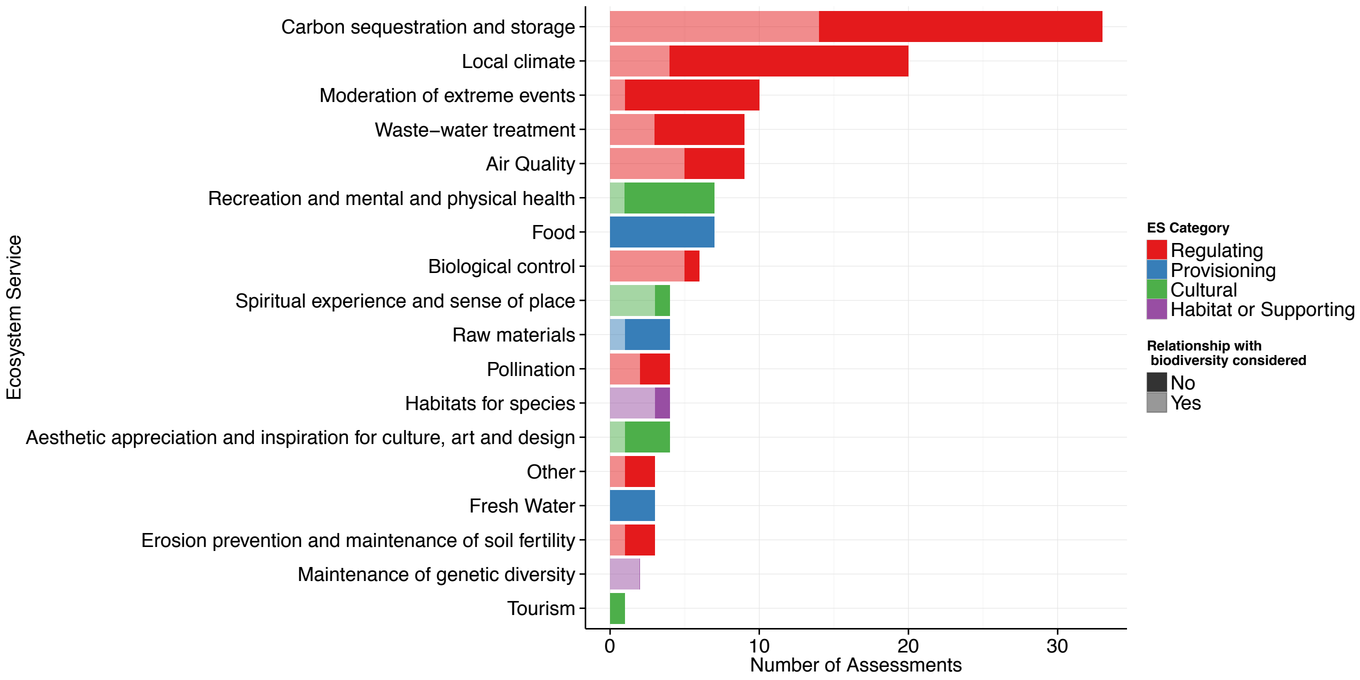

Carbon sequestration and storage
Local climate
Moderation of extreme events
Waste−water treatment
Air Quality
Recreation and mental and physical health
Food
Biological control
Spiritual experience and sense of place
Raw materials
Pollination
Habitats for species
Aesthetic appreciation and inspiration for culture, art and design
Other
Fresh Water
Erosion prevention and maintenance of soil fertility
Maintenance of genetic diversity
Tourism
Ecosystem Service
0
10
20
30
Number of Assessments
ES Category
Regulating
Provisioning
Cultural
Habitat or Supporting
Relationship with biodiversity considered
No
Yes

Figure 4

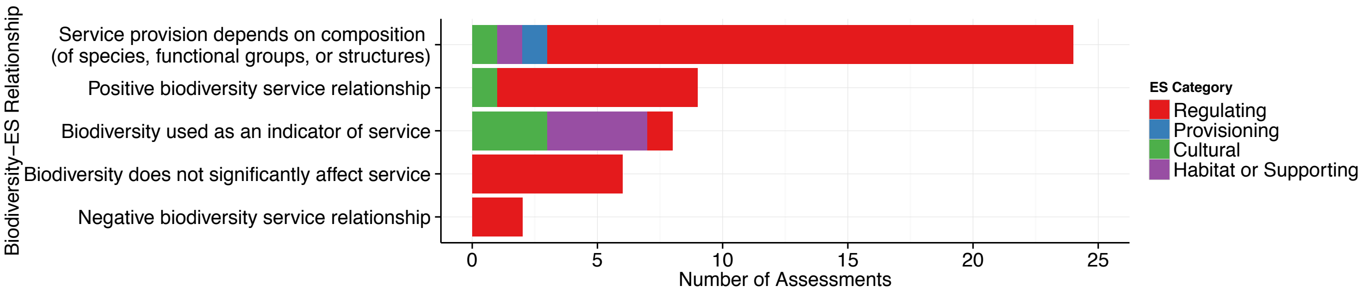
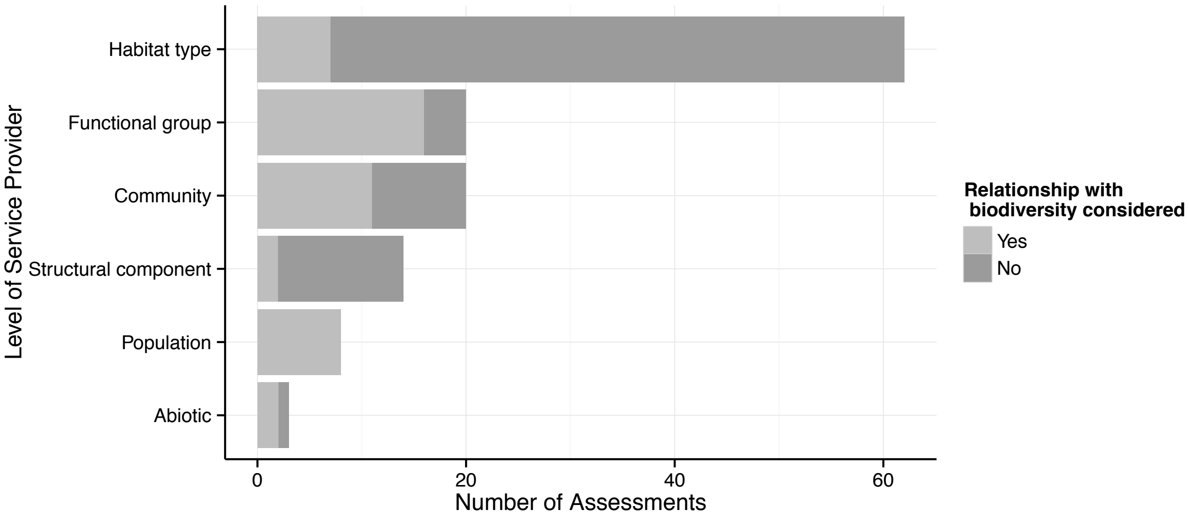

Biodiversity–ES Relationship
Service provision depends on composition
(of species, functional groups, or structures)
Positive biodiversity service relationship
Biodiversity used as an indicator of service
Biodiversity does not significantly affect service
Negative biodiversity service relationship
0
5
10
15
20
25
Number of Assessments
ES Category
Regulating
Provisioning
Cultural
Habitat or Supporting

Figure 5


Level of Service Provider
Habitat type
Functional group
Community
Structural component
Population
Abiotic
0
20
40
60
Number of Assessments
Relationship with biodiversity considered
Yes
No

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Supplementary Material

Appendices for: Ziter, C. 2016. The biodiversity-ecosystem service relationship in urban areas: a quantitative review. Oikos doi: 10.1111/oik.02883

Appendix 1

List of data sources used in meta-analysis

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Appendix 2

Appendix 2 contains the dataset used in the meta-analysis, and is available as an independent file (Appendix2.xls) at <www.oikosjournal.org/appendix/oik-02883>

Appendix 3

Table A1. Number of assessments for each ecosystem service that considered a biodiversity–ecosystem service (BES) link, and the type of biodiversity considered. Total (n) represents the total number of assessments, while BES (n) represents the number of assessments that considered a BES link. Note that a single assessment may measure more than one type of biodiversity, leading to a mismatch between BES (n) and the number of assessments per biodiversity type

Ecosystem service	Total (n)	BES (n)	No. of assessments per biodiversity type					
			Genetic	Species	Community	Functional	Structural	Habitat
Carbon sequestration and storage	(33)	(14)	0	12	3	2	6	1
Local climate	(20)	(4)	0	3	1	3	0	1
Moderation of extreme events	(10)	(1)	0	1	1	1	0	0
Waste-water treatment	(9)	(3)	2	1	2	0	0	0
Air quality	(9)	(5)	0	4	0	5	1	0
Recreation and mental and physical health	(7)	(1)	0	1	0	0	0	0
Food	(7)	(0)	0	0	0	0	0	0
Biological control	(6)	(5)	0	5	2	0	1	0
Spiritual experience and sense of place	(4)	(3)	0	2	0	0	1	0
Raw materials	(4)	(1)	0	1	0	0	0	0
Pollination	(4)	(2)	0	2	1	1	0	0
Habitats for species	(4)	(3)	0	1	0	0	0	2
Aesthetic appreciation/inspiration for culture, art, design	(4)	(1)	0	1	0	0	0	0
Other	(3)	(1)	0	1	0	0	0	0
Fresh water	(3)	(0)	0	0	0	0	0	0
Erosion prevention and maintenance of soil fertility	(3)	(1)	0	1	1	1	0	0
Maintenance of genetic diversity	(2)	(2)	0	2	1	0	0	0
Tourism	(1)	(0)	0	0	0	0	0	0

Table A2. The number of assessments within each service provider category for each ecosystem service.

Ecosystem Service	(n)	No. of assessments per service provider category						
		Population	Community	Habitat type	Functional group	Structural component	Abiotic	NA
Carbon sequestration and storage	(33)	2	7	14	4	5	1	0
Local climate	(20)	2	0	13	1	4	0	0
Moderation of extreme events	(10)	0	0	7	1	1	0	1
Waste-water treatment	(9)	0	4	4	0	0	1	0
Air quality	(9)	0	0	2	4	3	0	0
Recreation and mental and physical health	(7)	0	1	4	1	0	0	1
Food	(7)	0	1	5	1	0	0	0
Biological control	(6)	0	1	1	3	0	1	0
Spiritual experience and sense of place	(4)	1	1	0	1	0	0	1
Raw materials	(4)	0	0	2	1	1	0	0
Pollination	(4)	0	2	1	1	0	0	0
Habitats for species	(4)	0	0	4	0	0	0	0
Aesthetic appreciation and inspiration for culture, art and design	(4)	1	1	0	1	0	0	1
Other	(3)	1	0	0	0	0	0	2
Fresh Water	(3)	0	0	3	0	0	0	0
Erosion prevention and maintenance of soil fertility	(3)	0	0	2	1	0	0	0
Maintenance of genetic diversity	(2)	1	1	0	0	0	0	0
Tourism	(1)	0	1	0	0	0	0	0

Chapter 2 – Current and historical land use influence soil-based ecosystem services in an urban landscape

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Abstract

Urban landscapes are increasingly recognized as providing important ecosystem services (ES) to their occupants. Yet, urban ES assessments often ignore the complex spatial heterogeneity and land-use history of cities. Soil-based services may be particularly susceptible to land-use legacy effects. We studied indicators of three soil-based ES – carbon storage, water quality regulation, and runoff regulation – in a historically agricultural urban landscape and asked: (1) How do ES indicators vary with contemporary land cover and time since development? (2) Do ES indicators vary primarily among land-cover classes, within land-cover classes, or within sites? (3) What is the relative contribution of urban land-cover classes to potential citywide ES provision? We measured biophysical indicators (soil carbon (C), available phosphorus (P), and saturated hydraulic conductivity (Ks)) in 100 sites across 5 land-cover classes, spanning an ~125 year gradient of time since development within each land-cover class. Potential for ES provision was substantial in urban green spaces, including developed land. Runoff regulation services (high Ks) were highest in forests; water quality regulation (low P) was highest in open spaces and grasslands; and open spaces and developed land (e.g., residential yards) had the highest C storage. In developed land covers, both C and P increased with time since development, indicating effects of historical land-use on contemporary ES and tradeoffs between two important ES. Among-site differences accounted for a high proportion of variance in soil properties in forests, grasslands, and open space, while residential areas had high within-site variability – underscoring the leverage city residents have to improve urban ES provision. Developed land covers contributed most ES supply at the citywide scale, even after accounting for potential impacts of impervious surfaces. Considering the full mosaic of urban green space and its history is needed to estimate the kinds and magnitude of ES provided in cities, and to

augment regional ES assessments that often ignore or underestimate urban ES supply.

Key Words: Carbon; Ecosystem services; Historical ecology; Land-use change; Phosphorus; Runoff regulation; Saturated hydraulic conductivity; Soil; Urban ecosystems; Water quality

Introduction

Urban areas are complex mosaics of land-cover types with different land-use histories and vegetation conditions (Zhou et al. 2016), all of which can influence ecosystem services (ES) (Gaston et al. 2013) – the benefits people receive from ecosystems (MA 2005). Urban ecosystems are temporally and spatially heterogeneous at fine scales, have distinct climates, and can differ greatly in their biodiversity compared to surrounding natural and rural ecosystems (Forman 2014). Moreover, as urban areas expand, new green space is incorporated into existing cities, often on former agricultural land. Thus, cities are ideal for exploring the sensitivity of ES to current and past drivers (Dallimer et al. 2015), and assessing the degree to which land-use legacies may be unappreciated but important influences on ES (Ziter et al. 2017). However, studies of urban ES rarely address the high spatial heterogeneity and complex land-use histories of cities, particularly when considering multiple services (Gaston et al. 2013, Haase et al. 2014, Ziter 2016).

Many studies rely on land-cover based proxies to map ES (Haase et al. 2014, Ziter 2016) because of data constraints, and this can be an important first step towards inclusion in management or policy (Chan et al. 2006, Raudsepp-Hearne et al. 2010). However, land-cover based proxies are often poor surrogates for ES (Eigenbrod et al. 2010). This may be particularly true in urban ecosystems, given the lack of empirical data for many services, and high within-land-cover variability driven by differences in land-use and management (Loram et al. 2008). For example, various types of green space (i.e. non-impervious areas) within a city may be classified as the same land cover, but differ in plant community composition, number and size of trees, and soil conditions – leading to differences in ES. In Leicester, UK, researchers observed higher soil carbon stocks in residential yards than public green space, and under trees and shrubs compared to other vegetation (Edmondson et al. 2014). In Melbourne, Australia, degree of habitat complexity in urban parks influenced hydrological ES such as runoff regulation (Ossola et al. 2015). Yet such ecological differences are rarely considered in a land-cover based approach (Haase et al. 2014). A better understanding of the extent to which ES indicators vary among and within land-cover classes is needed to assess potential for current ES provision and to determine the degree to which changes in management might alter ES in heterogeneous urban landscapes.

Approaches based on current landscapes also ignore the role of past land-use in explaining contemporary distribution of ES. Time lags and land-use legacies are widespread ecological phenomena (Foster et al. 2003, Burgi et al. 2017), with historical land-use affecting ecosystem functions for decades to millennia (Dambrine et al. 2007, Rhemtulla et al. 2009, Mladenoff and Clayton 2009). Despite this knowledge, ES research has only recently begun to adopt temporal approaches (but see Díaz-Porras et al. 2014, Dallimer et al. 2015, Renard et al. 2015, Tomscha and Gergel 2016). Urban areas have undergone shifts in land use/land cover during development, and thus can be excellent systems for assessing effects of land-use legacies on ES. Indeed, in one of the few studies incorporating historical land use, five of eight ES in the city of Sheffield, UK were better predicted by past land-use than current patterns, with lag times ranging from 20 to 100 years (Dallimer et al. 2015). Understanding such legacies is central to understanding the extent that ES can be inferred from contemporary landscape pattern, as well as how ES and relationships between them may shift over time as landscapes continue to change (Ziter et al. 2017).

Urban ES dependent on soil and soil-vegetation relationships may be particularly susceptible to legacy effects and time lags in ES supply, as these services are underlain by slow ecological processes (Ziter et al. 2017). This is especially relevant in former agricultural areas (Raciti et al. 2011), which characterize many contemporary urban landscapes in North America. Agricultural activities (e.g., tillage, fertilization) fundamentally change soil nutrient pools such as carbon (C), nitrogen, and phosphorus (P). These legacies can last for decades to millennia following cessation of agriculture and re-establishment of forests or grasslands (Fraterrigo et al. 2005, McLauchlan 2007). However, few data exist regarding legacy effects in areas that subsequently urbanized (but see Golubiewski 2006, Pouyat et al. 2008, Raciti et al. 2011) – with existing studies often focusing on soil C in residential lawns. Urban lawns in both Colorado's Front Range and the city of Baltimore, Maryland (USA) store more soil C than native grassland or forest ecosystems, and older lawns store more C than young lawns (Golubiewski 2006, Raciti et al. 2011). Phosphorus has been hypothesized to follow the opposite trend, with soil P levels expected to decrease following agricultural conversion. However, legacy effects on urban soil P have been studied to a lesser extent than C, and the relationship is less clear (Bennett 2003, Kara et al. 2011), despite known implications for water quality (Hobbie et al. 2017, Motew et al. 2017). Urban ES research would benefit from further understanding of the effects of agricultural legacies on a greater number of services, across different types of urban green space.

We measured multiple soil-based indicators across 5 land-cover classes in a historically agricultural urban landscape to determine the extent to which current and past drivers influence three ES – carbon storage, water quality regulation, and runoff regulation (Table 1) – that are expected to be sensitive to patterns in land use/land cover and land-use legacies. These regulating services are socio-culturally valuable (Martín-López et al. 2012), and are among the most frequently researched ES in urban systems globally (Ziter 2016); yet to our knowledge, they have not previously been measured in the same study. We asked:

1. How do indicators of soil-based urban ecosystem services vary with contemporary land cover and time since development?
2. Do indicators of soil-based urban ecosystem services vary primarily among land-cover classes, within land-cover classes, or within sites?
3. What is the relative contribution of urban land-cover classes to soil-based ecosystem services at the citywide scale?

We expected agricultural legacies to be an important driver of ES, but that effects would differ among services. We anticipated that C storage and water quality regulation – ES based on soil pools (C and P) known to change slowly over time – would be more susceptible to legacy effects than runoff regulation. We expected runoff regulation to be more responsive to current land-cover, however, as we did not anticipate a strong legacy effect on soil texture, which is a key component of saturated hydraulic conductivity. We also expected the scale of variability to differ among soil properties, as well as between more- and less-developed land-cover types. Regarding soil properties, we expected C storage to show high within-site variability due to close association with litter inputs and thus fine-scale patterns of vegetation, and available P to show lower within-site, but high among-site variability due to agricultural legacies of fertilizer application (which tends to be applied evenly within fields, but vary between farms/farmers, e.g. Bennett et al. 2005). We expected saturated hydraulic conductivity to show high among-land-cover variability, as we anticipated differences in soil texture and compaction to be more pronounced at this scale. We also anticipated more developed land-cover types (e.g., residential yards) to show higher within-site variability in soil properties, due to higher anticipated fine-scale heterogeneity in vegetation and management than in semi-natural (e.g., forest, grassland) sites, where we anticipated higher between-site variability.

Methods

Study area description

This study was conducted during summer 2015 in Madison, Wisconsin, USA (Fig. 1), which encompasses 244 km^2 (199 km^2 land, 45 km^2 water) (US Census Bureau 2010), and is bordered by several suburbs (city population 245,000; urban area population 407,000). The climate is continental, characterized by warm humid summers, and cold winters (1981-2010 mean temperature 22°C July, -7°C January, annual precipitation of 87.6-cm; National Climatic Data Center). Situated in an urbanizing, agricultural watershed, much of the City of Madison was developed on former farmland, and the surrounding county remains primarily in agricultural production. Current land cover in the city is dominated by low- and medium-density developed land and open space, but also includes deciduous forest, high-density developed land, and grassland (Table 2). The remainder of the city is made up of agricultural land at the city's outskirts, wetlands, and barren land.

As in many urban landscapes, cultural and socio-economic variability in the city's many distinct neighbourhoods underlies management and aesthetic decisions that contribute to ecological variability of yards and other private green space. Madison also has a strong legacy of appreciation for urban natural areas, including a network of 250 parks and over 700 ha of conservancy land (Park Division 2012). Bolstered by the University of Wisconsin Arboretum and Lakeshore Preserve, this wealth of green space places Madison among the nation's highest ranked cities for per capita parkland. Combined with the considerable area of private yards and gardens in this mid-sized city, this variety and abundance of green space provides ample opportunity to study urban ES.

Soils in the region developed under the influence of past glaciation, which left behind a sandy-loam, calcareous till in the eastern two-thirds of Dane County. Soils in the greater Madison area are predominantly Alfisols (Hapludalfs in particular), and to a lesser extent Mollisols (predominantly Argiudolls and Endoaquolls) – which are associated with the forest and oak-savanna vegetation that dominated the region prior to European settlement – along with pockets of wet sedge meadows (Bockheim and Hartemink 2017; Fig. S1). Soils underlying study sites are largely Typic Hapludalfs (50% of sites, predominantly Dodge, McHenry, St. Charles series) and Mollic Hapludalfs (21% of sites, predominantly Batavia series). Comprising a further 20% of sites are Typic Argiudolls (7%, predominantly Plano series), Typic Endoaquolls (7%, predominantly Colwood series), and Udollic Endoaqualfs (6%, Virgil series) (Table S1; Data available from the Soil Survey Geographic (SSURGO) database (NRCS, 2017)).

Study design

We used a stratified design including five land-cover classes – forest, grassland, open space, and low- and medium-density developed land (Table 2) – with sites spanning an ~125 year gradient of time-since-development within each land-cover class. A total of 100 sites (n=20 within each land-cover class) were selected to span these gradients and cover the geography of the city (Fig. 1a). Sites within each land-cover class were well distributed geographically throughout the city to avoid bias due to underlying soil type or other edaphic features. We obtained landowner permission for all sites prior to sampling.

Selected land-cover classes represent a continuum from semi-natural to more developed green space, and include both private and public land. Given the predominantly agricultural history of the region, we chose time since development as a proxy of time since conversion from agricultural use. For low- and medium- density developed land covers, comprised of residential property, this gradient was based on the year built (City of Madison Assessor's Office; Fig. 1b). We identified suitable candidate sites using GIS software, and canvassed for permission. To again avoid underlying spatial patterns that may bias our results, we deliberately ensured that sites of similar ages were geographically distributed throughout the city to the extent possible. Similar methods were followed for open space and grassland sites – however, the temporal gradient was based on available historical records, as well as consultations with the City of Madison parks department and private land managers. For forest sites, we used three sets of aerial photos (from 1937, 1974, and 2013) to choose sites that were in forest cover prior to 1937, between 1937 and 1974, and post-1974.

Field sampling

Each site consisted of a 30 x 30m area, within which we established four 5x5m subplots (one in each quarter) to assess the effect of fine-scale heterogeneity on soil properties. In each subplot, we conducted vegetation surveys to account for variability in vegetation type and structure within and among sites, with the specific assessment dictated by the land-cover class (Appendix S1).

We collected soil samples for chemical analysis (C, P) at 0-5, 5-10, 10-25 cm fixed soil-depth intervals. Three 2-cm diameter cores were collected from each 5x5 m subplot, then composited into one sample per depth per subplot (i.e., four samples per depth per site). We also collected one 10-cm depth bulk density (g cm^{-3}) core from each 5x5m subplot using a 184-cm^3

stainless steel cylinder (4.8-cm inner diameter) connected to a slide hammer. Logistical and safety concerns precluded deeper sampling in an urban context, where buried utility or irrigation lines, etc., are a concern.

Soil preparation and analysis

Composite samples for chemical analysis were air dried, followed by oven drying for 24hrs at 60C. Samples were mechanically crushed to pass through a 2-mm sieve, and visible plant roots and residue discarded. For C analysis, soil samples were ground to a fine powder, and chemical analysis conducted on finely ground subsamples. Total C was analyzed by high-temperature catalytic combustion (Carlo-Erba Model NA 1500 C and N analyzer, CE Instruments, Milan, Italy). Percent C was converted to C mass for each site using soil bulk density. For P analysis, dried and ground subsamples were sent to the Soils and Plant Analysis Lab at the University of Wisconsin-Madison, where a Bray 1 extract procedure was used to analyze available P (Bray and Kurtz 1945). The Bray 1 method was generally developed as an estimate of P available to plants in agricultural systems, rather than as a reflection of P storage in soil or P runoff. However, Bray 1 P is related to dissolved P in runoff in several systems (Sharpley 1995; Ebeling et al. 2008; Wang et al. 2010), Bray 1 P is well correlated with total P in our system (Bennett 2003). Thus, Bray 1 P is likely to provide a good estimate of the sorbed P that accumulates in soils. Bulk density samples were air dried, followed by oven-drying at 70C for 48hrs, and weighed to determine soil mass on a dry-weight basis. Following bulk density determination, we analyzed samples for soil particle size. Sand, silt and clay content were measured using the hydrometer method, which uses sedimentation rates based on Stoke’s law (Bouyoucos 1962) (Table S2), and soil texture assigned according to the USDA major textural classes (Fig. S2). A pedotransfer function (Saxton and Rawls 2006) was used to estimate Ks from soil texture, bulk density, and organic matter (calculated from soil C measurements, under the assumption that 58% of soil organic matter is soil organic C).

Data analysis

To evaluate effects of land cover and time since development (Q1), we used linear mixed models (using R's "lme" in the "nlme" package) to test for significant differences in soil C (kg m^{-2}), P (ppm), and Ks (mm hr^{-1}) (significance level $\alpha = 0.05$). For all models, subplots were nested within sites as a random effect. First we tested for significant differences in each ES indicator among all five land-cover classes, with C and P aggregated over depth (R Core Team 2012). Second, we tested for significant effects of land-cover class, time since development, and depth (for C and P) on soil C, P, and Ks among the four land-cover classes for which the year of development was available (i.e. excluding forests – where limited temporal data was available to assess trends). Third, we modeled each land-cover class separately to assess the effects of time since development, depth, and their interaction on soil properties within each land-cover class. Model residuals were visually inspected for normality using diagnostic plots, and log transformations were performed as appropriate to improve normality. For open space sites, we also assessed historical aerial photos to determine whether or not the sites had been in agricultural use prior to development, and tested for significant differences in soil properties between those sites previously used for agriculture compared to those that had not been.

To account for potential spatial patterns beyond those accounted for by city structure, we re-ran all models as generalized additive mixed models (using R package "mgcv") with latitude/longitude added as a smoothing term. We used a penalized latitude/longitude term, so that variance was first attributed to the fixed effects (i.e. land cover, time since development), and then to latitude/longitude if not captured by the fixed effects. The spatial term was non significant in almost all cases, and did not substantively alter results after accounting for land cover and time since development (Appendix S1). Thus, we present results of the more easily interpretable, and slightly more conservative, mixed models here. Results were qualitatively similar for all soil properties. Additionally, analyses of percent C rather than mass showed qualitatively similar results, and are not presented here.

To identify the scales at which variance was most pronounced for each soil property (Q2), we used variance partitioning to assess relative variance in soil C, P, and Ks at three levels: among land-cover classes, among-sites, and within individual sites (using “VarCorr” in R’s “lme4” package). We also conducted this analysis separately by land-cover class to quantify relative variance in each soil property at two levels: among sites and within sites.

To estimate the relative contribution of each land-cover class to citywide ES (Q3), we accounted for the role of impervious surfaces – under various assumptions representing the effect of impervious cover on soil properties – followed by area-based extrapolations. Impervious surface was split into building cover and non-building impervious (e.g., roads, sidewalks, driveways, etc.), and calculated for each land-cover using QGIS. Impervious surfaces were quantified using NLCD percent impervious data (Xian et al. 2011, Haase et al. 2014), with building cover quantified using Lidar derived building footprint data for the City of Madison. For all soil properties, we assumed a value of zero under building footprints (sensu Edmondson et al. 2014). Basements are very common in our study region, which will preclude substantial soil nutrient pools under buildings at the depths considered here. For C under non-building impervious surfaces, we considered three alternatives to assess the sensitivity of our results to varying assumptions: (1) assume equivalent soil C as in non-impervious surfaces (consistent with findings by Edmondson et al. 2012); (2) assume 50% C (consistent with studies finding lower, but still substantial C pools under non-building impervious (Raciti et al. 2012, Wei et al. 2013), and (3) assume zero C under non-building impervious (a common assumption for urban areas, and the most conservative possible bound). For P under non-building impervious surfaces, we considered two alternatives: (1) assume equivalent soil P as in non-impervious surfaces (consistent with Wei et al. 2013), and (2) assume zero P under non-building impervious surfaces (i.e. assume any P under impervious surfaces does not influence water quality). For Ks, we assumed zero infiltration for any impervious surfaces.

Results

Urban vegetation

Vegetation differed among land cover categories (Appendix S1), but these differences were not strongly correlated with any measured soil properties.

Variation in ES indicators with land cover and time since development (Question 1)

Differences among land cover classes

All three ES indicators differed among land-cover classes (C ($F_{4, 95} = 7.16$, $P < 0.0001$); P ($F_{4, 95} = 2.96$, $P < 0.05$); Ks ($F_{4, 95} = 4.19$, $P < 0.01$); Fig. 2). Mean soil C (summed to 25-cm depth) ranged from 6.4 – 9.3 kg m^{-2} (Table 3, “original field values”). Carbon density was highest in more developed land covers, including both open space and residential areas (i.e. medium- and low-density developed), and lowest in semi-natural land covers (forests, grassland) (Fig. 2a). Mean available P (averaged over 25-cm depth) ranged from 38.6 – 62 ppm (Table 3, “original field values”). Phosphorus was highest in residential areas, lowest in open space and grasslands, and intermediate in forested areas (Fig. 2b). Mean saturated hydraulic conductivity ranged from 34.6 – 67 mm hr^{-1}(Table 3, “original field values”). Ks was highest in forests –

likely driven by relatively lower bulk density and lower clay content (Table S2), followed by grasslands. Ks was lowest in open space, with residential areas intermediate (Fig. 2c).

Differences with time since development and soil depth

Soil C density was consistently higher in shallow soils ($F_{2, 859} = 892.94$, $P < 0.05$; Fig. 3a-d). Soil C also varied with time since development, but that relationship differed among land-cover classes and with depth (Fig. 3a-d). Soil C increased over time in low-density developed sites, and the relationship was stronger in deeper soils (> 5 cm), where C increased by ~3.3 – 4.4% per decade of development (Fig. 3c). Soil C also increased over time in medium-density developed sites, again showing a depth-by-time interaction, and increasing by ~3.4% per decade of development (Fig. 3d).

Soil P concentration was consistently higher in shallow soils ($F_{2, 873} = 63.31$, $P < 0.0001$). Soil P concentration decreased or remained constant with time since development in grassland (Fig. 3e) and open space (Fig. 3f) sites, although open spaces used for agriculture prior to development had higher P than those that were not previously in agriculture (46 ppm (± 8.4 SE) vs. 26 ppm (± 8.7 SE), respectively; $F_{1, 18} = 6.48$, $P < 0.05$). In contrast, soil P increased with time since development in low- (by 7.4% per decade; Fig. 3g) and medium-density developed sites (by 4.9% per decade of development; Fig. 3h).

Saturated hydraulic conductivity increased with time since development in open space sites (Fig. 3j), but showed no relationship with time since development in grasslands (Fig. 3i), low- (Fig. 3k) or medium-density developed sites (Fig. 3l). In open space sites, Ks increased by 8.3% per decade of development (Fig. 3j).

Scale of variance in ES indicators (Question 2)

Most variation in ES indicators occurred among sites of the same land-cover class, followed by within-site, and lastly among land covers (Fig. 4a). However, variance was partitioned at different scales among land-cover classes. In forest, grassland, and open space land-cover classes (e.g. non-residential areas), most variance was among sites (broader scale) rather than within sites. In contrast, in low- and medium-density developed lands, most variance was within sites (finer scale) rather than among sites (Fig. 4b-d). These trends were consistent for all three soil properties.

Relative contribution of land-cover classes to citywide ES (Question 3)

The five land-cover classes considered encompass 76% of the City of Madison, and include the major areas of urban green space. However, land-cover classes differed in amount of impervious surface, which varied from 1 to 56% (Table 2). The relative contribution of each land-cover class to citywide ES depended on the assumed effect of impervious surfaces. Under the assumption that C is not present under buildings, but is stored in equivalent amounts under green space and non-building impervious surfaces, the relative contributions of the five land-cover classes remained consistent with measured field values (Table 3). Under the assumption that C is reduced by up to half under non-building impervious surfaces, open space remained the highest contributor to soil C stocks, and low- and medium density developed areas stored approximately equal C per unit area to semi-natural areas (6.0 – 6.2 kg m^{-2} for residential areas vs. 6.3 – 6.6 for grasslands and forests; Table 3). Only under the most conservative scenario (assuming zero soil C stocks under any type of impervious surface), did semi-natural land covers store more C per unit area than residential areas, although open space areas still stored the most C of any land-cover class (Table 3). Similarly for P, assuming equivalent P under non-building impervious surfaces resulted in minimal change to the relative contributions of different land-cover classes. Assuming zero P under any impervious surfaces altered the relative contributions, with residential areas then storing less P per unit area than forests (27.4-38.3 ppm for low/medium density residential vs. 48.6 ppm in forests), and medium-density developed areas in particular switching from the highest P values to the lowest (Table 3). Ks was the ES indicator most strongly influenced by impervious surfaces, with residential areas, and particularly medium-density developed demonstrating substantially lower Ks per unit area due to high impervious areas that provide no infiltration capacity (Table 3).

Accounting for the area of the city in each land-cover class, low-density developed areas account for the majority of C and P storage (~36% and 42%, respectively), and provide the greatest overall infiltration (36%) across the city (Table 4). Semi-natural areas contribute disproportionately to infiltration services, with grasslands and forests supplying 9% and 19% of Ks (respectively), despite comprising only 6% and 9% of considered land area (Table 4).

Discussion

Biophysical indicators of three soil-based ES – carbon storage, water quality regulation, and runoff regulation revealed considerable potential for ES supply in cities. Even developed land has substantial potential for ES provision. Urban soils stored more C on average than the agricultural soils that dominate the surrounding landscape (Kucharik and Brye 2013), and less P than agricultural soils (Bennett 2005) (although urban soil P was higher than in nearby remnant prairies; Bennett 2005). Soil properties also varied with time since development, indicating that land-use legacies can influence contemporary ES in cities. Given that urban areas comprise a substantial proportion of many landscapes (e.g., 25% of the Yahara watershed), excluding or undervaluing urban ES may lead to underestimates of regional ES.

Differences in ES indicators among land-cover classes

The higher C stocks in open spaces and residential areas relative to forests and grasslands (Fig. 2a) is consistent with previous work in urban and suburban landscapes (Golubiewski 2006, Raciti et al. 2011; Groffman et al. 2017). However, soil C did not differ between open spaces and residential areas in Madison, in contrast to other studies (Pouyat et al. 2006; Edmondson et al. 2014). High soil C in the three most developed land-cover classes studied may reflect high productivity of managed turfgrass systems (Poeplau et al. 2016), as well as irrigation and fertilization of residential yards (Groffman et al. 2016). Urbanization-driven increases in soil C stocks have the potential to increase ecosystem C stocks at regional through continental scales as cities expand (Groffman et al. 2014; 2017); however, lifecycle analyses are needed to determine whether increased C stocks are offset by C emissions from management practices (e.g. mowing, fertilizer production; Strohbach et al. 2012).

The high P stocks measured in residential areas compared to other urban land covers may also be a function of household-level management (Fig. 2b). Phosphorus fertilizer was banned within Madison city limits in 2005 (Dane County Code of Ordinances Chapter 80), but soil P from decades of prior use on residential lawns still persists in the contemporary landscape (see discussion of legacy P, below). Household pets can also increase soil P; nutrient inputs from pet waste contributed up to 76% of total P inputs in residential watersheds in Minnesota (Hobbie et al. 2017). Thus, lower P stocks in open spaces and grasslands may be explained in part by less fertilization and more removal of pet waste compared to residential yards. Exceptions to these general patterns, such as intensively managed golf courses, contribute to the high variability in open space P (Fig. 2b, gray dots). That soil P is highest in residential areas is worrisome for water quality, as the impervious cover and street density that characterize such areas can lead to high P in stormwater runoff (Pfeifer and Bennett 2011; Hobbie et al. 2017).

The relatively high Ks observed in forests and grasslands compared to developed land-cover classes is consistent with impairment of infiltration associated with urban development (Gregory et al. 2006; Zhou et al. 2008; Woltemade 2010) and higher average hydraulic conductivity compared to pasture, cropland, or urban land (Zimmermann et al. 2006; Zhou et al. 2008; Horel et al. 2015). In our system, the high Ks in forests is likely attributable to the somewhat lower bulk density and clay content in forest soils relative to other land covers (Table S2). Similarly, the lower bulk density of many prairie restorations, particularly older sites that had not been tilled, may explain the higher average Ks compared to more developed areas. Semi-natural areas are less likely to have undergone the compaction that often accompanies development of homes or parks.

Differences in soil properties among urban land-cover classes were sometimes counterintuitive and associated with surprising tradeoffs. For example, open spaces had both the highest C storage (corresponding to high organic matter) and the lowest Ks (Fig. 2ac), presenting a potential ES tradeoff where a synergy might have been expected due to the influence of organic matter on Ks (Fig. 2ac). Additionally, residential areas were high in both C and P, presenting a C storage/water quality tradeoff, but open spaces were high in C but low in P, indicating a synergy between these ES indicators (Fig. 2a,b). These results emphasize the difficulty of making assumptions about ES across land-cover types, even when vegetation is similar (e.g., residential lawn vs. public park), and point to the role of local land-use decisions in driving ES. Further, supply of a given ES does not necessarily extend to other services of interest (Nelson et al. 2009, Bennett et al. 2009, Qiu and Turner 2013). Thus, management for multiple ES in cities requires considering of the full mosaic of urban green space, including public and private land.

Effects of land-use legacies on ES indicators

Contemporary land cover was alone insufficient to predict soil-based ES in cities; historical land use had a strong effect, particularly in developed land covers. While land-use legacies are widely recognized in studies of land abandonment followed by succession, relatively few studies have considered effects of historical land use in cities (but see Dallimer et al. 2015). The increased C observed in older residential soils may represent C built up following cessation of agriculture (Raciti et al. 2011), as cultivation reduces soil C (Guo and Gifford 2002). Recovery from physical disturbance associated with construction may also play a role, with faster vegetation-driven recovery of surface soils compared to deeper soils (Fig. 3cd) (Golubiewski 2006, Johnston et al. 2016).

The steady increase of C and P with time since development in residential areas – but not in other turfgrass-dominated open spaces or grasslands – may be attributable in part to management history of irrigation, mowing, and fertilization (Groffman et al. 2016, Hobbie et al. 2017). Thus, historical land management is layered upon agricultural legacies. The 2005 P fertilizer ban may slow or halt the increase in urban soil P, but 12 years is likely too short relative to decades of P inputs to detect the benefit of this policy change (Bennett et al. 1999, Motew et al. 2017). Concomitant increases in C and P also suggests a stronger tradeoff between C storage (high C) and water quality regulation (low P) in older neighborhoods than in newer developments. Relationships among ES are not necessarily static (Tomscha and Gergel 2016) and accounting for history can improve understanding of contemporary and future ES patterns.

In non-residential green spaces, past land use/land cover seemed to better predict soil properties than time since development; i.e., knowing what pre-dated the green space mattered more than knowing when it was created. City parks established prior to agricultural conversion or on already developed land (e.g., donation of an estate; Mollenhoff 2004), had lower P, but parks that were farmed previously had high soil P, consistent with agricultural legacies (Bennett et al. 1999, Sharpley et al. 2013, Motew et al. 2017). Grassland P was likely also agriculturally driven. The two oldest grasslands in our dataset were prairies restored before industrial agriculture, thus avoiding high P inputs. Explanations for increased Ks with time since development in open spaces (Fig. 3j) are less clear. Many older city parks have sandy soils, as they were often developed along lakeshores. Soils in more recently developed open spaces, which are often used for organized sports, may also have been more compacted (Gregory et al. 2006). A lack of detailed data regarding management history precludes a stronger understanding of the relative roles of agricultural legacies vs. historical land management in explaining the observed trends. Future studies should consider the role of previous land-use compared to management or vegetation-driven trends over time, and also consider deeper soil samples, which may reveal further differences among land covers.

Spatial scales of variation among ES indicators and land-cover classes

Differences among land-cover classes in the spatial scales at which variance in soil properties was most pronounced offered insights into how urban lands are managed. Soil properties in forests, grasslands, and open spaces were most variable among sites, which aligns well with the typical scales at which vegetation and management vary in these urban green spaces. For example, two grassland sites may be composed of a grassy meadow and a restored forb-dominated prairie, or one site may be regularly burned while another is unmanaged (Fig. S3). Contrastingly, soil properties in low- and medium-density developed areas were most variable within-sites, reflecting the fine-scale heterogeneity of the residential urban landscape (Cameron et al. 2012, Polsky et al. 2014, Zhou et al. 2016). For example, a 30x30m site in a residential area may contain land parcels managed by different owners, or include front and back yards managed differently (Polsky et al. 2014; Fig. S4). This high fine-scale variability on private land highlights the potential for individuals to improve urban ES supply (Cerra 2017). Future research should focus on fine-scale drivers of urban ES (Grafius et al. 2016), including the social factors that play important roles (Larson et al. 2015, Groffman et al. 2016, Conway 2016, Aronson et al. 2017).

Relative contributions of urban land cover classes to citywide ES

Developed land covers were of high importance regarding citywide ES, even with relatively conservative assumptions regarding the impact of impervious surfaces. Low- and medium-density developed land accounted for over 50% of C stocks in urban green space, and contained ~60% of the city's available soil P. While the latter may negatively influence potential water quality regulation, the ultimate fate of soil P is influenced by the surrounding landscape. Soil erosion (which carries P-laden soil into waterways) may be decreased in areas dominated by turfgrass and impervious surfaces, in which case soil P in developed land could be sequestered for decades, and thus high soil P could be construed as a benefit. However, this same soil P stock could also contribute to a delayed effect of land use on ES supply (Ziter et al. 2017), whereby heavy rain events or other disturbance will facilitate movement of legacy P into surface waters (Motew et al. 2017). Construction or re-development of impervious areas, for example, would render previously protected P susceptible to loss through erosion (Betz et al. 2015). Impervious surfaces may also contribute indirectly to greater P loss by increasing runoff, although quantifying the impact of impervious surfaces on urban hydrology is complex, and the role and importance of permeable areas remains unclear (Booth and Jackson 1997, McGrane 2016). Potential interactions between built infrastructure and multiple ES is beyond the scope of this work, but remains an area ripe for future research (Svendsen and Northridge 2012).

Less-developed green spaces also have an important role in a city and may contribute disproportionately to urban ES. For example, urban forests comprised < 9% of the total land cover in Madison, but provided 19% of the citywide infiltration capacity. Consequently, the infiltration capacity of urban landscapes, while limited, is disproportionately attributable to forests (Maes et al. 2009). This reaffirms the importance of a mosaic of urban green space rather than a single solution for maximizing urban ES supply.

Conclusion

Ecosystem services can be substantial in urban landscapes, including on developed land. Considering the full mosaic of urban green space is needed to estimate the kinds and magnitude of ES provided in cities, and to augment regional ES assessments that often ignore or underestimate urban ES supply. And while land cover is important, it may be an unsuitable proxy for urban ES. The importance of past land use is recognized in ecology, but this temporal dimension is only recently considered in studies of ecosystem services and infrequently considered in urban ecosystems. Knowledge of historical land-use can improve estimates of contemporary ES and should be considered – especially in expanding urban areas. Future ES studies in urban ecosystems should also consider the fine-scale drivers of ES that can give landowners and managers further agency over the impact of their decisions.

Urban stakeholders and actors can also take an active role in increasing ES provision in urban landscapes. Planners and developers, for example, can encourage a diverse mix of land covers (e.g., forest and prairie in addition to turfgrass) in urban green spaces to capture a range of services; rather than plans that may maximize one service at the expense of others. Private land managers – including homeowners and residents – can also encourage ES provision on their property. Minimizing paved surfaces during building and landscaping decisions allows for maximum infiltration and carbon storage. Homeowners can also take precautions to reduce soil erosion during disturbances such as landscaping or construction, preventing legacy nutrients from being carried into waterways. Even simple actions such as reduced fertilizer application and diligent pet waste removal can contribute to reduced watershed nutrient loads over time. While seemingly small at the individual scale, such actions can scale up to make a positive difference well beyond single properties – contributing to more sustainable cities.

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Data Accessibility Statement

Data associated with this paper has been deposited in Dryad

Table 1. Ecosystem services, biophysical indicators, and rationale for three soil-based ecosystem services quantified across land-cover types and historical gradients in Madison, WI

Ecosystem Service	**Indicator**	**Description/Rationale**
Carbon storage	Soil carbon (C)	Soil carbon storage typically accounts for the majority of carbon storage in urban systems. Soil C acts not only as a climate regulation service, but is also indicative of general soil quality, underlying a range of benefits
Water quality regulation	Available phosphorus (P)	Phosphorus is a key driver of surface water quality in the Madison region (Motew et al. 2017). Soil phosphorus levels are indicative of potential P runoff into water bodies. While available P (Bray 1-P) is not a direct measure of total P or P runoff, available P is closely correlated with total P in our study area (Bennett 2003), and is also comparable with historically available data.
Runoff regulation	Saturated hydraulic conductivity (Ks)	Soil condition is a key factor linking land use and runoff/ flood regulation (Depietri et al. 2011). Ks, derived from soil texture, organic matter, and bulk density, is a key control over potential infiltration rates.

Table 2. Five land-cover classes encompassing the majority of urban green space in Madison, WI, including the proportion of each land-cover class comprised of building-cover, non-building impervious cover, and non-impervious cover.

Land cover	**Classification description (from Gillon *et al.* 2016)**	**Percent of Madison landscape**	**Percent of land-cover class comprised of:**		
			Building cover	**Non-building impervious cover**	**Non-impervious cover (i.e. greenspace)**
Deciduous forest	Dominated by trees generally > 5 meters tall, and > 20% of total vegetation cover. More than 75% of tree species shed foliage simultaneously in response to seasonal change	6.83	1.24	1.31	97.45
Grassland	Dominated by gramanoid or herbaceous vegetation, generally > 80% of total vegetation. Sites in our study include unmowed meadows, as well as restored prairies	4.55	0.12	1.27	98.61
Open space	A mixture of constructed materials, but mostly vegetation in the form of lawn grasses. Impervious surfaces account for < 20% of total cover. Sites in our study include city parks (n=17), golf courses (n=2), and cemeteries (n=1)	18.09	3.68	9.95	86.37
Low density developed	A mixture of constructed materials and vegetation. Impervious surfaces account for 20% to 49% percent of total cover. Sites in our study are residential lots	30.06	11.18	23.99	64.83
Medium density developed	A mixture of constructed materials and vegetation. Impervious surfaces account for 50% to 79% of the total cover. Sites in our study are residential lots	17.08	13.96	41.92	44.12

Table 3. Mean values of ecosystem service indicators for five land-cover classes, under varying assumptions for the impact of impervious surfaces on ES. All assume zero ES under buildings. Italicized sub-headings refer to the assumed percentage of ES under non-building impervious surfaces (NB-IMP). Original field-derived values for each service (i.e. assuming no effect of impervious surfaces on ES) are included for reference.

	Ecosystem service indicator Mean (SE)								
	C (kg m^{-2}, to 25 cm depth)				**P (ppm, from 0-25 cm depth)**			**Ksat (mm hr^{-1}, 0-10 cm depth)**	
Land cover	*Original field values*	*100% under NB-IMP*	*50% under NB-IMP*	*Zero under NB-IMP*	*Original field values*	*100% under NB-IMP*	*Zero under NB-IMP*	*Original field values*	*Zero under NB-IMP*
Forest	6.7 (0.46)	6.6 (0.45)	6.6 (0.45)	6.6 (0.45)	49.8 (9.05)	49.2 (8.94)	48.6 (8.82)	67.0 (6.72)	65.3 (6.55)
Grassland	6.4 (0.46)	6.4 (0.46)	6.3 (0.45)	6.3 (0.45)	38.6 (4.87)	38.5 (4.86)	38.1 (4.80)	49.3 (7.35)	48.6 (7.24)
Open space	9.3 (0.82)	8.9 (0.79)	8.5 (0.74)	8.0 (0.71)	39.3 (6.48)	37.9 (6.24)	33.9 (5.59)	34.6 (3.75)	29.9 (3.24)
Low density	8.0 (0.43)	7.1 (0.38)	6.2 (0.33)	5.2 (0.28)	59.1 (7.69)	52.5 (6.83)	38.3 (4.99)	43.5 (4.72)	28.2 (3.06)
Medium density	9.2 (0.54)	7.9 (0.46)	6.0 (0.35)	4.0 (0.24)	62.0 (5.75)	53.4 (4.95)	27.4 (2.54)	42.2 (3.06)	18.62 (1.35)

Table 4. Relative contribution of each land-cover class to ES considering varying assumptions of the impact of impervious surfaces on ES indicators. All assume zero ES under buildings. Italicized sub-headings refer to the assumed percentage of ES under non-building impervious surfaces (NB-IMP). Percent of area considered represents percent of total city area of each land-cover class divided by the total area covered by the 5 considered land-cover classes, such that all columns sum to 100%. Soil properties used as ES indicators are indicated in parentheses under each ES

		Proportion of total ES contributed by each land-cover class (%)					
		Carbon storage *(Soil C)*			**Water quality regulation** *(Soil P)*		**Runoff regulation** *(Ksat)*
Land cover	**Percent of city area considered**	*100% under NB-IMP*	*50% under NB-IMP*	*Zero under NB-IMP*	*100% under NB-IMP*	*Zero under NB-IMP*	*Zero under NB-IMP*
Forest	8.9	7.8	8.8	10.1	9.1	12.1	18.8
Grassland	5.9	4.9	5.6	6.4	4.8	6.3	9.3
Open space	23.6	27.7	29.8	32.7	18.6	22.4	22.8
Low density	39.3	36.6	36	35.2	42.8	42.1	35.7
Med density	22.3	23	19.8	15.6	24.7	17.1	13.4

Figure Legends

Figure 1. Map of study area. (a) Land cover in the City of Madison, WI. Legend indicates land cover classes included in the present study. White circles indicate site locations. (b) Year of development for residential lots within the City of Madison, WI. Blue areas in both (a) and (b) are lakes.

Figure 2. Variation in biophysical indicators of soil-based ecosystem services among land-cover classes (forest, grassland, open space developed, low density developed, medium density developed), in Madison, WI. (a) Mean soil C (kg m^{-2}) summed to 25-cm depth. (b) Mean available soil P (ppm) averaged over 25-cm depth. (c) Mean Ks (mm/hr) over 10-cm depth. Bars represent standard error. Grey points represent mean value of each of the 20 sites sampled per land-cover class (mean of four subplots per site).

Figure 3. Effect of time since development on three biophysical indicators of ES – carbon (C), available phosphorus (P), and saturated hydraulic conductivity (Ks) – across four land-cover classes in urban Madison, WI. Points represent the mean of four composite soil samples taken from each 30x30m site (n=20 sites). Lines and shading indicate the smoothed conditional mean and 95 % confidence interval for the mean, respectively. Solid lines represent statistical significance. Relationships that are not statistically significant are represented with dashed lines.

Figure 4. Percent of total variance in biophysical indicators of ecosystem services accounted for at scales of measurement. (a) Percent of total variance accounted for at the among land cover,

among site, and within site scale for each of three ecosystem service indicators: soil carbon (C), soil available phosphorous (P), and saturated hydraulic conductivity (Ks). Percent of total variance accounted for at the among site vs. within site scale for each of 5 land-cover classes for (b) carbon, (c) Phosphorus, and (d) Saturated Hydraulic Conductivity. Land-cover classes include: Forest (F), Grassland (G), Open Space Developed (O), Low Density Developed (L), and Medium Density Developed (M).

Figure 1

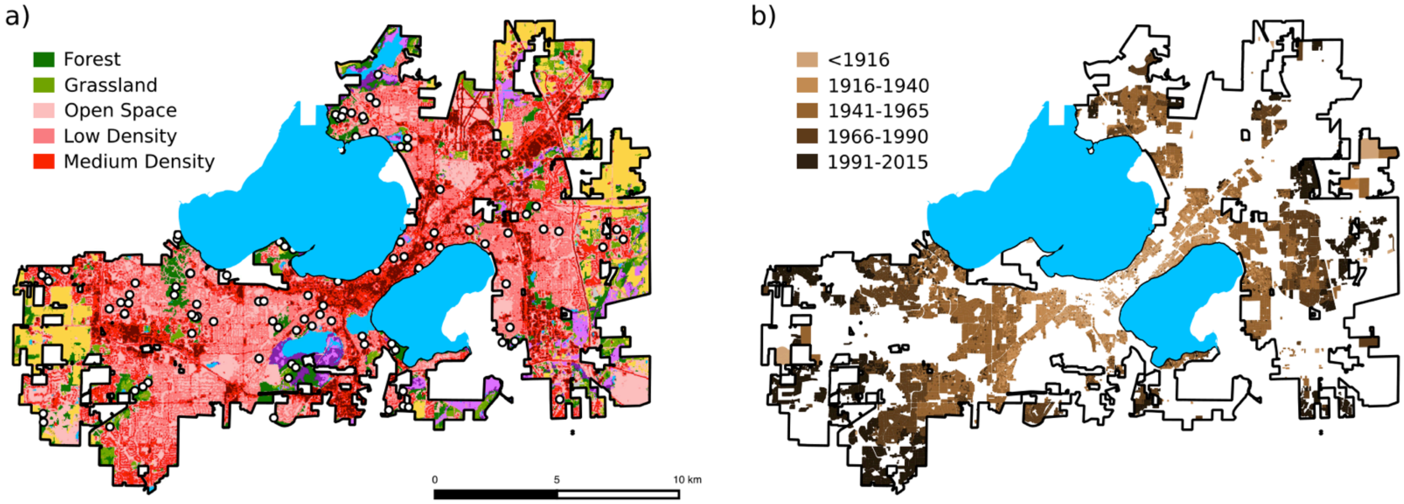

a)
Forest
Grassland
Open Space
Low Density
Medium Density
0
5
10 km
b)
<1916
1916-1940
1941-1965
1966-1990
1991-2015

Figure 2

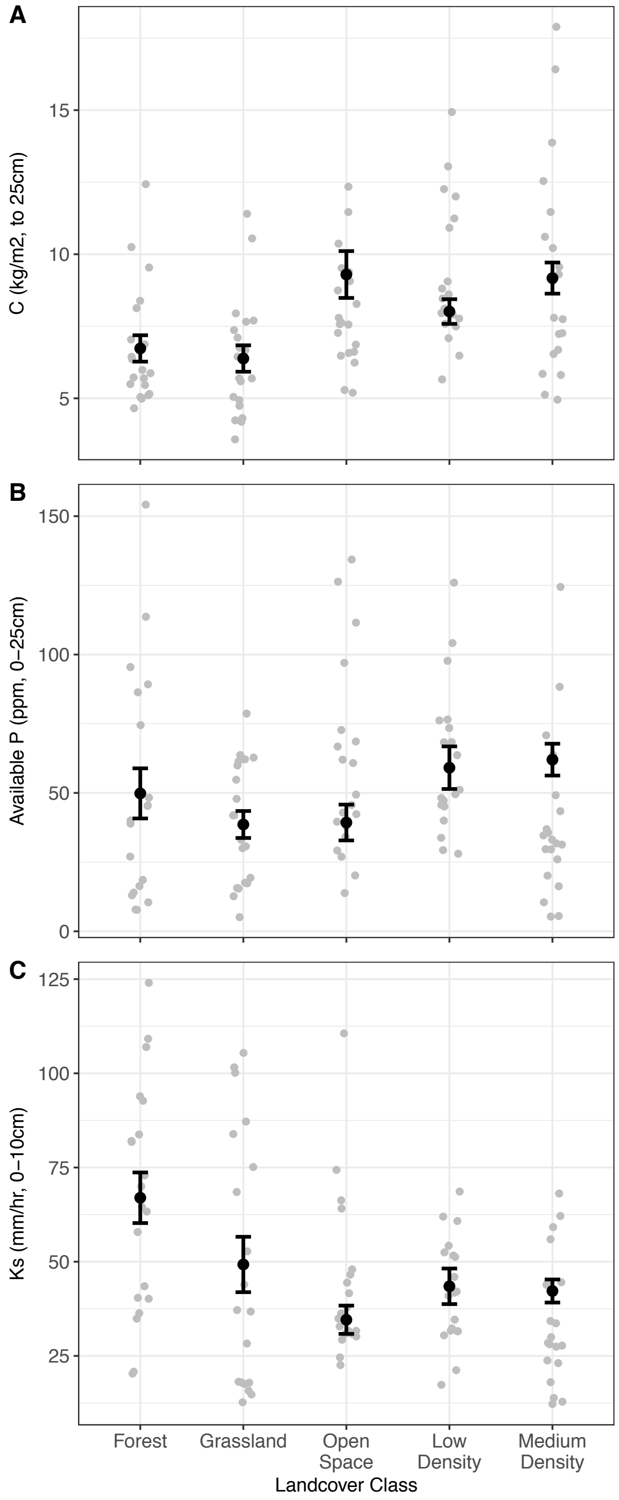

A
C (kg/m2, to 25cm)
15
10
5
B
Available P (ppm, 0–25cm)
150
100
50
0
C
Ks (mm/hr, 0–10cm)
125
100
75
50
25
Forest
Grassland
Open Space
Low Density
Medium Density
Landcover Class

Figure 3

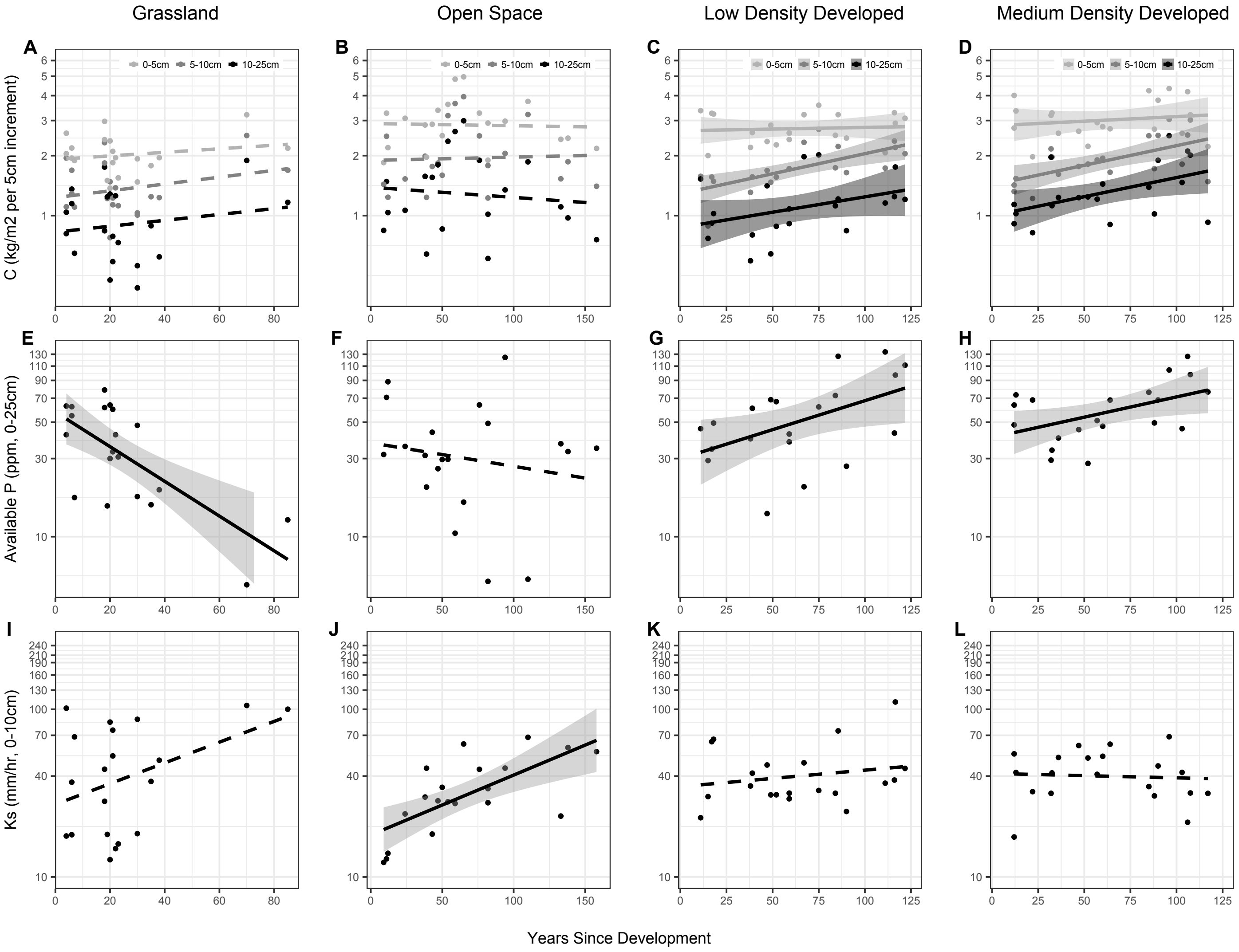
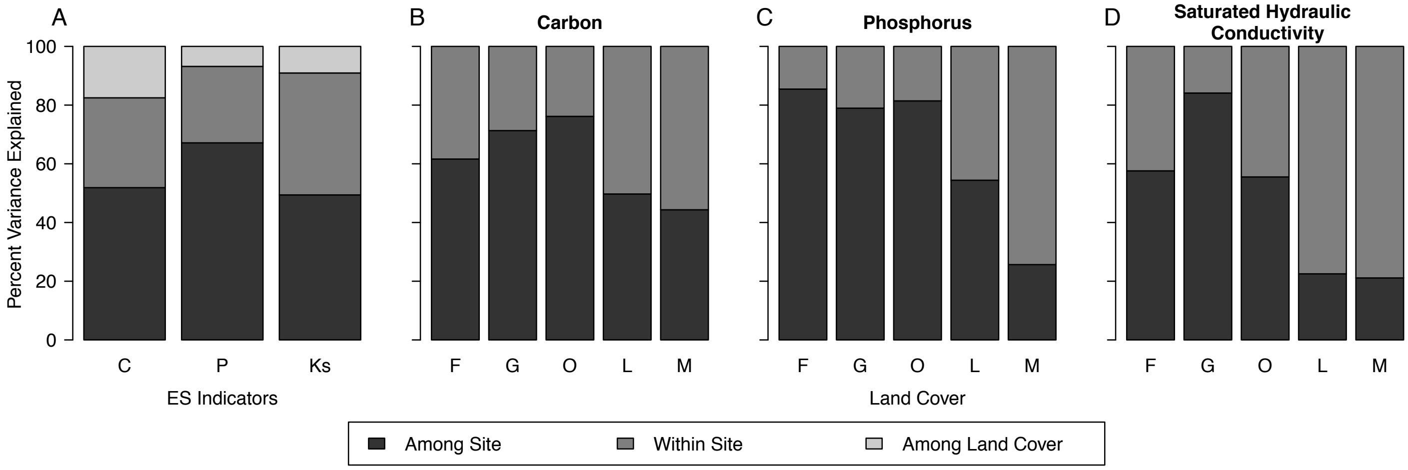

Grassland
Open Space
Low Density Developed
Medium Density Developed
A
B
C
D
0-5cm
5-10cm
10-25cm
C (kg/m2 per 5cm increment)
1
2
3
4
5
6
E
F
G
H
Available P (ppm, 0-25cm)
10
30
50
70
90
110
130
I
J
K
L
Ks (mm/hr, 0-10cm)
10
40
70
100
130
160
190
210
240
0
20
40
60
80
0
50
100
150
0
25
50
75
100
125
Years Since Development

Figure 4


A
B
Carbon
C
Phosphorus
D
Saturated Hydraulic Conductivity
Percent Variance Explained
0
20
40
60
80
100
C
P
Ks
ES Indicators
F
G
O
L
M
Land Cover
Among Site
Within Site
Among Land Cover

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Appendix S1

Appendix for: Ziter, C, and Turner, MG. Current and historical land use influence soil-based ecosystem services in an urban landscape. Ecological Applications *(In press)*

Vegetation survey details

Methods: Each site consisted of a 30 x 30m area, within which we established four 5x5m subplots (one in each quarter) to assess the effect of fine-scale heterogeneity on ES indicators. In each subplot, we conducted vegetation surveys to account for variability in vegetation type and structure within and among sites, with the specific assessment dictated by the land-cover class. In open space, low-density developed, and medium-density developed sites, vegetation structural complexity was assessed for each 5x5m subplot, following the methodology of Dale and Frank (2014). The vegetation structural complexity index is a rapid field assessment accounting for the presence/absence of 5 structural layers (groundcover, herbaceous layer, shrub, understory tree, and overstory tree) in each $1m^2$ grid cell of a plot; thus, the maximum structural complexity of a $25m^2$ plot would be 125, if each $1m^2$ cell contained all 5 structural layers. We also recorded the genus and diameter at breast height (DBH) of trees present within each subplot. In grassland sites, we recorded the percent grass and forb cover for each 5x5m plot, as well as 3-5 dominant species. For forests, the vegetation assessment took place at the full 30x30m site, as 5x5m plots are too small to measure forest structure. Three 30m x 2m belt transects were run within each site, and the species ID and diameter at breast height (DBH) (>1cm) were recorded for each tree.

Results: Forested sites were dominated by woody vegetation, containing a mean 3894 stems/ha (SE 504), with a mean basal area of 58 m^2/ha (SE 4.9). Tree/large shrub species richness ranged from 3 to 13 per site (mean 7.7 (SE 0.60)), with invasive shrubs such as

Rhamnus cathartica and *Lonicera* spp. prevalent throughout most sites. Grassland sites were composed primarily of restored prairies, as well as three meadow sites. Twelve of the 20 grassland sites were maintained by the city, while the remaining were on private land. There was a relatively even distribution between grass and forb dominated sites, with subplots having slightly higher forb coverage on average (53% vs. 46%). Common species were representative of prairies in the region, including *Solidago* spp., *Silphium* spp., *Monarda*, *Andropogon gerardii*, *Poa pratensis*, and *Rudbeckia* spp. Open space sites were characterized by mowed turfgrass, often with occasional trees (50% of sites had trees present in at least one sub-plot); however, no herbaceous, shrub, or understory trees were present in any open space sites. Resultantly, structural complexity in open space sites was relatively low, ranging from 25-50 within subplots (mean site structural complexity 30 (SE 1.4)). Low- and medium-density developed sites had similar vegetation patterns, and were generally more structurally diverse than open space sites (site structural complexity 38 (SE 1.3) for low density, 37 (SE 1.2) for medium density). Sites were typically dominated by turfgrass, as well as some herbaceous cover; but all five structural layers were represented among developed sites overall. Trees were common, with tree cover present in at least one subplot in all but one developed site.

Generalized additive mixed model results

To account for potential spatial patterns in soil properties beyond those accounted for by city structure, we re-ran all models as generalized additive mixed models (using the “gamm” function in R package “mgcv”) with latitude/longitude added as a smoothing term. We used a penalized latitude/longitude term (using a thin plate spline with a null space penalty), so that variance was first attributed to the fixed effects (i.e. land cover, time since development), and then to latitude/longitude if not captured by the fixed effects. All models were fit using maximum likelihood, using the default 10 basis functions. In model results, EDF = effective degrees of freedom for the regression spline, Ref.df = referenced degrees of freedom to compute the p-value.

Differences among land cover classes

All three ES indicators differed among land-cover classes (C ($F_4 = 6.97$, $p<0.0001$); P ($F_4 = 2.85$, $p<0.05$); Ks ($F_4 = 4.19$, $p<0.01$)), with the smooth lat/long terms non-significant in all cases (C (EDF = 0.59, Ref.df = 9, F = 0.1, p=0.22); P (EDF = 0.58, Ref.df = 9, F = 0.1, p=0.21); Ks (EDF = 0, Ref.df = 9, F = 0, p=0.52)). GAMM results are qualitatively and quantitatively very similar to linear mixed model results reported in the manuscript.

Differences with time since development

Carbon varied with time since development, but the magnitude and significance of the relationship differed both with depth and among land-cover classes ($F_6 = 2.20$, $p<0.05$) – consistent with mixed model results. The smooth lat/long term was non-significant (EDF = 0.18, Ref.df = 9, F = 0.02, p=0.31). Results for individual land-cover models were again consistent with mixed model results. Soil C increased over time in low-density developed sites, but the strength of the relationship depended on depth ($F_2 =7.12$, $p<0.001$). Soil C varied similarly in medium-density developed sites, again showing a depth by time interaction ($F_2 =4.70$, $p<0.01$). The smooth lat/long terms were non significant in both cases (Low density (EDF = 0.02, Ref.df = 9, F = 0.002, p=0.38), Med density (EDF = 0, Ref.df = 9, F = 0, p=0.77)). There was no effect of time since development on C in either grassland sites or open space developed sites, with the smooth lat/long term again non-significant in both cases.

P concentrations also varied with time since development, but the direction depended on land-cover class (F_3 = 7.5, $p<0.0001$) – consistent with mixed model results. The smooth lat/long term was non-significant (EDF = 0, Ref.df = 9, F = 0, p=0.63). In grassland sites, P concentrations declined with time since development (F_1 = 17.65, $p<0.0001$); a trend driven in part by two 70+ year old prairie restorations with very low P concentrations. The smooth lat/long term was non significant (EDF = 0, Ref.df = 9, F = 0, p=0.68). In open space sites, there was no relationship with time since development, nor was the spatial term significant. In both low and medium density developed sites, P concentrations increased with time since development (Low density (F_1 =4.94, $p<0.05$), Medium Density (F_1 =4.56, $p<0.05$). The smooth lat/long terms were non significant in both cases (Low density (EDF = 0, Ref.df = 9, F = 0, p=0.66), Med density (EDF = 0.34, Ref.df = 9, F = 0.05, p=0.29)).

Variation in Ks with time since development depended on land-cover class (F_3 = 3.3, $p<0.05$) – consistent with mixed model results. Here, the smooth lat/long term was significant (EDF = 1.36, Ref.df = 9, F=0.49, $p<0.05$), driven largely by the results in grassland sites. In grassland sites, there was a positive effect of time since development on Ks (F_1 = 5.3, $p<0.05$), with a significant lat/long term (EDF = 1.25, Ref.df = 9, F=0.47, $p<0.05$). This result is inconsistent with mixed model results, which were qualitatively similar, but non significant (p=0.09). As this trend seems to depend heavily on two older grassland sites in the UW-Arboretum, we have chosen to include the more conservative results in the manuscript. The remaining results were again consistent with the linear mixed models. In open space sites, Ks increased with time since development (F_1 = 19.9, $p<0.0001$), but the lat/long term was non significant (EDF = 1.08, Ref.df = 9, F=0.22, p=0.18). Ks showed no relationship with time since development in low- or medium-density developed land-cover classes, and neither lat/long term was significant.

Table S1. Number of sites within each soil subgroup for each decade of development.

Decade Built	Aquic Argiudolls	Fluvaquentic Hapludolls	Mollic Hapludalfs	Typic Argiudolls	Typic Endoaquolls	Typic Hapludalfs	Udollic Endoaqualfs	*Total Sites*
1890s			1			3		***4***
1900s			1		1	1		***3***
1910s						1	1	***2***
1920s						3	1	***4***
1930s			1			1		***2***
1940s			1				1	***2***
1950s			2			2	1	***5***
1960s			2	1		2		***5***
1970s		1	1			1		***3***
1980s			2					***2***
1990s			1			1		***2***
2000s	1			1		4		***6***
Total Sites	***1***	***1***	***12***	***2***	***1***	***19***	***4***	***40***

Table S2. Mean values of soil texture (percent sand, silt, and clay) for five land-cover classes, determined using the hydrometer method. For each land cover class, n=20 sites.

Land Cover	Percent Sand Mean (SE)	Percent Silt Mean (SE)	Percent Clay Mean (SE)
Forest	40.3 (1.64)	51.5 (1.44)	8.2 (0.59)
Grassland	42.9 (1.74)	46.8 (1.42)	10.3 (0.62)
Open Space	42.4 (1.81)	47.5 (1.51)	10.12 (0.53)
Low Density	41.8 (1.43)	47.2 (1.14)	11.0 (0.54)
Medium Density	43.6 (1.27)	47.0 (1.05)	9.4 (0.42)

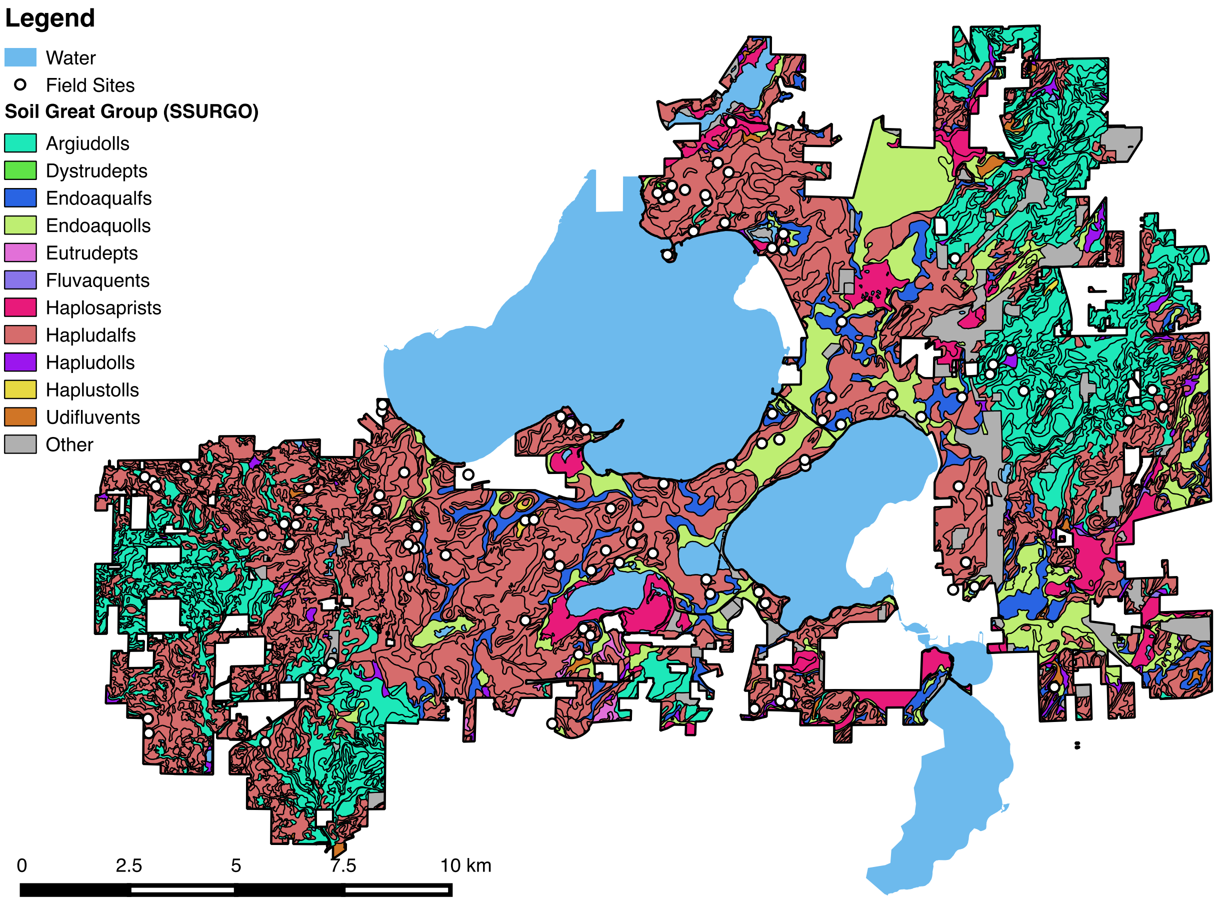

Figure S1. Map of soil types within the study area (City of Madison, WI). Soils underlying study sites are largely Typic Hapludalfs (50% of sites, predominantly Dodge, McHenry, St. Charles series) and Mollic Hapludalfs (21% of sites, predominantly Batavia series). Comprising a further 20% of sites are Typic Argiudolls (7%, predominantly Plano series), Typic Endoaquolls (7%, predominantly Colwood series), and Udollic Endoaqualfs (6%, Virgil series). “Other” category includes alluvial land, cut and fill land, gravel pits, landfills, made land, marsh, and quarry. Data available from the Soil Survey Geographic (SSURGO) database (NRCS, 2017).

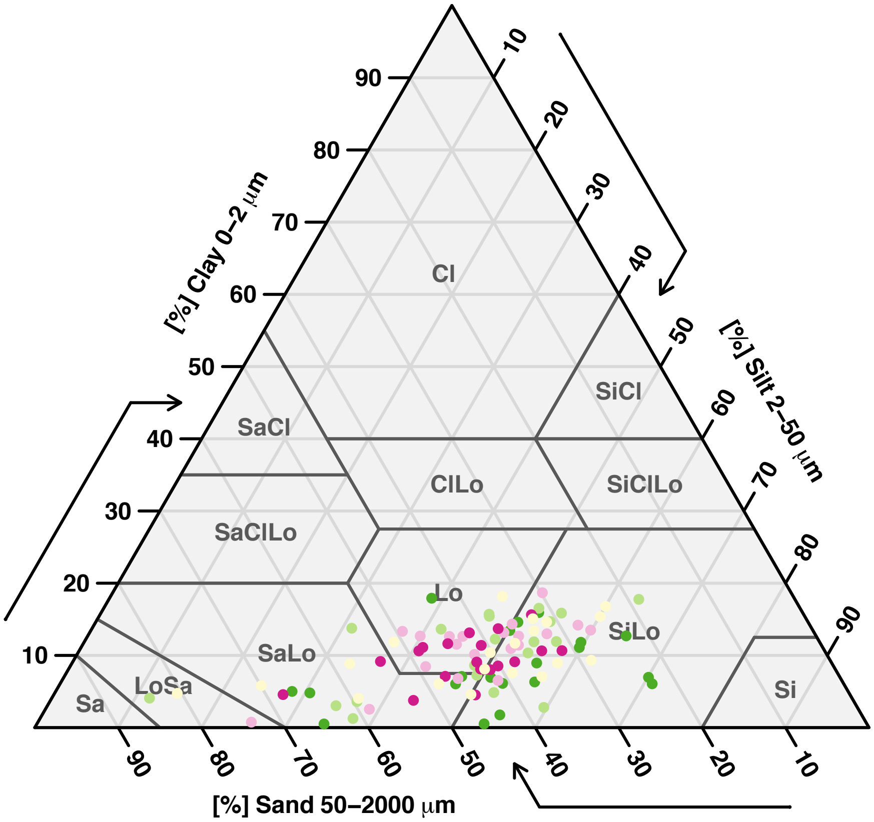

Figure S2. Soil texture for five land-cover classes, measured using the hydrometer method and plotted on the USDA soil texture triangle. Each point represents the average texture of 4 samples from one 30x30 m site (n=20 sites for each land cover class). Dark green represents forested sites, light green represents grassland, yellow represents open space, pale pink represents low density developed sites, and dark pink represents medium density developed.

Figure S3. Example of among-site variability in 4 different urban grassland sites sampled for soil-based ecosystem services in Madison, WI. From left to right: An unmanaged meadow site, grass dominated; an unmanaged meadow, mixed grasses and forbs; a forb dominated restored prairie; a grass dominated restored prairie.

Figure S4. Example of within-site variability in low-density developed land sampled for soil-based ecosystem services in Madison, WI. The four images comprise 4 subplots within the same 30x30m sampling site.

Chapter 3 – No evidence of co-facilitation between a non-native Asian earthworm (*Amynthas tokioensis*) and invasive common buckthorn (*Rhamnus cathartica*) in experimental mesocosms

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Abstract

Non-native invasive earthworms are known drivers of forest change in north temperate forests. Much understanding of earthworm invasion is based on species of European origin, but concern about Asian pheretimoid earthworms (e.g. Asian jumping worms, *Amynthas* spp.) is increasing. Some effects of *Amynthas* spp. on soil properties and biota have been studied, but little is known about interaction of *Amynthas* spp. with plants. Potential interaction between *Amynthas* spp and invasive buckthorn *(Rhamnus cathartica*) is of particular interest given hypothesized co-facilitation between *R. cathartica* and European earthworms – cited by some as components of an "invasional meltdown". We used reciprocal mesocosm experiments in Wisconsin, USA, to test for co-facilitation between *Amynthas tokioensis* and *R. cathartica*. We asked: (1) Are jumping worms more successful in environments invaded by buckthorn? (2) Does jumping worm activity increase buckthorn germination and establishment? Counter to expectations, co-facilitation was not supported, and we found evidence to the contrary. There was no increase in litter loss (indicative of consumption by jumping worms) or jumping worm fecundity in buckthorn-invaded environments, and buckthorn germination was unaffected by increased jumping worm densities. Counter to our hypothesis, jumping worm fecundity was greater in buckthorn-free soils than in buckthorn-invaded soils. Our results have encouraging implications for conservation and management regarding these species, and highlight potential differences in ecological impact of non-native invasive earthworm taxa that vary in life-history and functional dynamics.

Key Words: Asian jumping worm; *Amynthas tokioensis*; Earthworms; *Rhamnus cathartica*; Wisconsin

Introduction

Biotic invasions can considerably alter forest ecosystem structure and function (Vitousek 1990). In north temperate forests, invasive earthworms in particular are gaining attention as a driver of forest change. Prior to European settlement, many north temperate forests of North America lacked earthworm populations, with current earthworm communities dominated by species from Europe and Asia (Hendrix and Bohlen 2002; Bohlen et al. 2004). Invasive earthworms have large ecological impacts on forest ecosystems, including mixing organic and mineral soil horizons, decreasing soil carbon storage, and altering nitrogen cycling, soil food webs, and native plant communities (Bohlen et al. 2004; Hale et al. 2006; Blouin et al. 2013).

Much understanding of earthworm invasion is based on studies of European species (particularly family Lumbricidae; Bohlen et al. 2004; Hale et al. 2006), however, managers and ecologists are increasingly concerned about earthworms of Asian origin in temperate deciduous forests (Callaham et al. 2003; Snyder et al. 2011; Greiner et al. 2012; Qiu and Turner 2016). Asian pheretimoid earthworms (e.g. *Amynthas* and *Metaphire* spp.) were first recorded in the United States in 1939 (Gates 1982), and their invasion now spans several northern and southern states (Chang et al. 2016a). While *Amynthas agrestis* is frequently cited as the culprit of invasion in north temperate forests, recent work shows *A. agrestis* often co-occurs with morphologically similar *Amynthas tokioensis* and *Metaphire hilgendorfi*, with high possibility of misidentification (Schult et al. 2016; Chang et al. 2016a; Chang et al. 2017a). Referred to as “Asian jumping worms” for their characteristic rapid, snake-like movements, these co-invading species are thought to share several traits, and may change forest ecosystems in ways distinct from European species as a result of differences in life-history and functional dynamics (Greiner et al. 2012; Chang et al. 2016b).

A. agrestis, *A. tokioensis*, and *M. hilgendorfi* reproduce parthenogenetically, and unlike more commonly studied European species, have an annual lifecycle. They emerge from cocoons in spring and grow rapidly to sexual maturity before reproducing and dying in fall (Burtelow et al. 1998; Greiner et al. 2012). They are epi-endogeic, living in litter and surface soils rather than deep burrows. However, jumping worms are larger than many epigeic species of European origin (Greiner et al. 2010), and jumping worms live at much higher densities than their European counterparts (Callaham et al. 2003). The combination of greater body size and density and their wide dietary flexibility (Zhang et al. 2010) may increase their effects on ecosystems relative other earthworm taxa (Chang et al. 2016c). Thus, jumping worms have the potential to markedly change forest ecosystems in ways distinct from European earthworms, yet comparatively less is known about their ecosystem impacts and habitat preferences (Chang et al. 2016a). Initial studies reveal jumping worms can substantially reduce leaf litter, accelerate decomposition, and alter nutrients pools in forest and prairie soils (Greiner et al. 2012; Qiu and Turner 2016). Invasion of jumping worms also alters organic matter and forest floor structure (Burtelow et al. 1998), and results in a long-lasting granular soil signature (Chang et al. 2016a) that has been hypothesized to negatively impact plant growth.

Ecological consequences of exotic Asian earthworm invasions will depend in large part on how they interact with other native and invasive species, as species interactions can amplify or dampen impacts of invasive species on ecosystem function (Simberloff and Holle 1999; Richardson et al. 2000; Levine et al. 2003; Brooker et al. 2008). Studies have documented interaction between *A. agrestis* and/or *M. hilgendorfi* and European earthworm species (Zhang et al. 2010; Greiner et al. 2012; Chang et al. 2016b; Chang et al. 2017b; Laushman et al. *in press*), as well as a variety of soil and aquatic predators including millipedes, salamanders, and crayfish

(Snyder et al. 2011; Snyder et al. 2013; Gorsuch and Owen 2014; Ziemba et al. 2015; Ziemba et al. 2016). However, few studies have investigated potential interaction of Asian earthworms with forest plants (but see Laushman et al. *in press*), despite well-documented occurrence of plant-earthworm interactions more generally (Scheu 2003; Bezemer and van Dam 2005; Hale et al. 2006). Of particular interest in Midwestern forests is potential co-facilitation between Asian earthworm species and invasive plants, such as common buckthorn (*Rhamnus cathartica*).

Native to Europe, buckthorn is common in human-dominated landscapes, and is considered among the most abundant and harmful forest invaders in the Midwestern US (Knight et al. 2007; Roth et al. 2015). Its physiology – including rapid growth, shade tolerance, and high photosynthetic rates – and unique phenology allow it to outcompete native plant species (Knight et al. 2007), while modifying soil and leaf litter in ways that encourage further invasion (Heneghan et al. 2006). Buckthorn can fundamentally alter forest structure by forming dense, monospecific thickets (Mascaro and Schnitzer 2007), or by preventing native tree establishment in open sites that would otherwise undergo succession to native-dominated forest. Ultimately, buckthorn dominance can reduce aboveground carbon storage by up to half compared to native communities (Mascaro and Schnitzer 2011). Additionally, buckthorn is an important overwintering host of the invasive soybean aphid (*Aphis glycines*), an economically important crop pest (Bahlai et al. 2010; Heimpel et al. 2010). Thus, buckthorn impacts several ecosystem services provided by Midwestern landscapes.

European earthworm species (e.g. *Lumbricus terrestris*) are often assumed to interact with buckthorn such that each species facilitates the other (Heneghan 2003; Frelich et al. 2006; Kurylo et al. 2007; Knight et al. 2007, but see Wyckoff et al. 2014; Iannone et al 2015). This interaction has been proposed as an example of "invasional meltdown", in which a group of non-native species facilitates each other's success (Simberloff and Holle 1999; Simberloff 2006; Heimpel et al. 2010). European earthworms are hypothesized to aid buckthorn spread via alterations to the forest floor that enhance germination, including thinning of leaf litter, increased pH, and increased nutrient cycling and availability (Heimpel et al. 2010; Roth et al. 2015). In turn, buckthorn is hypothesized to facilitate earthworm invasion via nutrient-rich litter, and the creation of a desirable soil environment (Heneghan et al. 2007; Mueller et al. 2017). Supporting this hypothesis, buckthorn and European earthworm populations are positively correlated in woodlands in northeastern Illinois (Heneghan et al. 2007) and Minnesota (Mueller et al. 2017), and removal of buckthorn reduced European earthworm populations by over 60% the following year in Wisconsin forests (Madritch and Lindroth 2009). However, other studies fail to support the putative invasional meltdown. Wycoff et al. (2014) found greater evidence of negative relationships than positive between buckthorn and earthworms at the prairie-forest border in west central Minnesota. Similarly, with the exception of accelerated litter decomposition, Iannone et al. (2015) found a lack of evidence that buckthorn invasion altered soils – a frequently cited mechanism for earthworm facilitation – in a well-replicated regional study in Illinois. Thus, whether co-facilitation occurs between earthworms and buckthorn remains contested in the literature.

If the hypothesized relationship between European earthworm and buckthorn is correct, co-facilitation might also be expected between jumping worms and buckthorn, with potential consequences for Midwestern landscapes. Because jumping worms occur at higher densities, grow faster, and consume more leaf litter than European species (Zhang et al. 2010; Greiner et al. 2012; Qiu and Turner 2016), jumping worms could facilitate buckthorn germination and establishment in much the same manner, and perhaps to a greater extent, as European earthworms. Whether the opposite side of this potential relationship – facilitation of earthworms by buckthorn – is likely to hold is less clear, and two alternatives are plausible. Early seasonal decomposition of buckthorn litter (Heneghan et al. 2002) relative to mid-season jumping worm maturity may weaken the effect of buckthorn on jumping worms, as nutrient-rich buckthorn litter is less available as a food source. However, residual pieces of buckthorn litter are still likely to persist in invaded soils, and soil changes including increased nitrogen, calcium, and pH (Mueller et al. 2017) could still influence jumping worm success consistent with expectations based on European earthworms. Contrastingly, faster overall litter decomposition (and thus lower litter quantities) observed in buckthorn-invaded environments could provide a less favorable environment for jumping worms, which consume a more litter than their European counterparts.

The presence of both buckthorn and jumping worms at the University of Wisconsin Arboretum – where *A. tokioensis* and *A. agrestis* were discovered in 2013 (Chang et al. 2016a) – provided an opportunity to test this species interaction. We used mesocosm experiments to ask: Does a positive feedback exist between *Amynthas tokioensis* and *Rhamnus cathartica*? Specifically (1) Are jumping worms more successful in environments that have already been invaded by buckthorn? (2) Does jumping worm activity increase buckthorn germination and establishment? We hypothesized increased foliage litter loss in buckthorn-invaded soils due to higher feeding activity of *A. tokioensis* in the presumed more favourable conditions, as well as increased jumping worm fecundity (cocoon production). We further hypothesized increased buckthorn germination and establishment under conditions of higher jumping worm densities, consistent with studies of European earthworms.

Methods

Mesocosm experimental design

We conducted two separate replicated 3x2 factorial mesocosm experiments during summer and fall 2016 in the UW-Madison Arboretum's open field facility (adapted from the methods of Qiu and Turner 2016). Mesocosms consisted of intact soil cores (20cm diameter x 25cm depth) collected from forest sites.

Experiment 1 (Q1):

We tested *A. tokioensis* leaf litter consumption rates and fecundity (cocoon production) in buckthorn invaded vs. buckthorn free environments experimentally by manipulating leaf litter mass consistent with variability in buckthorn invaded vs. uninvaded sites in the field (Appendix Table A1), and using soil from paired invaded and buckthorn-free forest sites (3x2 factorial, *n*=9 replicates per treatment combination). We aimed to distinguish the hypothesized positive effects of buckthorn soil environments on jumping worm success with the potentially negative effects of reduced litter availability in buckthorn-invaded environments. The mesocosm environment ensured control over worm density. This is important, as variation in worm density, activity and movement could confound results. Additionally, litter remained on top of soil as in natural settings, allowing for continuous assessment.

Intact soil cores (n=54) were collected in late spring from 9 representative forest sites uninvaded by jumping worms in the UW-Madison Arboretum (as per earthworm surveys from the previous summer, Laushman et al. *in press*). Each forest site contained a buckthorn invaded and buckthorn free subsite (separated by ~10m), with similar canopy species composition. Within each subsite we recorded diameter at breast height (DBH) and species identity of all saplings and trees (>2.5cm DBH) within a 100m^2 circular plot. Common overstory species in the study sites included *Acer saccharum*, *Quercus alba*, *Prunus serotina*, *Fagus grandifolia,* and

Carya spp. We also recorded density of buckthorn seedlings in three 1m^2 quadrats – one at the plot center, and two at 1m from the center in a randomly determined compass direction. In buckthorn-invaded subplots, *R. cathartica* occurred at a mean density of 8.3 stems per m^2 (± 1.5SE). Large buckthorn stems (>2.5cm DBH) ranged from 0 (only stems <2.5cm present) to 21 per 100m^2 plot (mean 9 ± 2.7SE).

At the center of each circular plot a set of three intact soil cores was collected within a 1m radius (n=6 cores per site). All cores were collected at least 1m from any edge (e.g. walking paths, obvious vegetation transitions). Cores were cleared of leaf litter, woody debris, and undergrowth, and returned to the Arboretum field facility for the remainder of the experiment.

Leaf litter for treatments was collected from non-buckthorn invaded forests surrounding each soil-sampling site (so as not to contaminate non-buckthorn cores with fragments of buckthorn litter and/or soil from heavily invaded areas). Litter from each site was gently mixed to homogenize species composition (litter composition was consistent with common overstory species, above) and sizes of litter pieces, air-dried, and a low (1.5g), medium (20g), or high (40g) litter treatment was randomly allocated to each set of 3 cores from the corresponding collection site. Low, medium, and high litter treatments were representative of field conditions, based on field surveys of litter in buckthorn-invaded and uninvaded environments, whereby leaf litter from 2 randomly located 30cm x 30cm quadrats within each subsite was collected, dried, and weighed (Appendix Table A1). Subsamples of litter were oven-dried to establish an oven-dry/air-dry correction factor.

Each PVC core was outfitted with landscaping cloth (bottom), and mesh "worm screens" (top) to prevent worm escape and allow vertical water flow, and the 6 cores for each treatment were placed into completely randomized blocks to account for variation across the field facility.

Shade cloth was installed above the facility, and soil piled surrounding each core to mimic forest conditions (Appendix Fig. A1). Mesocosms were monitored weekly for soil moisture, and deionized water was added as needed to prevent earthworm death by desiccation.

We added five *A. tokioensis* individuals to each core initially, supplemented with 2 additional earthworms 1 month into the experiment to account for possible earthworm death early in the experiment (following Qiu and Turner 2016). All individuals were collected in late June from a known invasion site within the Arboretum using standard mustard extraction methods (Lawrence and Bowers 2002). Densities of up to 7 worms per core, while high, are consistent with natural populations – supported by recorded field densities within the Arboretum (Appendix Fig. A2, Table A2).

Litter percent cover and depth of surface litter (calculated as an average of 4 random points per mesocosm) were recorded weekly for 18 weeks, ending following the first hard freeze in late October. At 18 weeks, remaining litter was collected from each soil core, oven dried, and weighed to determine total litter mass loss. Percent cover and depth of soil signature – the grainy, visible signature indicative of *Amynthas* activity – was measured within each core following litter removal. We then excavated the top 5 cm of each core in two 2.5cm increments, and *A. tokioensis* cocoons were isolated and counted by wet sieving through a 1.0mm standard soil sieve.

Experiment 2 (Q2)

Buckthorn germination trials were also conducted in mesocosms (n=30) as described above. Here we again varied litter mass (consistent with experiment 1) and also varied worm density (3x2 factorial experiment, 5 replicates per treatment combination). Reduced litter is the primary mechanism by which earthworms are hypothesized to increase buckthorn germination and establishment. Intact cores (same size as above) were collected from 5 representative buckthorn-free forest sites in the Arboretum (buckthorn completely absent from a 10m radius surrounding site, to ensure buckthorn seeds were not present in the seed bank, dominant canopy species consistent with above). Within each site, 6 intact soil cores were collected. Cores were collected in 3 pairs of two within a 1m radius, such that each pair could be randomly allocated one of three litter treatments, and *A. tokioensis* allocated to one core of each pair while the other served as a control. Paired cores were collected from no more than 15cm apart. With the exception of earthworm allocation to only one of each pair, cores and experimental setup were treated as described above. Unfortunately, we became aware throughout the course of the experiment that the sampling region assumed uninvaded by *A. tokioensis* based on the most recent survey of earthworm distribution (Laushman et al. *in press*) had become invaded prior to soil collection, such that a low number of jumping worms were present in the "control" cores. Given the life history of the organism, this incipient invasion was undetectable until after the experiment had already started. Thus, we refer to earthworm treatments as "low density" and "high density" throughout the remainder of the work. While precise measurement of jumping worm densities was not possible without destructive sampling, no more than one jumping worm per core was noted visually in low-density treatments throughout the course of the summer.

Representing natural seed rain, we sowed 40 buckthorn seeds (cold stratified for 42 days, (Stewart and Graves 2005)) on top of the litter or soil in each mesocosm, and recorded germination and survival weekly for 18 weeks. Cumulative buckthorn germination was calculated as an indicator of germination success, and final number of surviving seedlings as an indicator of establishment success (Roth et al. 2015). As with Experiment 1, litter percent cover and depth were measured weekly, and remaining litter was collected from each soil core, oven dried, and weighed at the end of the experiment to determine total litter mass loss. We measured percent cover and depth of soil signature following litter removal as an indicator of earthworm activity, confirming the modified low- vs. high-density earthworm treatments.

Data Analysis

To evaluate effects of buckthorn invasion on jumping worm success (Q1), we used general and generalized linear mixed effects models (using the lme4 package in R, Bates et al. 2015) to test for significant differences in litter mass loss (total and percent loss between end and initial measurements), depth and percent cover of soil signature (log and logit transformed, respectively), and fecundity (number of cocoons produced and cocoon presence/absence). For all models, soil origin and litter mass were included as fixed effects, and site was included as a random effect to account for treatments nested within each sampling site.

To evaluate effects of jumping worm activity on buckthorn germination and establishment (Q2), we used general and generalized linear mixed effects models to test for significant differences in litter mass loss (total and percent loss between end and initial measurements), depth and percent cover of soil signature (log+1 and logit transformed, respectively), and buckthorn germination (number of buckthorn seeds germinated throughout the experiment, log+1 transformed) and establishment (buckthorn seedlings surviving at the end of the experiment). Here, earthworm density and litter mass were included as fixed effects, and site was again included as a random effect.

All analyses were performed using R statistical software (R Development Core Team 2009). Linear models were fit using Maximum Likelihood and significance of fixed effects was evaluated using model comparisons using likelihood ratio tests, which generate *P* values using a chi-square test. We use a statistical significance level of $\alpha = 0.05$ to indicate strong support, and

$\alpha = 0.1$ to indicate marginal support. Model residuals were visually inspected for normality and homogeneity of variance. Count data were analyzed using a Poisson distribution where it improved model fit (cocoon number and buckthorn establishment), and cocoon presence was analyzed using a binomial distribution.

Results

Effects of buckthorn invasion on jumping worm success (Q1):

There were no significant effects of initial litter mass ($\chi^2(2) = 0.251$, P = 0.88) or soil origin ($\chi^2(1) = 1.23$, P = 0.27 on percent litter mass loss over the season (Fig. 1a). Total litter mass loss was positively correlated with initial litter mass, with greater litter loss from mesocosms with higher initial litter treatments ($\chi^2(2) = 115$, P < 0.001; Fig. 1b). There was also a marginal positive effect of soil origin on total litter mass loss after accounting for litter mass, with higher litter loss in mesocosms containing soil from buckthorn-free areas, particularly in medium and high litter treatments ($\chi^2(1) = 3.08$, P = 0.08; Fig. 1b).

Soil signature depth (indicative of earthworm activity) was greater in mesocosms containing higher initial litter mass ($\chi^2(2) = 8.71$, P = 0.013), as well as in mesocosms containing soils from buckthorn-invaded areas after accounting for litter mass ($\chi^2(1) = 4.58$, P = 0.03) – with differences driven largely by the lowest litter treatment (Fig. 1c). Percent cover of soil signature showed similar patterns, with greater soil signature in higher initial litter conditions ($\chi^2(2) = 20.0$, P < 0.001) and marginally greater soil signature in buckthorn-invaded soils after accounting for litter mass ($\chi^2(1) = 3.21$, P = 0.07) (Fig. 1d).

Cocoons were more likely to be present in cores with higher initial litter mass ($\chi^2(2) =$ 8.72, P = 0.01), although there was no difference in cocoon presence in buckthorn-invaded vs.

buckthorn free soils ($\chi^2(1) = 0.715$, $P = 0.40$) (Fig. 2b). The number of cocoons produced varied among cores (range 0-51, mean 5 $\pm$ 1.2SE). Cores with higher initial litter mass contained a greater number of cocoons on average ($\chi^2(2) = 178$, $P < 0.001$), as did cores containing soil from buckthorn-free areas ($\chi^2(1) = 15.9$, $P < 0.001$) (Fig. 2a). No more than 4 cocoons were found in any mesocosm under a low litter treatment. There was no difference in cocoon presence or number in the top 2.5 cm layer of soil compared to the next deepest 2.5cm.

There was no significant interaction between litter and soil treatments for any of the variables measured.

Effects of jumping worm activity on buckthorn germination and establishment (Q2):

Both percent and total litter loss were greater in mesocosms containing a higher initial litter mass (percent $\chi^2(2) = 10.1$, $P = 0.006$; total $\chi^2(2) = 87.8$, $P < 0.001$), and greater in the high-density earthworm treatment compared to low-density after accounting for litter amount (percent $\chi^2(1) = 4.99$, $P =0.03$; total $\chi^2(1) = 6.16$, $P = 0.01$). Litter loss ranged from 17-63% in low-density earthworm treatments, and 32-72% in high-density earthworm treatments. On average, litter mass loss was 14% greater in the high-density earthworm treatment across all initial litter mass treatments. Soil signature depth (Fig. 3a) and percent cover (Fig. 3b) were both greater in high-density earthworm conditions (depth $\chi^2(1) = 28.7$, $P < 0.001$; cover $\chi^2(1) = 17.9$, $P < 0.001$) and in mesocosms with higher initial litter depths after accounting for worm density (depth $\chi^2(2) = 13.2$, $P = 0.001$; cover $\chi^2(1) = 13.9$, $P < 0.001$).

Buckthorn germination was generally low, with a maximum of 5 seeds germinating in any individual mesocosm over the course of the experiment (12.5% germination success). Germination occurred in 15 out of 30 mesocosms. Fewer seeds germinated in mesocosms with a higher initial litter depth ($\chi^2(2) = 8.34$, $P = 0.015$), but earthworm density did not affect buckthorn germination ($\chi^2(1) = 1.96$, P = 0.16; Fig. 3c). Buckthorn establishment followed similar patterns to germination. Establishment ranged from 0 to 3 seedlings. Again, fewer seedlings established in mesocosms with a higher initial litter depth ($\chi^2(2) = 7.64$, P = 0.02), but earthworm density did not affect buckthorn establishment ($\chi^2(1) = 1.20$, P = 0.27; Fig. 3d). There was no significant interaction between litter and earthworm treatments for any of the variables measured.

Discussion

Contrary to expectations based on well-studied European earthworm species (Heneghan 2003; Heneghan et al. 2007; Madritch and Lindroth 2009; Heimpel et al. 2010; Roth et al. 2015; Mueller et al. 2017) but consistent with Wyckoff et al. (2014) and Iannone et al. (2015), we found no evidence of positive feedbacks between common buckthorn and Asian jumping worms in our mesocosm experiments. Soil and litter conditions representative of buckthorn-invaded areas did not facilitate *A. tokioensis* litter consumption or reproduction, and increased *A. tokioensis* density did not affect buckthorn germination or establishment. While these results should be replicated under more natural conditions, our work suggests that although jumping worms and buckthorn each present conservation challenges, interactive effects (e.g. the foundation of an “invasional meltdown”, (Simberloff and Holle 1999; Heimpel et al. 2010)) are unlikely in our system. Additionally, results support recent findings that Asian earthworms may have distinct ecological consequences from those of European origin (Laushman et al. *in press*, Qiu and Turner 2016) – cautioning against basing understanding of earthworm invasions on European species alone.

Litter loss – indicative of litter consumption by earthworms – was not increased in areas previously invaded by buckthorn as hypothesized, and was actually slightly lower than in soils from buckthorn-free areas (Fig. 1b). Interestingly, soil signature – a more direct indicator of earthworm activity – was often higher in buckthorn-invaded soils despite the lower litter loss (Fig. 1c,d), perhaps indicating that jumping worms were feeding on other sources of organic matter in addition to litter. Zhang et al. (2010) highlight the dietary flexibility of *Amynthas agrestis*, including soil organic matter and soil biota, and Snyder et al. (2013) note *A. agrestis'* direct consumption of the FH (i.e. surface organic) soil horizon. Thus, it may be that soil under buckthorn stands supports broader dietary options for *Amynthas* due to differences in soil properties (Heneghan et al. 2002; Knight et al. 2007). However, differences in both litter consumption and earthworm activity were slight in our experiment, and a more direct study of dietary habits would be needed to confirm this hypothesis. Additionally, recent studies have questioned the extent to which soil properties differ systematically under buckthorn invaded and buckthorn-free stands (Iannone et al. 2015), and a lack of strong differences may have contributed to our results.

Our measurements of jumping worm fecundity provide additional evidence refuting the hypothesis of increased earthworm success in buckthorn-invaded areas. Although highly variable, mean cocoon density was highest in soils from buckthorn-free areas (Fig. 2a). Possible mechanisms for this difference are unclear, although previous work shows that differences in faunal or microbial communities may influence jumping worm fecundity (Snyder et al. 2013). In addition to effects of soil origin, cocoons were more than twice as likely to be present in higher litter areas, and occurred in higher numbers when present (Fig. 2). These results are intuitive – higher resource availability leads to higher fecundity – and are consistent with previous findings of minimal *A. agrestis* cocoon production in soil alone compared to treatments containing both litter and soil (Ikeda et al. 2015). However, these results contrast those of Snyder et al. (2013) who found no significant difference in *A. agrestis* cocoon production in mesocosms with litter and the soil FH horizon compared to only the FH horizon. In our experiment, lower fecundity in low-litter environments is further evidence against earthworm facilitation by buckthorn, given that low litter conditions characterize many buckthorn-invaded areas due to the replacement of native understory species with rapidly-decomposing buckthorn (Heneghan et al. 2002; Table A1).

Overall, results from our first experiment imply a lower likelihood of *A. tokioensis* population growth and survival in buckthorn-invaded areas than those free of buckthorn. The relative lack of cocoons in low litter conditions also implies a possible dependence of *A. tokioensis* on leaf litter. While some research implies that that *A. agrestis* are not obligate litter feeders (Zhang et al. 2010; Snyder et al. 2013), other studies find litter an important food source (Ikeda et al. 2015). In our system, litter seems to play an important role in the lifecycle of *A. tokioensis*. Reproduction was below replacement in all low-litter mesocosms (only 4 of 18 low-litter mesocosms contained cocoons at all, and no more than 4 cocoons per mesocosm were recovered for 7 initial earthworms), either due to lack of resources to allocate to reproduction in these conditions, or failure of *Amynthas* individuals to survive to reproduction. This may be a result of an important microhabitat or refuge provided by leaf litter as well as a food source for this largely surface-dwelling earthworm. Further research on the habitat preferences of jumping worms is needed, particularly as they continue to expand their range in the US. Additionally, future research should investigate the potential for cocoons deeper in the soil profile – which was logistically infeasible in the present study.

Our hypothesis of increased buckthorn germination and establishment under higher jumping worm activity was also unsupported. The limited germination and establishment under medium and high litter treatments confirmed existing knowledge regarding the negative effect of leaf litter depth on buckthorn germination (Knight et al. 2007; Roth et al. 2015). However, increased earthworm activity did not moderate this effect as in other studies (e.g. Roth et al. 2015). Epigeic earthworms are hypothesized to increase germination through changes to soil environment and nutrient availability (e.g. patches of nutrient rich castings) (Asshoff et al. 2010), but in the case of buckthorn primarily through the reduction of leaf litter (Roth et al. 2015). Even under high-density earthworm treatments we saw less litter loss than anticipated based on field observations and previous studies (e.g. 32-72% loss vs. 84-95% loss in Qiu and Turner 2016). It may be that the jumping worms are eating more than just litter (Zhang et al. 2010; Snyder et al. 2013), or that the field conditions were unsuitable. The 2016 summer and fall were uncharacteristically cool and rainy, which may have influenced *A. tokioensis* feeding behaviour – particularly in mesocosms where options to seek more desirable conditions are limited. Alternatively, it may be that *A. tokioensis*, which is smaller than the more commonly studied *A. agrestis*, has less impact on litter than previously assumed. Future studies should investigate potential differences in the ecological impacts of different Asian jumping worm species (Chang et al. 2016b).

The absence of facilitation may also be a consequence not of total litter loss but of timing. Given the annual lifecycle of *Amnythas* spp., most litter loss occurs in the late summer/early fall (Qiu and Turner 2016). This contrasts with the more consistent feeding of European earthworm species throughout the growing season. While buckthorn does germinate throughout the summer and even into the fall in our study region, peak buckthorn germination in this region is mid-summer (Susan Carpenter, University of Wisconsin Arobretum, *personal* *communication*). Thus, even in cases where jumping worms ultimately consume enough litter to alter germination conditions, there is likely to be a mismatch in timing whereby the peak germination period has already passed by the time of peak litter consumption. However, yearly temperature variability may alter this relationship, with *Amynthas* maturation highly variable among years (e.g. mature worms present May 2017 vs. July 2016 in the UW-Madison Arboretum, *personal observation*).

Even in the lowest litter conditions, where neither amount nor timing of litter loss presents an obstacle, buckthorn germination and establishment were not significantly increased under high earthworm densities (Fig. 3). However, germination was much lower than anticipated in our experiment overall (Stewart and Graves 2005). Low germination can be partially attributed to ongoing issues with moulding seeds in very wet, rainy conditions during our experiment. There is also potential that earthworm predation of seeds and seedlings may have reduced germination and establishment rates (Eisenhauer et al. 2010; Cassin and Kotanen 2016), although we are unaware of any studies that look at seed or seedling predation by Asian earthworms specifically. Our findings should be confirmed in studies with higher germination success, as well as under more natural conditions. We also encourage future studies to consider a gradient of earthworm densities, including a true control treatment, and studies of movement patterns and rates of spread. Given the absence of a "no jumping worm" treatment in our study, we cannot rule out potential issues of non-linear or threshold effects. It may be that low-density and high-density jumping worm treatments tested here have similar ecological effects.

From a conservation and management perspective, these results are encouraging. While buckthorn and jumping worms are both found in abundance in southern Wisconsin, and each provides challenges, there does not appear to be risk of co-facilitation. The presence of buckthorn throughout southern Wisconsin is unlikely to facilitate jumping worm spread, particularly given the unfavorable low-leaf litter conditions characteristic of buckthorn stands. Similarly, the incipient jumping worm invasion is unlikely to worsen the challenges already posed by buckthorn, as jumping worms do not seem to be decreasing leaf litter enough, or at the right time, to facilitate buckthorn invasion. Future research should focus on determining the habitat preferences of *Amynthas* to better understand factors driving the spread and success of this rapidly expanding species.

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manuscript. Both authors contributed critically to all drafts and gave final approval for publication.

Figure Legends

Fig. 1 Effects of *Amynthas tokioensis* on litter loss and soil signature following an 18 week mesocosm experiment. Bars represent mean changes compared to initial conditions for mesocosms containing soils from buckthorn invaded areas (grey) and adjacent buckthorn free areas (black). Error bars are standard errors. (A) Percent litter loss does not differ significantly with initial litter mass or soil origin; (B) Total litter loss increases significantly ($P<0.001$) as initial litter mass increases, and is marginally higher ($P<0.1$) in buckthorn-free soils; (C) soil signature depth is significantly higher with higher initial litter mass ($P<0.05$) and in buckthorn-invaded soils ($P<0.05$); (D) soil signature percent cover is significantly higher with higher initial litter mass ($P<0.001$) and marginally higher in buckthorn-invaded soils ($P<0.1$).

Fig. 2 Number and presence of *Amynthas tokioensis* cocoons following an 18 week mesocosm experiment. Bars represent mean number of cocoons (A) or proportion of cores containing cocoons (B) in mesocosms containing soils from buckthorn invaded areas (grey) and adjacent buckthorn free areas (black). Error bars are standard errors. (A) Cocoons are present in significantly higher numbers with higher initial litter mass ($P<0.001$), as well as in soils from buckthorn-free areas ($P<0.001$); (B) cocoon presence is significantly more likely with higher initial litter mass ($P<0.05$), but unaffected by soil origin

Fig. 3 Effects of *Amynthas tokioensis* on soil signature and *R. cathartica* germination and establishment following an 18 week mesocosm experiment. Bars represent mean changes compared to initial conditions for mesocosms containing low density (grey) and high density (white) earthworm treatments. Error bars are standard errors. (A) Soil signature depth is significantly greater under high jumping worm density ($P<0.001$) as well as higher initial litter mass ($P< 0.01$); (B) soil signature percent cover is significantly greater under high jumping worm density ($P<0.001$) as well as under higher initial litter mass ($P<0.001$); (C) *R. cathartica* germination was lower with higher initial litter mass ($P<0.05$), but did not significantly differ with jumping worm density; (D) *R. cathartica* establishment was lower with higher initial litter mass ($P<0.05$), but did not significantly differ with jumping worm density.

Figure 1

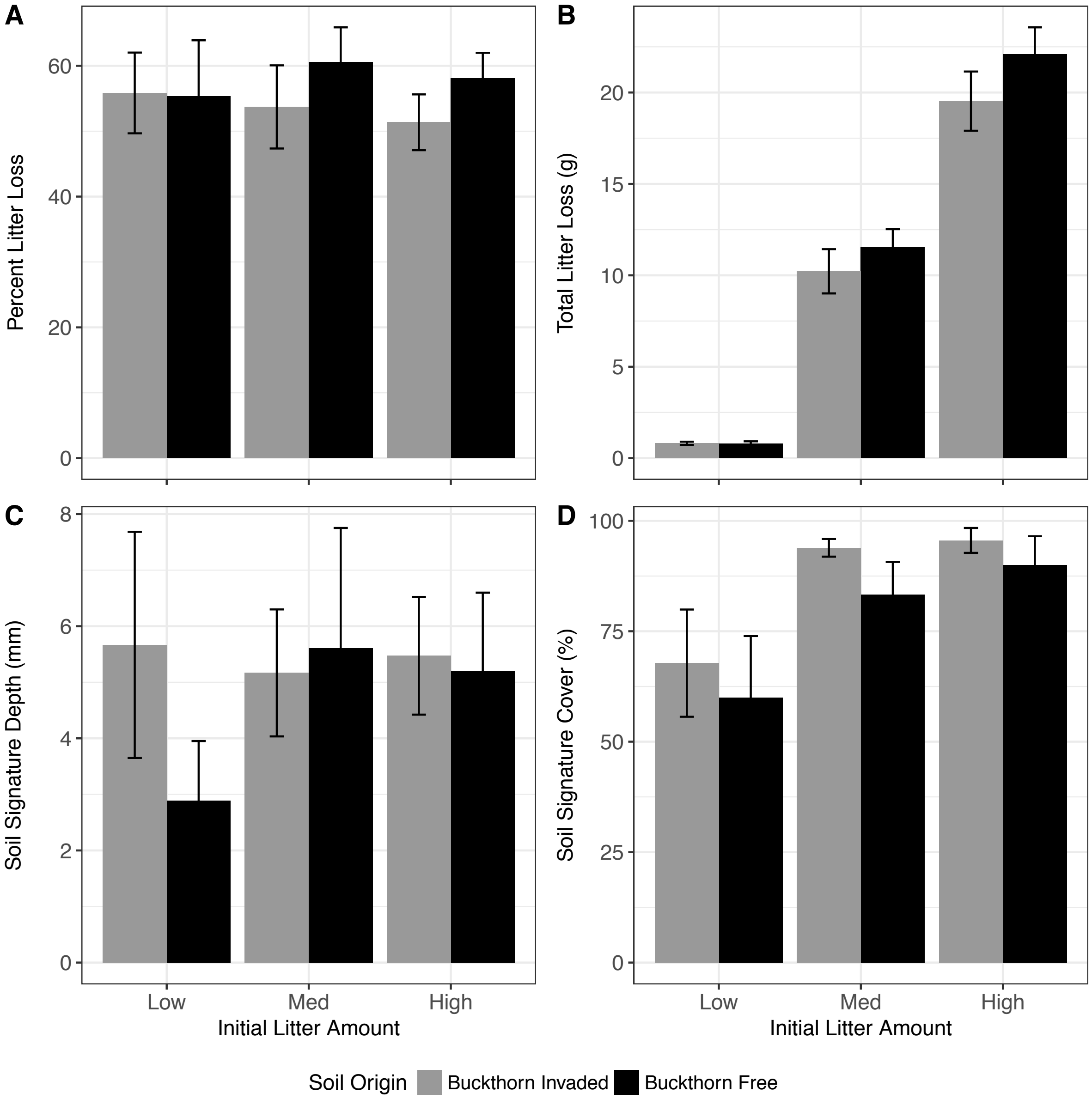

A
Percent Litter Loss
0
20
40
60
B
Total Litter Loss (g)
0
5
10
15
20
C
Soil Signature Depth (mm)
0
2
4
6
8
D
Soil Signature Cover (%)
0
25
50
75
100
Low
Med
High
Initial Litter Amount
Soil Origin
Buckthorn Invaded
Buckthorn Free

Figure 2

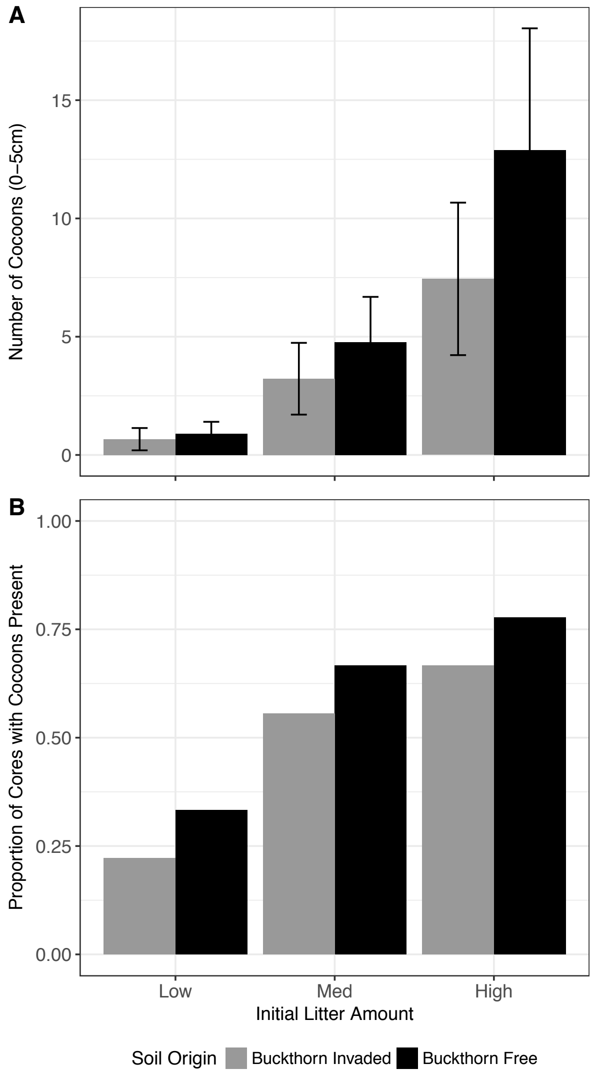
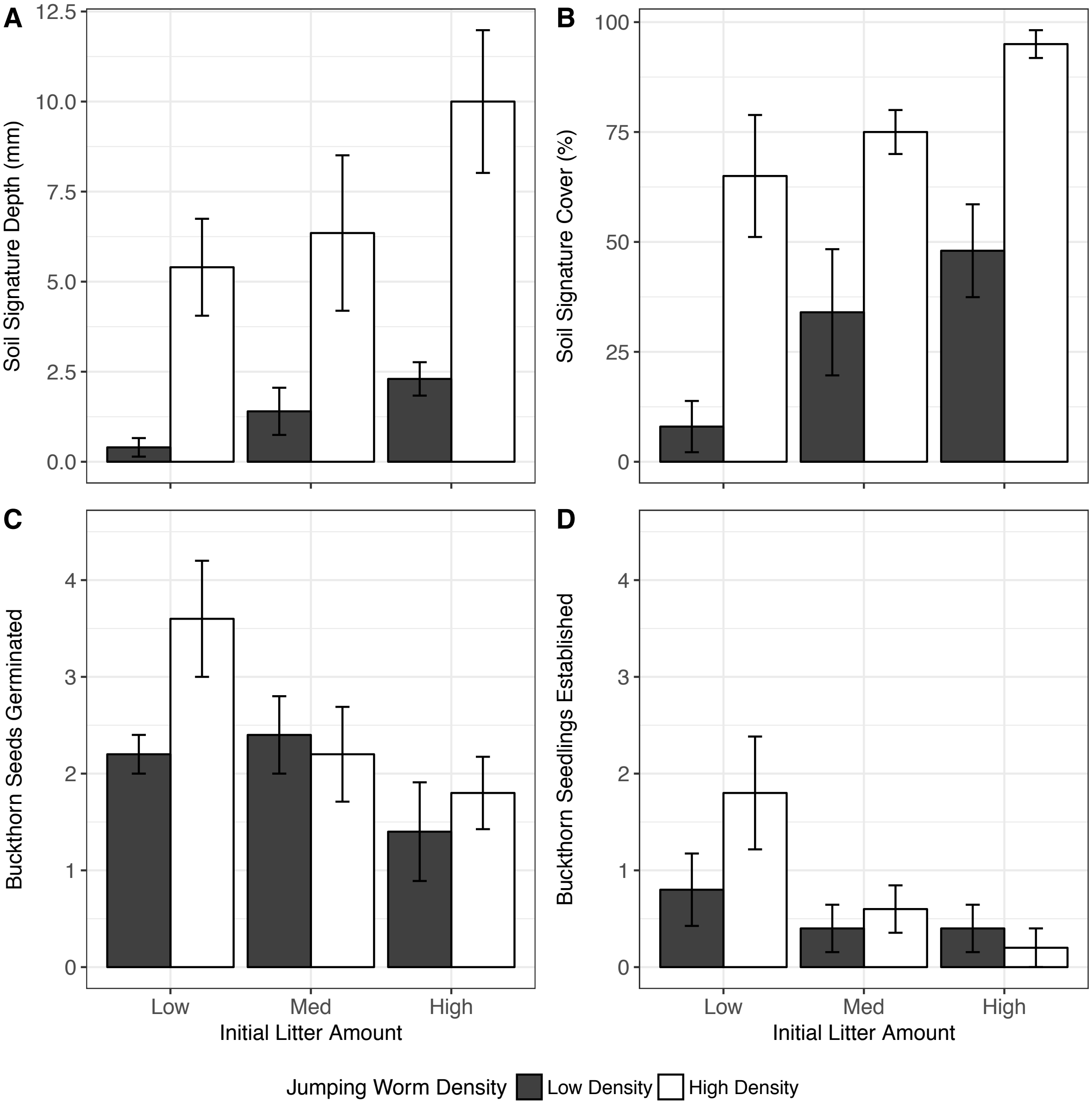

A
Number of Cocoons (0–5cm)
0
5
10
15
B
Proportion of Cores with Cocoons Present
0.00
0.25
0.50
0.75
1.00
Low
Med
High
Initial Litter Amount
Soil Origin
Buckthorn Invaded
Buckthorn Free

Figure 3


A
Soil Signature Depth (mm)
12.5
10.0
7.5
5.0
2.5
0.0
B
Soil Signature Cover (%)
100
75
50
25
0
C
Buckthorn Seeds Germinated
4
3
2
1
0
D
Buckthorn Seedlings Established
4
3
2
1
0
Low
Med
High
Initial Litter Amount
Low
Med
High
Initial Litter Amount
Jumping Worm Density
Low Density
High Density

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Appendix 1

Appendix for: Ziter, C, and Turner, MG. No evidence of co-facilitation between a non-native Asian earthworm (Amynthas tokioensis) and invasive common buckthorn (Rhamnus cathartica) in experimental mesocosms *(In Review – Biological Invasions)*

Table A1 Field leaf litter conditions in forests uninvaded and invaded by *Rhamnus cathartica.* Fallen leaf litter was collected from two randomly located 30x30cm quadrats from each of 23 field sites (9 invaded, 14 uninvaded) in the UW-Madison arboretum, and air-dried

R. cathartica invasion status	Air dry leaf litter mass (g/m2)	
	Range	Mean (SE)
Buckthorn-Free (N=28)	268 – 1468	667 (52.0)
Buckthorn-Invaded (N=18)	50 - 797	193 (40.8)

Table A2 *Amynthas tokioensis* field densities. *A. tokioensis* densities were sampled within an ~0.25 ha area of maple woods in the UW-Madison Arboretum thought to be near the initial location of invasion. Five haphazardly located mustard pours (30x30cm area) were conducted weekly during July through September (inclusive)

Sampling Date	*A. tokioensis* density (earthworms/m^2)	
	Range	Mean (SE)
July 5	43 – 183	86 (28.3)
July 13	75 – 172	127 (19.7)
July 20	43 – 86	60 (8.7)
July 27	75 – 248	149 (31.8)
Aug 2	32 – 150	84 (20.3)
Aug 10	10 – 172	90 (31.7)
Aug 17	22 – 182	86 (26.6)
Aug 24	32 – 108	65 (14.0)
Aug 30	32 – 194	99 (26.7)
Sept 7	22 – 86	56 (12.5)
Sept 14	43 – 140	90 (16.2)
Sept 22	43 – 152	97 (18.0)
Sept 28	53 – 140	84 (15.0)

Fig. A1 Mesocosm experimental setup in the field facility at the University of Wisconsin–Madison Arboretum (Photo credit: C. Ziter)

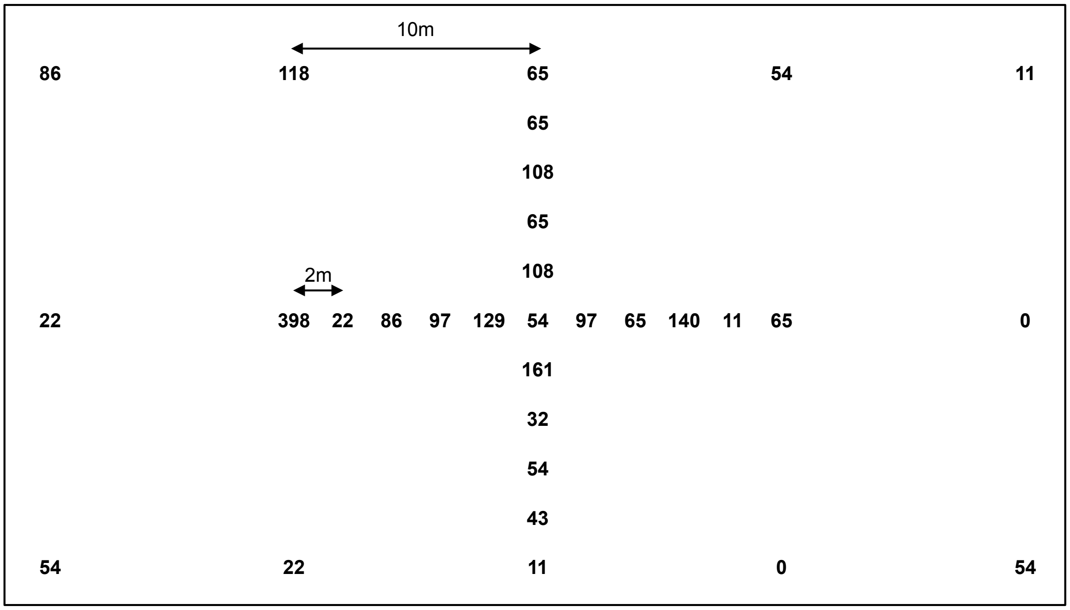

Fig. A2 Spatial pattern in *Amynthas tokioensis* field densities. *A. tokioensis* densities were sampled within an ~0.25ha area of maple woods in the UW-Madison Arboretum thought to be near the initial location of invasion. 31 mustard pours (30x30cm area) were conducted across an evenly spaced 10x10m grid, and 2x2m sub-grid on a single day in early October. Bold numbers represent *A. tokioensis* density (converted to earthworms/m^2)

Chapter 4 – Intra-urban variability in summer air temperature: interacting effects of canopy cover and impervious surfaces

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Abstract

Improving climate adaptation strategies in cities – critical as climate warms – requires a better understanding of how spatial variation in temperature aligns with residents' lived experience. However, few studies have measured intra-urban variability in air temperature at fine scales. We used a bicycle-mounted measurement system to repeatedly sample 10 urban transects spanning a range of impervious and canopy cover in Madison, WI, collecting air temperature observations every ~5 meters. Daytime air temperature varied considerably within a heterogeneous urban landscape, and was coolest where canopy cover was high; with canopy substantially moderating the effect of impervious cover. Effects of canopy were limited at night, however, suggesting that while urban forest management provides considerable mitigation potential during the day, reduction of impervious surfaces remains critical for reducing nighttime urban heat islands. Our results suggest that urban stakeholders have considerable agency over reducing daytime summer temperatures, with potential to improve the health and wellbeing of urban residents.

Introduction

The urban heat island effect (UHI), where temperatures are higher in urban compared to surrounding rural environments (Oke 1982), presents a major sustainability challenge for cities. Occurring mainly due to replacement of vegetation with impervious surfaces, high urban temperatures increase vulnerability of urban residents to heat waves and climate warming, and significantly influence energy demands and costs in cities globally (Patz et al. 2005, Memon et al. 2008, Jenerette et al. 2015). Strategies to improve cities' resilience to future climates are critical as urban areas expand, urban populations grow, and extreme heat events increase in frequency in a warming world (Mishra et al. 2015).

Although the broad-scale causes, magnitude, and spatial extent of urban-rural temperature differences have been studied extensively (Memon et al. 2008), less is known about how landscape heterogeneity affects temperature variation within cities. Research linking land-cover patterns and land surface temperature (i.e., from satellite imagery) shows that the UHI is often less an "island" than an "urban heat archipelago", with temperature differences between localized hot and cool spots as large as urban-rural differences (Buyantuyev and Wu 2010, Jenerette et al. 2015). However, measurements of air temperature – a critical metric for public health outcomes (White-Newsome et al. 2013) – have been limited at the within-city scales relevant to adaptation.

Studies of intra-urban air temperature have focused largely on either impervious surfaces or the "park cool island" phenomenon: green spaces are cooler than built-up areas, with temperature further modified by size, shape, and vegetation of urban parks (Bowler et al. 2010; Hiemstra et al. 2017). Cities are not neatly divided into green and impervious spaces, however. Urban heterogeneity is fine-scaled and integrates both natural and built features (Cadenasso et al. 2007). To better plan climate adaptation strategies in cities, studies are needed that consider effects of land cover on urban air temperature at fine spatial scales, including potential interactions between impervious cover and vegetation structure.

Urban forest management represents an important opportunity to mitigate high temperatures at the scale of urban residents' daily lives, and beyond traditional green spaces. Trees are prevalent throughout many cities, and unlike the relatively static size and shape of parks, the urban canopy is continually changing in response to policy, societal preference, and disturbance. The potential of trees to regulate temperature is widely acknowledged, with forested green spaces reaching considerably cooler temperatures than their non-treed counterparts (Bowler et al. 2010, Gago et al. 2013, Hiemstra et al. 2017). However, a detailed understanding of the magnitude and scale at which trees affect local air temperature throughout urban landscapes is hampered by the paucity of data along continuous gradients of urban land cover.

Advances in sensor-based methods – and mobile sensors in particular – provide an opportunity to collect air temperature measurements at data-sparse intra-urban scales (ACERE 2018). While stationary sensor networks are excellent for characterizing broad patterns and temporal dynamics of the UHI (Schatz and Kucharik 2014), mobile sensors facilitate access to areas otherwise difficult to sample, and allow measurement along continuous land-cover gradients. We used a custom bicycle-based sensor as a low cost, low impact method to characterize the intra-urban heat island in a mid-size temperate city – focusing on the mitigation potential of urban trees. While others have used bicycles to study the UHI (Brandsma and Wolters 2012, Heusinkveld et al. 2014, Rajkovich and Larsen 2016), we extended this method in multiple ways: sampling many transects across multiple days, considering continuous land-cover change rather than discrete categories, assessing effects of scale, and accounting for the complex spatial-temporal nature of mobile data. We asked how variability in canopy and impervious cover interact to influence both daytime and nighttime summer air temperature at multiple fine spatial scales.

Methods

Study area

Madison, Wisconsin is a mid-size city (urban area population ~400,000) in the north-central United States. The climate is humid-continental, with warm humid summers and cold winters. Characterized predominantly by low-density housing, Madison also contains mid- and high-density development, and green spaces including forest, wetland, and prairie. The surrounding landscape is largely agricultural, but includes remnant native vegetation (forests and grasslands), wetlands, and several lakes.

Mobile measurements

We built two bicycle-mounted temperature sensors (Fig 1b) equipped with instrumentation to quantify human thermal exposure. A fast-response, high-accuracy temperature probe (Campbell Scientific 109SS) equipped with solar shield was mounted at 1.5m high, with a response time of < 7.5s in 3m/s wind and an accuracy of ± 0.1°C. This sensor and a GPS device (Campbell Scientific GPS16X-HVX) were integrated directly with a data logger (Campbell Scientific CR-850) and SLA rechargeable battery, enabling simultaneous recording of temperature and location while riding.

Ten urban transects were selected to cover the city geographically (Fig 1a) and span a wide range of variability in canopy and impervious cover. Mean transect length was 7km (mean cycling time 28min), preventing large changes in background temperature during measurement periods. During summer 2016 (May 30th – September 6th) each transect was sampled at least three (but up to 12) times during the hottest portion of the day (always between 1:30-7pm, but usually 4-6pm), for 64 total daytime rides. Four transects (Fig 1a) were also sampled at night (minimum 2-hours after sunset, ~10pm-12am), for 12 total nighttime rides. Maximum daily temperature averaged 29°C on sampling days (range: 22 – 34°C).

Data were collected at 1-second intervals – corresponding to air temperature observations approximately every 5-meters. Repeated measurements at any particular location (e.g., while at a stoplight) were removed to avoid potential measurement errors, for example due to exhaust from surrounding cars. To facilitate comparison of measurements collected at different times, measurements were converted to temperature anomalies using mean temperature of five stationary sensors in the city center as a reference data set (Fig 1a; WebPanel 1). Thus, a temperature anomaly of -1°C corresponds to temperature at the measurement location 1°C lower than the average temperature of the reference sensors at the same time.

Landscape structure

We calculated percent canopy and impervious cover (Fig 1a, inset) within a series of buffers (of 10, 30, 60, and 90m radius) surrounding each temperature measurement. Canopy cover was calculated from a 1m-resolution urban land-cover raster derived from NAIP data. Impervious cover was calculated from a custom layer comprised of (LiDAR-derived) building footprints, and City of Madison open data for stormwater impervious areas, roads, and bicycle paths (https://data-cityofmadison.opendata.arcgis.com). This layer was hand-corrected by referencing high-resolution satellite imagery, and rasterized at 1m-resolution. For each measurement, we also calculated distance to water and relative elevation (relative to mean elevation of the corresponding transect; from National Elevation Dataset 10m DEM). Analysis was done using QGIS.

Data Analysis

To evaluate effects of canopy and impervious cover on summer air temperatures at each scale of interest, we used generalized additive models (GAMs, using the “bam” function in R package “mgcv” version 1.8.17; Wood 2011, Wood 2017). GAMs are a flexible, nonparametric technique that use penalized regression splines to fit smooth relationships between response and explanatory variables. We assumed temperature was normally (Gaussian) distributed.

Percent impervious cover, canopy cover, and their interaction were included as smooth terms, as was distance from water. Smooths for single variables were fit using thin plate splines with a null space penalty. The interaction term was fit using a tensor product interaction (ti) term. We restricted the maximum degrees of freedom below mgcv defaults (allowing three basis functions per smooth term and nine for the interaction) to account for the fact that GAMs can overestimate nonlinearity of functional relationships in the presence of strong spatial autocorrelation (Wood 2017). Spatial coordinates were also included as a smooth term to account for unspecified spatial structure beyond that explained by land-cover variables. This term was fit using a Gaussian process spline with the default Matern covariance function (Wood 2017), using 29 basis functions to allow considerable flexibility in the shape of this relationship. Elevation was not a significant driver of temperature in our low topographic-relief system, and was excluded from final models. For all models, rides were nested within transect as a random effect (intercept), to account for differences in underlying weather conditions during different sampling periods. Models were fit using restricted maximum likelihood.

Due to measurement frequency, considerable temporal autocorrelation was present in model residuals. To account for the fact that positive spatial or temporal autocorrelation effectively reduces sample size (Fortin and Dale 2005), data were partitioned into 100 subsets of 1% of the data; each comprised of equally spaced measurements (e.g., model one included measurements 1, 101, 201… model two included measurements 2, 102, 202…). We averaged the predictions from each model to determine the response of temperature to explanatory variables (Fig 2). Including only every 100th point in each model considerably reduced residual autocorrelation (based on assessment of pacf plots), while averaging responses across 100 models ensured full use of available information, and incorporated inter-model variation in our estimate of uncertainty in the shape of functional responses.

We repeated this approach for the hottest days (where mean temperature for 4-hours prior to sampling exceeded 30°C) to determine whether UHI effects were exacerbated under high heat conditions. We also repeated our approach with nighttime measurements (excluding distance from water, as the effect was not significant at night).

Results

Intra-urban air temperature varied considerably (Fig 1c). Mean within-ride temperature range (i.e., difference between the hottest and coolest areas of each transect) was 3.5°C (SE 0.13; range 1.1-5.7°C), whereas temperature differed by only 0.2°C on fixed reference sensors during the same measurement periods. Variability was diminished at night, with a mean within-ride difference of only 2.1°C (SE 0.13; range 1.2-3.0°C). Model results for both day and night showed little variation among the 10 transects surveyed, but substantial differences among individual rides (i.e. driven by conditions during the sampling period).

Land-cover effects on daytime UHI

Air temperature decreased nonlinearly with increasing canopy cover (Fig 2a-d), with larger effects at broader compared to more localized scales. Increasing canopy cover from 0% to 100% within a 10m radius corresponded to a mean decrease of 0.7°C (Fig 2a), compared to 1.3°C when considering a 30m radius (Fig 2b), and over 1.5°C considering a 60 or 90m radius (Fig 2cd). The relationship was also increasingly non-linear at larger scales – particularly 60 and 90m – with canopy cover over 40% leading to substantially cooler temperatures (Fig 2cd).

Air temperature increased linearly with increasing impervious cover, but at each scale the magnitude of temperature change was less than for the effect of canopy (Fig 2). Effects were again larger at broader scales; increasing impervious cover from 0% to 100% within a 10m radius corresponded to a mean increase of 0.5°C (Fig 5e), compared to 0.7°C, 1.0°C, and 1.3°C when considering a surrounding area of radius 30, 60, and 90m respectively (Fig 2fgh).

Lakes decreased adjacent temperatures by only ~0.25°C on average, and effects were largely restricted to shoreline locations. Influence was quickly lost with increasing distance from the lake, with no consistent effect remaining at distances over ~700m from shore (WebFigure 1).

Overall, canopy cover substantially moderated the UHI effect at all scales considered (Fig 3). Variation in canopy and impervious cover at local scales led to mean temperature differences of 1.3°C (10m radius; Fig 3a) to 2.7°C (90m radius; Fig3d) across the urban landscape (30 and 60m radii intermediate at 1.9 and 2.3°C, respectively; Fig 3bc). On days exceeding 30°C, these temperature differences were even more pronounced; mean temperature differences across the impervious/canopy gradient increased by an additional 0.2-0.6°C (WebFigure 2).

Effects of land cover on nighttime UHI

Intra-urban air temperature was considerably less variable at night (WebFigure 3). The effect of canopy cover was limited, with increasing canopy from 0% to 100% cover corresponding to a linear decrease of 0.3-0.5°C (magnitude increasing with scale, WebFigure 3a-d). At night, impervious cover influenced air temperature to an equal or greater extent as canopy cover; temperature increased linearly from 0.3-0.7°C (magnitude increasing with scale, WebFigure 3e-h) as impervious cover increased from 0% to 100%. Consequently, variation in canopy and impervious cover at local scales led to mean nighttime temperature differences of only 0.5°C (10m radius) to 1.1°C (90m radius) across the urban landscape (30 and 60m radius intermediate at 0.7 and 0.9°C, respectively) (WebFigure 4).

Discussion

Improving climate adaptation strategies in cities – critical as climate warms – requires a better understanding of how spatial variation in temperature aligns with residents' lived experience (Jenerette et al. 2015). However, few studies have measured intra-urban variability in air temperature at fine scales. Using a mobile measurement system (Figure 1), we showed daytime air temperature varied considerably within a heterogeneous urban landscape, and was coolest where canopy cover is high (Figure 3). Air temperature increased with impervious cover, but canopy moderated this effect substantially. Fine-scale effects of land-cover on air temperature were consistent across the urban landscape, and temperature differences within the city were comparable to broad-scale difference between Madison and surrounding rural areas (Schatz and Kucharik 2014). Our results highlight potential for urban forestry to enhance temperature regulation services within temperate cities. Furthermore, our methods provide guidance for affordable, low-impact measurement of the intra-urban heat island, and could be replicated to test mitigation strategies in other geographic regions.

Within-city temperature differences were largest during conditions when health and energy impacts are most consequential – on the hottest days – further emphasizing the importance of mitigation efforts. This is analogous to Madison's broader UHI (Schatz and Kucharik 2015), where variability in daytime air temperature was greater during high-heat events than average summer days. Intra-urban temperature differences were diminished at night, however, in contrast to the strong nighttime urban-rural differences in Madison (Schatz and Kucharik 2014) and elsewhere (Memon et al. 2008). Effects of canopy were particularly limited at night, suggesting that while urban forest management provides considerable mitigation potential during the day (Hiemstra et al. 2017, Adams and Smith 2014), reduction of impervious surfaces remains critical for reducing the nighttime UHI (Memon et al. 2008).

The mitigation potential of land-cover modifications even at very fine scales gives urban stakeholders (e.g. residents and property managers) agency over reducing daytime summer temperatures. We show that increasing canopy even within only a 10-30m radius (comparable, in Madison, to the area of a single downtown lot (10m) or 2 to 3 suburban properties (30m)) can yield measurable cooling effects. However, our results also highlight the need for collective action to achieve a higher magnitude of cooling within cities. At scales where temperature differences were strongest, and where increasing canopy cover had the greatest effect (i.e., 60-90m, comparable to a typical city block) meaningful cooling will require multi-stakeholder collaboration; a persistent challenge of urban ecology (Aronson et al. 2017). Canopy cover in excess of ~40% had a larger effect on temperature reduction. Thus, trees planted along streets, on private property and in public parks may all be required to increase canopy cover above a threshold where meaningful reduction in summer temperatures occurs.

While it is important to be cognizant of the negative impacts of urban sprawl, combatting urban heat where people live also requires incorporation of enough greenspace within our cities to achieve effective levels of canopy cover; particularly difficult in higher density neighbourhoods. The strong and non-linear effect of canopy suggests balance is needed in urban planning and design between the compact urbanization suggested for maintaining many ecosystem services, and the more sprawling urbanization where built and natural spaces are interspersed (Stott et al. 2015). Furthermore, due to the long-lived nature of trees and persistence of pavement, current decisions – from homeowner preferences, to urban planning choices and urban forest policy – are setting up the urban heat riskscape of the future. Thoughtful choices today are needed to ensure the resilience of our future cities.

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Figure Legends

Figure 1. A mobile temperature sensor was used to measure variability in air temperature in Madison, WI. (A) Ten transects were sampled during summer days. Pink and yellow transects (marked “N”) were also sampled at night. White dots represent stationary reference sensors. Inset shows example of canopy and impervious cover. (B) Instrumentation including a fast-response, high-accuracy temperature sensor was mounted on a rear bicycle rack to facilitate continuous sampling at fine spatial scales, and allow exchange among bicycles. (C) Raw

temperature data (1 measurement/second) along a portion of one transect (same as Panel A inset), demonstrating fine-scale variation in air temperature with changing land cover. Photos show land cover at various locations (indicated with arrows).

Figure 2. Estimated smooth curves for the effect of increasing canopy cover (A-D), and impervious cover (E-F) within a surrounding radius of 10m, 30m, 60m, and 90m, on daytime summer air temperature in Madison, WI. Black lines represent the mean, and shaded areas represent ± 2 standard errors, both averaged across 100 models each containing 1% of the data. Mean and standard errors were generated using type =“iterms” in mgcv, such that standard errors returned for smooth components include uncertainty about the intercept/overall mean (Wood 2017). Edf represents effective degrees of freedom, averaged over all 100 models.

Figure 3. Difference in daytime urban air temperature achieved through altering impervious and canopy cover within a radius of (A) 10m, (B) 30m, (C) 60m, and (D) 90m, from generalized additive model responses. Right-hand images in each panel show the scale of measurement using an example of a typical medium-density neighbourhood in downtown Madison, WI. Models showed a strong relationship between observed and fitted values, with measures of model fit (adjusted R^2 and root mean square error (RMSE) – labeled underneath scale bar) consistent both among the 100 models at each scale, and across scales.

Figure 1

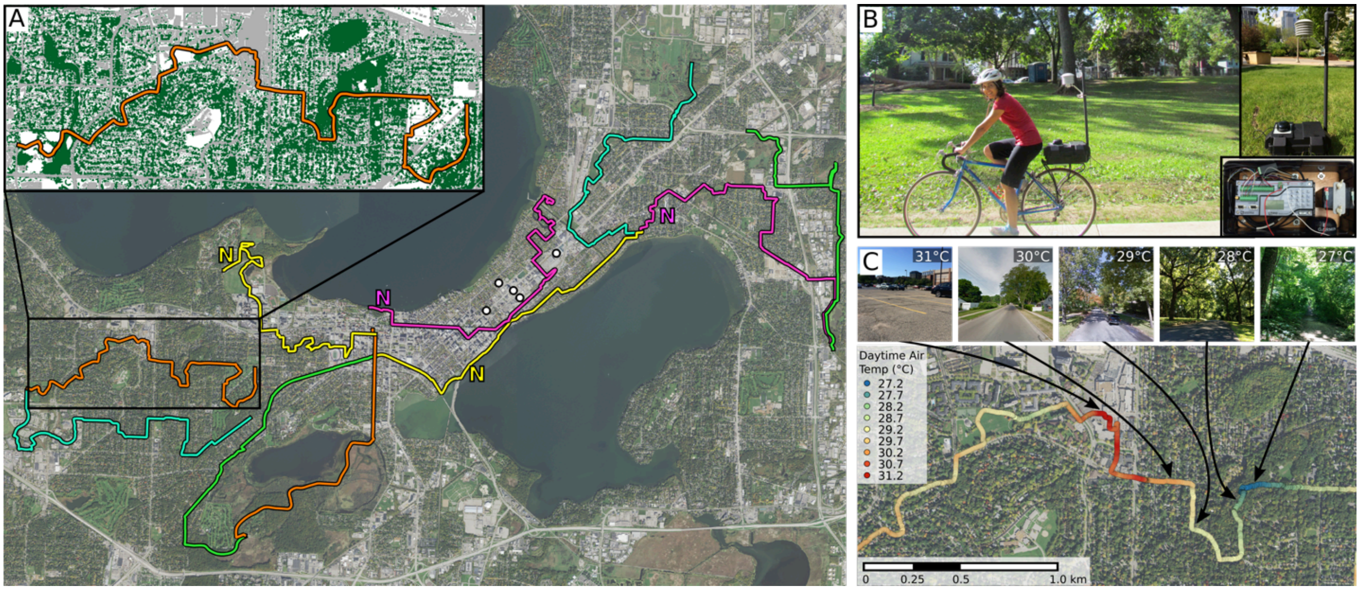

A
N
N
N
N
B
C
31°C
30°C
29°C
28°C
27°C
Daytime Air Temp (°C)
● 27.2
● 27.7
● 28.2
● 28.7
● 29.2
● 29.7
● 30.2
● 30.7
● 31.2
0
0.25
0.5
1.0 km

Figure 2

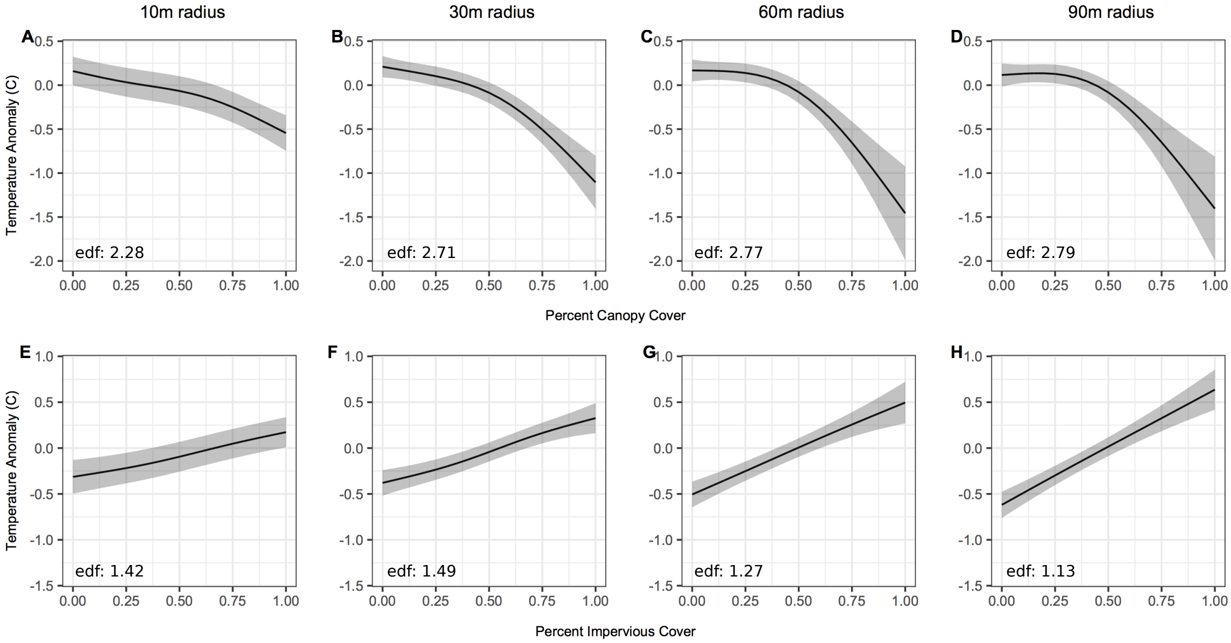
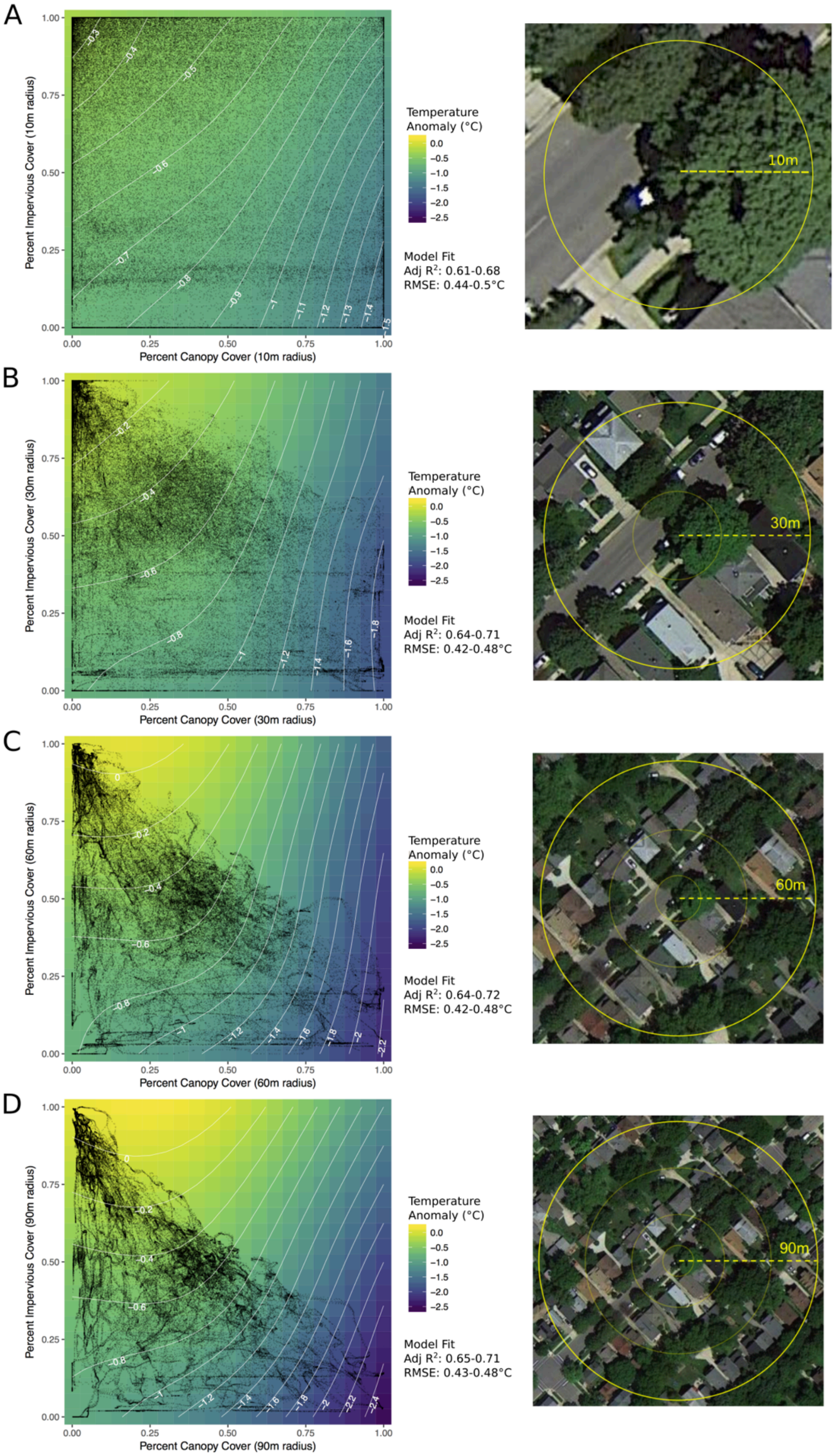

10m radius
30m radius
60m radius
90m radius
A
B
C
D
E
F
G
H
Temperature Anomaly (C)
edf: 2.28
edf: 2.71
edf: 2.77
edf: 2.79
Percent Canopy Cover
edf: 1.42
edf: 1.49
edf: 1.27
edf: 1.13
Percent Impervious Cover
0.5
0.0
-0.5
-1.0
-1.5
-2.0
1.0
0.00
0.25
0.50
0.75
1.00

Figure 3


A
Percent Impervious Cover (10m radius)
Percent Canopy Cover (10m radius)
Temperature Anomaly (°C)
0.0
−0.5
−1.0
−1.5
−2.0
−2.5
Model Fit
Adj R²: 0.61-0.68
RMSE: 0.44-0.5°C
10m
B
Percent Impervious Cover (30m radius)
Percent Canopy Cover (30m radius)
Temperature Anomaly (°C)
Model Fit
Adj R²: 0.64-0.71
RMSE: 0.42-0.48°C
30m
C
Percent Impervious Cover (60m radius)
Percent Canopy Cover (60m radius)
Temperature Anomaly (°C)
Model Fit
Adj R²: 0.64-0.72
RMSE: 0.42-0.48°C
60m
D
Percent Impervious Cover (90m radius)
Percent Canopy Cover (90m radius)
Temperature Anomaly (°C)
Model Fit
Adj R²: 0.65-0.71
RMSE: 0.43-0.48°C
90m
0.00
0.25
0.50
0.75
1.00

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Supplementary Material

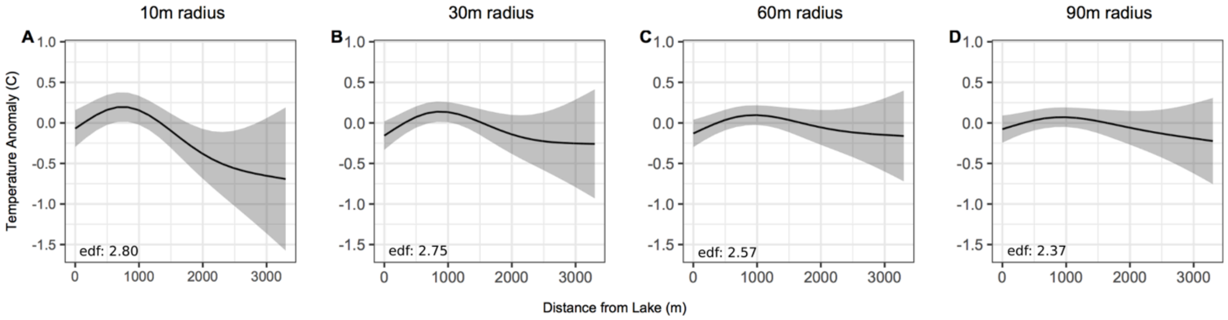
WebPanel 1. Temperature Anomaly Calculations

To enable relative comparisons of air temperature within and across transects, we used a set of fixed reference sensors to calculate the “temperature anomaly” for all measurements. This accounted for minor changes in background temperature over the sampling period, and facilitated comparison among measurements taken at different times. We chose 5 sensors from a 150-sensor array of stationary temperature sensors in Madison (see Schatz and Kucharik 2014) – located close together in the built-up city center (Fig 1a) – as reference sensors for this study.

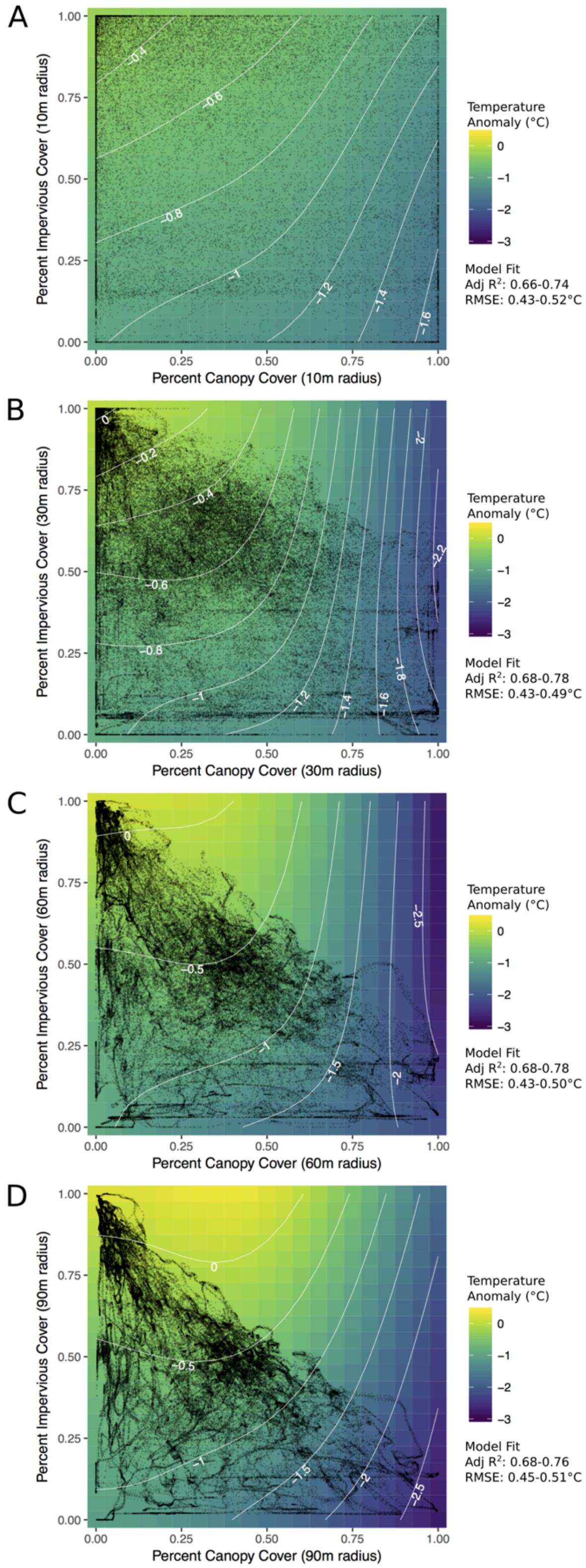
Reference sensors recorded air temperature simultaneously every 15 minutes, requiring reconciling the temporal resolution with the 1-second resolution of mobile sampling. For each sampling period (e.g. each bike ride along a given transect), we isolated measurements recorded by the reference sensors immediately preceding, during, and after the ride. This ranged from 3-5 measurements per ride, depending on ride length and start/end times. For example, if a ride occurred from 4:27 – 4:55pm, we isolated the reference temperature measurements from 4:15, 4:30, 4:45, and 5:00pm on the same day. To account for minor fluctuations in temperature between 15min recordings, we assumed a linear change in temperature between time points, and estimated the temperature at 1-second intervals for each of the 5 reference sensors. We then calculated the mean temperature across the 5 sensors at each time point to create a single reference dataset that matched the temporal resolution of the bicycle-collected data.

We subset the reference dataset to the same start and end point as each ride. This allowed us to estimate any change in background temperature over each sampling period, and also calculate a temperature anomaly for each measurement that accounted for this change (by subtracting the bicycle-measured temperature from the reference temperature at each time point).

WebFigures

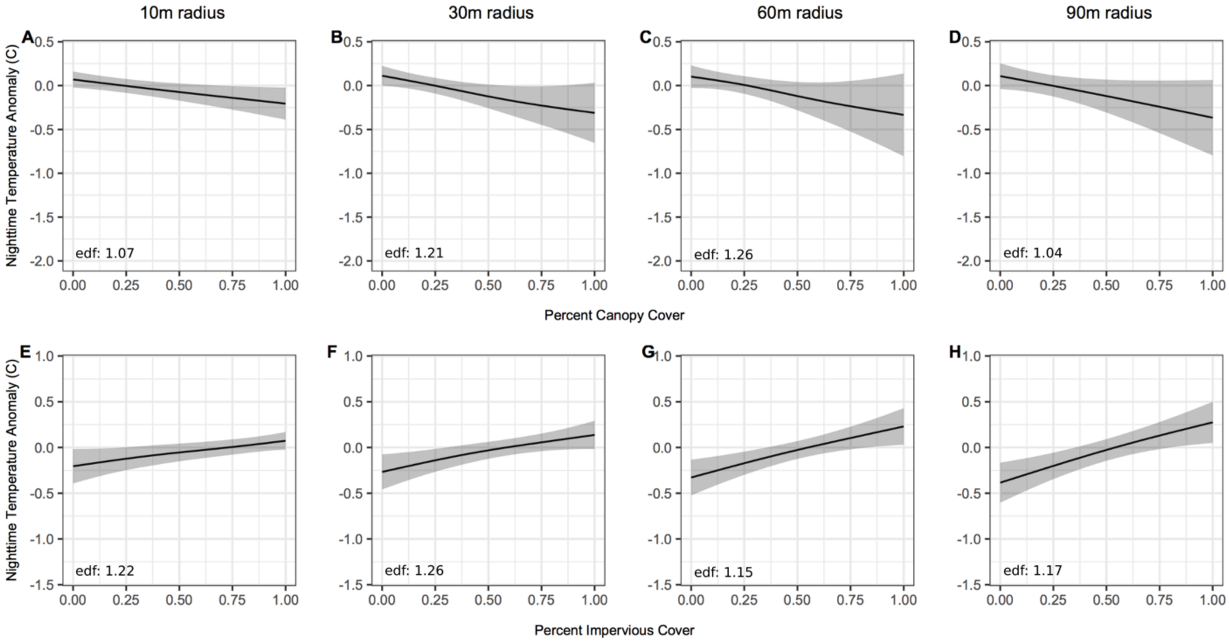


WebFigure 1. Estimated smooth curves for the effect of increasing distance from the lake within a surrounding radius of (A) 10m, (B) 30m, (C) 60m, and (D) 90m. Black lines represent the mean, and shaded areas represent ± 2 standard errors, both averaged across 100 models each containing 1% of the data. Mean and standard errors were generated using type =“iterms” in mgcv, such that standard errors returned for smooth components include uncertainty about the intercept/overall mean (Wood 2017). Edf represents effective degrees of freedom, averaged over all 100 models.

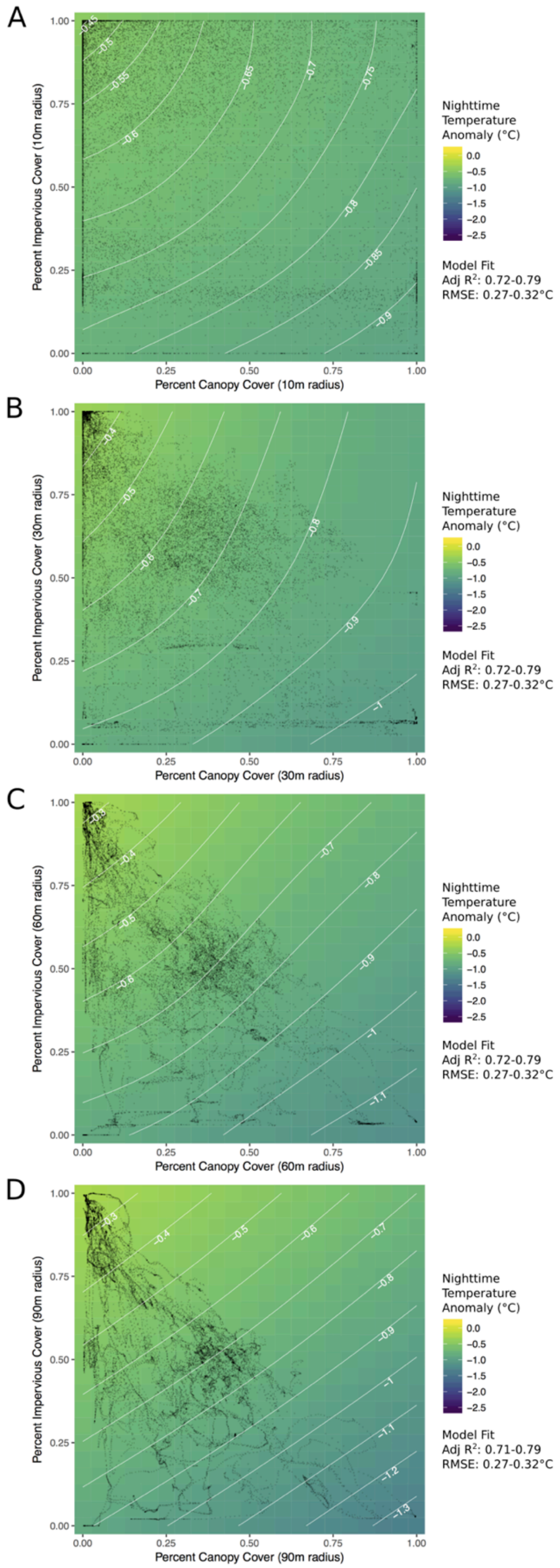


WebFigure 2. Difference in daytime urban air temperature on hot summer days (over 30°C) achieved through altering impervious and canopy cover within a radius of (A) 10m, (B) 30m, (C)

60m, and (D) 90m, from generalized additive model responses. Models showed a strong relationship between observed and fitted values, with measures of model fit (adjusted R^2 and root mean square error (RMSE) – labeled underneath scale bar) consistent both among the 100 models at each scale, and across scales. Temperature range is greater on hot days than for models across all sampling days (i.e., Fig 3), by 0.17°C (10m scale), 0.43°C (30m scale), 0.59°C (60m scale), and 0.36°C (90m scale).



WebFigure 3. Estimated smooth curves for the effect of increasing canopy cover (A-D), and impervious cover (E-F) within a surrounding radius of 10m, 30m, 60m, and 90m, on nighttime summer air temperature in Madison, WI. Black lines represent the mean, and shaded areas represent ± 2 standard errors, both averaged across 100 models each containing 1% of the data. Mean and standard errors were generated using type ="iterms" in mgcv, such that standard errors returned for smooth components include uncertainty about the intercept/overall mean (Wood 2017). Edf represents effective degrees of freedom, averaged over all 100 models.



WebFigure 4. Difference in nighttime urban air temperature achieved through altering impervious and canopy cover within a radius of (A) 10m, (B) 30m, (C) 60m, and (D) 90m, from

generalized additive model responses. Models showed a strong relationship between observed and fitted values, with measures of model fit (adjusted R^2 and root mean square error (RMSE) – labeled underneath scale bar) consistent both among the 100 models at each scale, and across scales.

Dissertation Conclusions

Unprecedented urban growth has markedly changed ecosystem structure, function, and biodiversity, and consequently the ecosystem services that our health and wellbeing depend on. To work towards more sustainable, liveable cities, it is important to identify opportunities to manage cities for increased ecosystem service provision. This requires an understanding of urban areas as spatially heterogeneous and temporally dynamic ecosystems. Integrating synthesis, observational, and experimental approaches, this dissertation provides insight into the implications of landscape structure, historical land-use, and biodiversity for ecosystem services in urban landscapes. Results are relevant for ecosystem service management in Madison and other temperate, mid-size cities, and also contribute to advances in ecosystem service science more broadly. Several key findings are summarized below.

1. Understanding biodiversity-ecosystem service relationships requires a more mechanistic focus, including accounting for the potential impacts of non-native and invasive species.

There are many calls to conserve biodiversity in urban areas, often with the expectation that such efforts will align with increased supply of ecosystem services. However, my results show that biodiversity can have positive, negative, or neutral impacts on ecosystem services in urban areas, with services more commonly dependent on measures of composition than correlated with the magnitude of any given biodiversity metric (Chapter 1). These findings suggest that research should focus on mechanisms by which biodiversity change may influence ecosystem services, rather than the common assumption that a greater number of species will by default increase services as well. Considering multiple aspects of biodiversity is also important, particularly regarding non-native species that are widespread in urban areas – but understudied with respect to ecosystem service impacts (Chapter 1). Consequences of invasive species for ecosystems are often assumed despite limited evidence. However, we found that contrary to the dominant "invasional meltdown" hypothesis concerning earthworms and invasive plants, an incipient urban invader, *Amynthas tokioensis*, did not interact with *Rhamnus cathartica* in our system – with positive conservation implications (Chapter 3). Our results emphasize the need to think critically regarding the influence of invasive – and other – species on ecosystem services, including consideration of species traits and life history.

2. Both contemporary and historical land-use influence ecosystem services and their interactions, with cities providing an excellent study system for the effects of spatial and temporal heterogeneity. Ecosystem service research and management often relies on simple land-cover or habitat based proxies, including in cities (Chapter 1). Using empirical data on soil properties (Chapter 2) and air temperature (Chapters 4) we showed that ecosystem services were highly variable at fine scales, and within typical land cover categories. This may be particularly problematic in urban ecosystems – characterized by fine-scale variability – but our results also highlight the importance of thinking beyond land cover or habitat-based proxies and considering multiple spatial scales in ecosystem services research more broadly. Furthermore, we showed that historical land-use can play a strong role in shaping contemporary patterns of ecosystem services, including altering relationships among services over time (Chapter 2). Particularly when slow process underlay service provision (Chapter 2), or services depend on slow-growing species (Chapter 4), thoughtful choices today are needed to ensure ecosystem services are sustained in our future cities.

3. We need to "think outside the park" when it comes to urban ecosystem services; it is important to consider the full mosaic of greenspace in cities, including both public and

private land. While many urban ecology studies have relied on parks as the de facto example of urban greenspace, the ecological fabric of cities is in fact much broader, including a considerable amount of land owned and managed by private citizens and businesses. Our results show that ecosystem services can differ in important ways in private compared to public greenspaces (Chapter 2), and that consideration of multiple types of greenspace led to a better understanding of multiple services at the scale of an urban landscape. We also found that considering land-cover variables along continuous, rather than categorical, scales yielded important insights into ecosystem service provision (Chapter 4). Interstitial urban spaces (e.g. street trees outside the "built up" vs. "green space" dichotomy) can provide important benefits to urban residents. A stronger understanding of these within-city drivers of ecosystem services will allow ecologists to better speak to the situations and scales at which urban stakeholders have agency over ecosystem service provision – aligning with a major goal of ecosystem service science to design research that better addresses the questions of decision-makers.