# Urban Microbiomes and Urban Agriculture: What Are the Connections and Why Should We Care?

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A large percentage (~50 %) of the global human population lives in urban systems. The transition from largely rural to urban lifestyles began gradually, but has accelerated. Given the magnitude of anthropogenic changes in the Earth system as a whole and concerns about resource availability and continued population growth, questions about the sustainability of urban systems have become a focal point for a variety of research and civic efforts, including programs promoting urban agriculture as a means to provide local food sources and to better manage critical nutrients such as nitrogen and phosphorus. The last decade or so has also witnessed a remarkable transformation in our understanding of the centrality of microbes for virtually all aspects of human life and wellbeing. However, this transformation has not yet been incorporated into a fuller understanding of the biology and ecology of urban life. Research on microbial assemblages (or microbiomes) in the built environment, particularly building interiors, has provided compelling examples of the importance of microbes, but these results provide at most an incomplete picture of microbial distribution and activity in urban systems. For example, though very little is known about microbial interactions with urban agriculture, the success of urban agriculture and its potential to contribute to urban sustainability will depend in part of incorporating new knowledge about soil and plant microbiomes to optimize production and to minimize some of the adverse effects of agriculture in traditional settings (e.g., greenhouse gas emission, nitrogen and phosphorus eutrophication). To that end, this review defines and provides examples of the microbiome concept and the significance of microbiomes in urban systems; it also identifies large knowledge gaps and unanswered questions that must be addressed to develop a robust and predictive understanding of urban biology and ecology.

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## Introduction and Definitions

Microbes in natural and managed systems have long been recognized for their critical biogeochemical functions, e.g., decomposition and nutrient cycling (Fenchel et al. 2012). These functions are among numerous diversity-dependent "ecosystem services," many of which provide benefits for humans at little or no cost (Bell et al. 2005; Balvanera et al. 2006; Langenheder et al. 2010). Indeed, some services, e.g., nitrogen fixation, have been exploited to improve soil fertility and food production resulting in substantial economic benefits (Fig. 1).

The services provided by microbes result from the activities of individual populations or groups of populations (i.e., guilds) acting in complex assemblages, or communities. Many microbial communities (e.g., those in soils) harbor thousands of populations (or "species") that form interacting and interdependent networks. These networks and their services are sensitive to natural and anthropogenic disturbances, which elicit a variety of responses that depend in part on community composition, species richness and evenness (Yeager et al. 2005; Wittebolle et al. 2009).

**Fig. 1** Using a winter cover crop of crimson clover to fix nitrogen in a raised bed curbside garden in Seattle, WA (Photo by Sally Brown)

## *Microbiome Definition and Examples*

Although the term "microbial community" remains widely used when referring to assemblages of microbes, the term "microbiome" has been used synonymously to refer to assemblages associated with macroorganisms. More specifically, it has been used to refer to members of the domains Bacteria and Archaea associated with organs (e.g., rumen, colon, vagina), surfaces of organisms (e.g., epithelia), or in some cases organisms as a whole. This usage has been credited to Joshua Lederberg, a 1958 Nobel Laureate in Physiology, who described the intimate relationships between humans and microbes, stressing their profound importance and mostly beneficial service roles in human health (Relman et al. 2009).

Recognition of the importance of microbes in the human gut stimulated a major investment in the Human Microbiome Project, which has established biogeographic maps of microbial communities on and within humans of different age, ethnicity, gender and geography (Sears 2005; Gill et al. 2006; Diaz et al. 2012; Fierer et al. 2012; Faith et al. 2013). Numerous related studies have developed strong linkages between microbiome composition and activity, and diseases including certain cancers, diabetes and obesity (Armougom et al. 2009; Larsen et al. 2010; Hu et al. 2011). These studies have not simply documented relationships between microbes and disease states; rather they have shown that some members of the human microbiome contribute beneficially to health in a variety of ways (Fierer et al. 2012).

In parallel, a large number of studies have explored microbial associations with plants and animals (e.g., Rawls et al. 2004; Thompson et al. 2010; Kelley and Dobler 2011; Yashiro et al. 2011; King et al. 2012). Some of the latter have helped inform human studies. Collectively, they have transformed our understanding of organismal biology by illustrating the extent to which multicellular organisms depend on bacterial associates or symbionts to function optimally.

Microbiome research has also expanded beyond organisms to consider assemblages of microbes that are resident on or in inanimate objects with which specific organisms interact. Thus, the microbiomes of cleaning sponges, shower curtains, kitchen and bathroom surfaces, cell phones, and computers have all been analyzed to better understand the microbial populations with which humans come in contact (Feazel et al. 2009; Corsi et al. 2012; Hospodsky et al. 2012; Kelley and Gilbert 2013; Berg et al. 2014; Fujimura et al. 2014; Kembel et al. 2014; Meadow et al. 2014). Results from these studies have revealed a surprising level of diversity in the "built environment" (referring to human-produced structures), and documented reservoirs of pathogens in sometimes surprising contexts (Feazel et al. 2009).

The microbiome concept is extended here beyond individuals and the objects and structures with which they interact in an immediate sense to the urban scales that define the geographic boundaries within which most people currently spend most of their time. The urban scale is increasingly important due to the ongoing worldwide urbanization of human populations, and growing concerns about urban sustainability. Extension of the microbiome concept to this scale draws from a rich literature that recognizes urban environments as distinct, complex ecosystems,

which necessarily include important, but mostly underappreciated roles for microbes (Groffman et al. 2002; Kaye et al. 2006; Pickett et al. 2008; Pouyat et al. 2010; King 2014).

## *Urban Microbiomes*

What then are urban microbiomes? In what ways do they matter? What do we need to know about them? Questions such as these were not asked a mere decade ago, and for all practical purposes, they could not have been answered if they had been asked. Methodological and conceptual limitations constrained studies on microbes in urban environments largely to pathogens, pathogen indicators, bio-threat agents and waste treatment (e.g., Werner et al. 2011; Dobrowsky et al. 2014). Exceptions include studies that have addressed biogeochemical processes in urban settings (Milesi et al. 2005; Groffman and Pouyat 2009; Harrison et al. 2011; Bettez and Groffman 2012), and that have addressed the role of microbes in the degradation of culturally or artistically valuable sculpture and building surfaces (Saiz-Jimenez 1997; Papida et al. 2000; Herrera and Videla 2004; Herrera et al. 2004; Webster and May 2006; Fujii et al. 2010). However, most urban microbe studies have focused on individual populations and their effects; few studies have been integrative, and those have been eclectic in nature (Braun et al. 2006; Knapp et al. 2009; Hou et al. 2013).

At present, only limited information exists about urban microbiomes, and most of the recent observations have emphasized interiors of the built environment. However, urban microbiomes not only encompass microbial assemblages within buildings, they also include assemblages associated with the highly diverse exterior environments that characterize urban systems (e.g., Ramirez et al. 2014). Among many others, the latter include building surfaces, roads, streets and other passages; surface and sub-surface soils; the phyllosphere of plants; animal and human waste; water distribution systems, streams, drainage systems and other aquatic habitats.

The atmosphere of urban environments also harbors microbes, even if its populations are transient (Brodie et al. 2007). Because the urban atmosphere can exchange microbes with both the physical and biological components of urban systems, it contributes to the collective urban microbiome. The atmosphere also represents a medium or "teleconnection" for exchange of microbes between urban and rural systems, and provides a pathway for the introduction of microbes from distant or remote systems (Bowers et al. 2011). For example, in March 2013, a dust storm originating in China's Gobi Desert deposited sand with associated microbes in Los Angeles, California, more than 10,000 km away. The extent to which such events impact urban systems is essentially unknown, though a variety of consequences can easily be imagined.

Urban microbiomes are thus comprised of the vast and diverse assemblages of microbes that occur as resident or transient members of numerous habitats within urban systems. Today detailed characterizations are conceivable using "next gen" approaches for metagenetic and metagenomic sequencing. However, this capability

begs important questions: Why do urban microbiomes matter? Why would one want to characterize them in the first place? Are there connections with new initiatives in urban sustainability, i.e., urban agriculture?

## Urban Microbiomes: Why Do They Matter?

Urban microbiomes are important for numerous reasons, some of which directly involve human wellbeing. For example, microbial communities in waste treatment systems have contributed greatly to improvements in public health. Urban microbiomes also indirectly affect human wellbeing. For instance, certain microbial biogeochemical transformations produce greenhouse gases (e.g., nitrous oxide, $N_2O$) that contribute to global warming and its adverse impacts (Kaye et al. 2004; Townsend-Small et al. 2011), while other processes contribute beneficially to pollutant detoxification (Kolvenbach et al. 2014). Human life in urban systems is inextricably linked to microbes. Several examples of the importance of urban microbiomes are summarized briefly below.

### *Microbial Biomass and Diversity*

In undisturbed terrestrial systems, microbial biomass, largely found in soils, typically accounts for a substantial fraction of total non-plant biomass (Tate 2000). Although biomass inventories have not been reported for urban systems, the relatively small amount of exposed soil surface suggests that microbial biomass might be modest at most, and distributed very differently than in undisturbed systems. The consequences of different distributions are unknown; similarly unknown is the extent to which soil beneath built surfaces contributes to the biogeochemical "footprint" of urban systems.

Nonetheless, with thousands of microbial species per gram of soil, microbes undoubtedly constitute the greatest reservoir of urban species and genetic biodiversity, exceeding the diversity of all urban plants and animals combined, and this does not even consider microbes that colonize or are otherwise associated with plants and animals themselves. Urban microbial diversity includes species that contribute important ecosystems services (e.g., waste treatment, pollutant biodegradation, nitrogen fixation) from which humans benefit, as well as species that have adverse impacts (e.g., plant and animal pathogenesis and building deterioration). Reasonably complete inventories exist for plant and animal diversity in urban systems, but comparable assessments for microbes are lacking.

Regardless, a recent survey of in soils of Central Park, New York City revealed a level of microbial diversity similar to that observed in natural (i.e., unmanaged) soils across the globe (Ramirez et al. 2014). Not only were the numbers of microbial species in Central Park soils equivalent to numbers in other soils, the composition

of the soil communities were similar; this was true both for bacteria (domains Bacteria and Archaea) and fungi (Fig. 2a, b). Although more comprehensive analyses of urban soils are needed, initial results confirm that they are a major reservoir of species and genetic diversity.

## *Microbial Interactions with Plants*

Irrespective of their biomass, soil microbes play profoundly important roles in plant production, and thus must be considered in the development of sustainable urban agriculture. Soil microbes complete with plants for nitrogen and other nutrients, but they also promote plant growth by facilitating nutrient uptake through a variety of symbiotic or associative relationships that have been thoroughly documented for many natural and agricultural systems (Tate 2000). Plant growth-promoting rhizobacteria (PGPR) also aid in plant defenses against disease by regulating some plant pathogen populations and contributing to "induced systemic resistance" (Faure et al. 2008; Belimov et al. 2009; Doornbos et al. 2011; Hassan and Mathesius 2012; Carvalhais et al. 2013) (Fig. 3).

In addition, urban soils are often degraded relative to managed agricultural and unmanaged natural soils, usually due to elevated toxic metals and organics (e.g., copper, lead, polycyclic aromatic hydrocarbons – PAH), which can limit their productivity. In some cases, soil microbes have been successfully exploited to enhance metal and organic phytoremediation in brownfield and other contaminated soils (Di Gregorio et al. 2006; Gerhardt et al. 2009). Microbially-enhanced phytoremediation might thus prove generally useful as a pre-treatment to improve urban soil quality for agricultural applications. Targeted selection of plants and bacterial inoculants, along with strategies to enhance naturally-occurring microbial biodegradation, could increase the inventory of agriculturally suitable soils with little to moderate cost. Similar approaches could also be used to "condition" microbial communities to optimize and sustain urban production, but this will require new knowledge about urban soil microbes.

## *Microbes and Biogeochemical Transformations*

In addition to their interactions with plants, urban microbes mediate a variety of biogeochemical processes that affect mass and energy flows within urban systems, and exchanges of mass and energy between urban systems and their surroundings. Some of these processes occur within waste treatment systems, which affect forms and masses of carbon, nitrogen, phosphorous, trace metal and pollutant exchanges.

Other processes associated with urban soils, riparian systems and structures engineered for controlling water movement (e.g., storm runoff) are also important (Arango et al. 2008; Cadenasso et al. 2008; Harrison et al. 2011; Li et al. 2014).
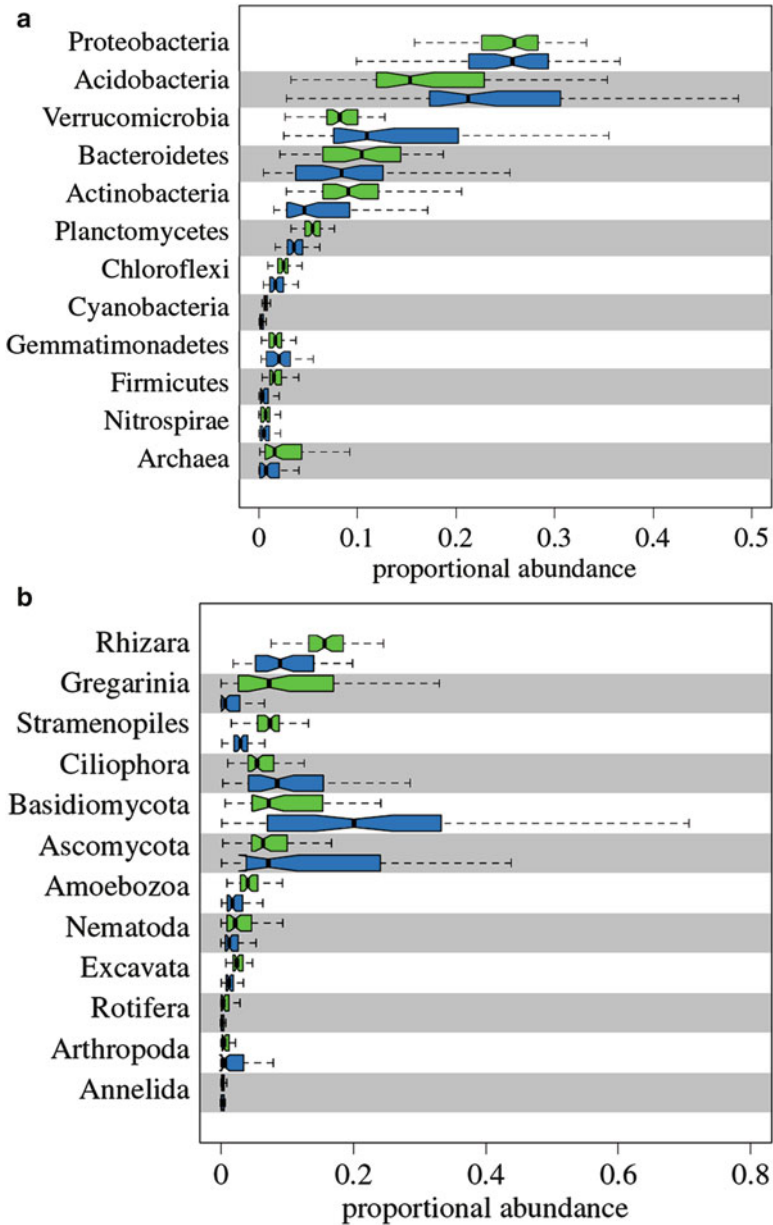
**Fig. 2** (**a**) Relative abundances of common bacterial phyla and Archaea in Central Park, New York City soils. *Box* and *whisker plots* show average abundances (*bar*) and *upper* and *lower* limits (*dashed lines*) for Central Park (*green*) and a global soil inventory (*blue*). (**b**) As for (a), but illustrating relative abundances of fungi and other eukaryotes (From Ramirez et al. (2014))

**Fig. 3** A garden constructed using municipal biosolids at a wastewater treatment plant in Tacoma, WA (Photo by Dan Eberhart)

Denitrification rates, which are elevated in urban systems, are particularly significant, because denitrification can limit nitrogen (nitrate) exports to receiving systems, such as inland and coastal waters (Klocker et al. 2009; Harrison et al. 2011). However, denitrification can also contribute to $N_2O$ formation. Denitrification and the coupled process of nitrification are both stimulated by nitrogen fertilization, whether fertilizers are applied for lawns or crop and vegetable production. $N_2O$ formation from these processes, and fluxes from urban agriculture, must be considered carefully and controlled to the extent possible, since $N_2O$ emissions can potentially vitiate any benefits from carbon storage (sequestration) or reduced $CO_2$ emissions accompanying urban agriculture (Livesley et al. 2010). While rigorous management of nitrogen fertilization might represent the primary mechanism for controlling urban $N_2O$ emissions, a deeper understanding of the relevant microbial populations, their activities and controls is also essential.

## Microbes and Water Distribution Systems

The role of microbial communities in water distribution systems has been a subject of increasing attention, largely due to the recognition that "premise plumbing" systems (i.e., the water distribution systems of buildings) harbor distinct microbiomes

(Wang et al. 2013). A variety of opportunistic pathogens, including various myco-bacteria, *Pseudomonas*, *Legionella* and protozoans such as *Acanthamoeba*, occur in these assemblages, and can contribute to disease outbreaks. Recently, for example, the protist *Naegleria fowleri*, which causes a nearly always-fatal primary amebic meningoencephalitis, has been found in premise plumbing at two locations in Louisiana, USA.

While much remains unknown about premise plumbing microbiomes, it has been suggested that they might be manipulated using a form of probiotic treatment to limit opportunistic pathogens (Wang et al. 2013). To accomplish this successfully will require a level of understanding comparable to that now emerging for the human gut microbiome. Success will also hinge on a new recognition of the integral role microbes play in all built systems, and our routine and intimate associations with those microbes.

## *Exposures to Microbes and Consequences*

Because they are ubiquitous, humans interact directly and indirectly with microbes in the urban environment, as do all urban plant and animal populations. These interactions occur routinely and often with no obvious consequences. However, recent results suggest that some exposures to airborne microbes can have beneficial consequences for immunological fitness. In particular, exposures to microbes in rural atmospheres have been associated with lower incidences of asthma than exposures to microbes in urban atmospheres (Riedler et al. 2001; Ege et al. 2011; Illi et al. 2012). This difference might be due to a number of factors, including the concentration and diversity of airborne microbes and durations of exposure. In addition, the results indicate that increased urbanization could be associated with future increases in asthma incidence. Interestingly, the protective benefit of rural atmospheres has been attributed to farming environments and activities. This intriguing observation suggests that urban agriculture could provide similar protective benefits if agricultural activity is incorporated appropriately within urban systems (Brown and Jameton 2000).

## Urban Microbiomes: What Do We Need to Know?

Urban microbiome analyses are in their infancy. A small, but rapidly growing number of studies have characterized urban atmospheres, waste treatment systems and the interiors of buildings. They have provided new and unanticipated insights about the types and distributions of bacteria in the built environment, including observations that could improve health outcomes through microbiome-informed building design (e.g., Kembel et al. 2014). Nonetheless, these studies represent just the tip of the proverbial iceberg. In parallel, a larger but still limited number of studies

embedded in the discipline of urban ecology have begun to define both the unique characteristics of urban ecosystems as well as characteristics shared with unmanaged systems. Again, however, much remains to be done to understand the ecological and biogeochemical dynamics of urban systems. Some of the knowledge gaps and unanswered questions involving urban microbiomes are summarized below.

> A.1. What are the major reservoirs of urban microbes (e.g., the atmosphere, plants, soils, humans and other animals, waste treatment systems, exteriors and interiors of buildings) and how does their relative importance vary with space and time within and among urban systems?
>   2. How do the individual contributors to urban microbiomes interact across space and time?

As noted previously, the composition and dynamics of urban microbiomes remain largely unexplored and thus represent large knowledge gaps. One can surmise that soils are the greatest locus of genetic and functional diversity in urban microbiomes overall, but this assumption has yet to be evaluated empirically and likely varies across and among cityscapes with changes in soil distribution and mass. Although interactions between indoor and outdoor microbiomes as mediated through the urban atmosphere are now being explored, they represent only two of numerous interaction pathways; identifying and analyzing other interactions will be crucial for developing explanatory and predictive models and determining the factors that contribute to changes in them.

Addressing these questions is now feasible using next-gen sequencing approaches and computational advances for metagenetics (16S rRNA and other genes) and metagenomics. With continuing decreases in sequencing costs and the availability of high performance computing platforms, large-scale urban microbiome analyses are not only possible, but should be undertaken along with complementary urban ecological analyses.

> B.1. What major biological, ecological and biogeochemical functions occur in urban microbiomes? How do they differ from the microbiomes of unmanaged systems, how do they vary across space and time, and what controls their expression?
>   2. Can microbiomes of building surfaces and other structures be manipulated or controlled to improve resistance to deterioration or to promote beneficial services (e.g., pollutant remediation)?

If little is known about the diversity of urban microbiomes, even less is known about their functions. A few biogeochemically important functions (e.g., denitrification and methane oxidation) have been identified through process-based approaches, but function is often inferred from phylogenetic marker genes (e.g., 16S rRNA genes), which provide only broad diagnoses and are notoriously unreliable for spe-

cific processes in specific taxa. Thus, the possibility of manipulating microbiomes or their functions to achieve particular goals, e.g., decreased structural degradation, remains a distant though desirable goal. Greater understanding of function, like greater understanding of microbiome diversity, is now feasible using next-gen sequencing. However, the depth of sequencing necessary for comprehensive analyses, along with constraints of sequence assembly and annotation likely mean that in the near future relative few systems will be characterized in detail. However, this should not delay implementation of metagenomic, metatranscriptomic and metabolomics analyses of urban microbiome function; indeed these studies should be given a high priority.

> C.1. How connected with (or isolated from) the microbiomes of surrounding regions are urban microbiomes, and what are the pathways or mechanisms for connections?

Urban systems do not exist in isolation, nor do their microbiomes. The atmosphere represents one obvious route for exchanges between urban systems and their surroundings. A growing body of information has addressed the importance of short- and long-range atmospheric transport as a means for microbe dispersal, but there are other transport mechanisms, the relative importance of which is unknown, but which likely vary among urban systems and for specific microbial groups. For example, riverine transport might be important as a source of some bacteria in some urban systems (e.g., New York, NY; Portland, OR; St. Louis, MO), but play smaller roles in other cities (e.g., Denver, CO, Indianapolis, IN and Phoenix, AZ). Microbial transport directly and indirectly due to fluxes of humans, vehicles and plants and animals into and out of cities might also be important in some cases.

> D.1. Can soil microbiomes be manipulated to optimize urban agricultural production while minimizing or eliminating nitrous oxide production and emission?
> 2. Can the potential health benefits from exposure to rural-agroecosystem microbial aerosols be reproduced in urban environments at scales large enough to benefit urban populations?

While urban agricultural production is attractive for a number of reasons, its success in the context of sustainability will depend on a full accounting of costs and benefits. Greenhouse gases, especially $N_2O$ and methane, will need to be included in the costs. As a result of their large GWP values, relatively small changes in $N_2O$ and methane fluxes can either negate or amplify benefits gained from nitrogen recycling, carbon sequestration, and energy efficiencies derived from local agricultural production.

In traditional agricultural settings, significant $N_2O$ production occurs largely as a result of inefficient fertilizer nitrogen use by plants; agricultural land use also sub-

stantially reduces atmospheric methane uptake. Similar patterns have been documented for urban land use. Both phenomena add to atmospheric radiative forcing and global warming. While these impacts can be reduced in part by improved management of fertilizer nitrogen applications, they might also be reduced by specific manipulations of rhizosphere and bulk soil microbiomes. The latter has not been attempted for conventional agricultural production, but might be feasible on the scales of urban agriculture, particular in systems designed *de novo*. Of course, successful manipulation of microbiomes to manage greenhouse gases will require advances in understanding of the structure, function and controls of microbial communities and their activities.

Although not fully understood, a number of observations suggest that asthma incidence can be reduced by exposure to microbes in rural atmospheres, particularly those associated with agriculture. Whether this or other potential health benefits can be reproduced in urban environments is unknown, but important to consider in evaluating the total costs and benefits of urban agriculture. It is worth remembering that urbanization is a recent and growing phenomenon in human history, and that human immunological systems evolved in markedly different environments with exposures to different suites of antigens. Reproducing at least some of those exposures could contribute to larger efforts to improve urban health outcomes and urban sustainability.

## Summary

Microbes are both the foundation and fabric of all life, human life included. Thus, individual microbes have long been a focus of health concerns, and they have also long been exploited beneficially (e.g., *Streptomyces griseus* for drug production). Nonetheless, microbes exist naturally in complex communities, or microbiomes, and it is in this context that their significance arises. Whether in the human gut or broadly distributed across cityscapes, microbiomes play profoundly important roles in the activities and functions of the hosts and systems they inhabit. The composition and dynamics of urban microbiomes are largely unknown at present, but it is clear that they contribute basic services that make urban life possible. It is also clear that a greater understanding of urban microbiomes is essential for promoting urban sustainability and ensuring the success of rapidly expanding initiatives such as urban agriculture.

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