

MINIREVIEW

Urban Microbiomes and Urban Ecology: How Do Microbes in the Built Environment Affect Human Sustainability in Cities?

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Humans increasingly occupy cities. Globally, about 50% of the total human population lives in urban environments, and in spite of some trends for deurbanization, the transition from rural to urban life is expected to accelerate in the future, especially in developing nations and regions. The Republic of Korea, for example, has witnessed a dramatic rise in its urban population, which now accounts for nearly 90% of all residents; the increase from about 29% in 1955 has been attributed to multiple factors, but has clearly been driven by extraordinary growth in the gross domestic product accompanying industrialization. While industrialization and urbanization have unarguably led to major improvements in quality of life indices in Korea and elsewhere, numerous serious problems have also been acknowledged, including concerns about resource availability, water quality, amplification of global warming and new threats to health. Questions about sustainability have therefore led Koreans and others to consider deurbanization as a management policy. Whether this offers any realistic prospects for a sustainable future remains to be seen. In the interim, it has become increasingly clear that built environments are no less complex than natural environments, and that they depend on a variety of internal and external connections involving microbes and the processes for which microbes are responsible. I provide here a definition of the urban microbiome, and through examples indicate its centrality to human function and wellbeing in urban systems. I also identify important knowledge gaps and unanswered questions about urban microbiomes that must be addressed to develop a robust, predictive and general understanding of urban biology and ecology that can be used to inform policy-making for sustainable systems.

Keywords: microbiome, urban, public health, diversity, ecosystem services

Introduction and definitions

Humans now live predominantly in cities. Whether planned or not, the late 20th and early 21st centuries have become an era of urbanization. The global average urban population currently exceeds 53% of the total population, with a growth rate of 2% annually (World Bank, <http://wdi.worldbank.org/table/3.12>). In the United States (US), the urban population has begun to plateau at about 83%, but it continues to grow slowly. Urbanization also accounts for about 83% of the Republic of Korea's total population (hereafter Korea), although growth to that level occurred much more rapidly than it did in the US. In addition, population densities in Korea's cities are generally much greater than they are in the US; indeed, they are among the highest in the world.

While some have argued that urbanization represents a path towards a sustainable future, largely due to economies of scale, especially for energy, urbanization does not come without problems (Chakarrabarti, 2013). For Korea, as elsewhere this has been evident in concerns about socioeconomic issues, as well as resource availability, water quality, "heat island" exacerbation of global warming, changing patterns of disease and other factors that influence human health (Foster, 2001; Jeong, 2001; Yusuf *et al.*, 2001; Choi *et al.*, 2006; Vlahov *et al.*, 2007; Kim and Kim, 2011). These concerns have led to policies intended to promote some level of deurbanization, however, it remains to be seen to what extent such policies will result in sustainable solutions rather than simply creating new concerns.

Regardless of the policy choices made about urbanization in Korea and elsewhere, it is clear that humans largely will remain in urban systems for the foreseeable future. These systems, sometimes referred to as "built environments", retain the basic features of natural ecosystems though they are quite distinct from them in many respects. For example, specific mass and energy flows characterize the built environment just as they do natural systems along with networks of internal and external connections that determine fundamental properties such as biodiversity, stability, resistance, and resilience.

Among the many constituents of natural systems, microbes are notable for their long recognized critical contributions to biogeochemical functions, e.g., decomposition and nutrient cycling (Fenchel *et al.*, 2012). Many of these functions play important roles in the overall dynamics of urban systems, and some constitute critical "ecosystem services,"

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which provide benefits for humans at little or no cost (Bell *et al.*, 2005; Balvanera *et al.*, 2006; Langenheder *et al.*, 2010). For example, nitrification and denitrification have even been exploited extensively for urban wastewater treatment (Bitton, 2011), resulting in substantial economic and health benefits.

Nonetheless, many roles of microbes in urban systems have been largely unappreciated. Moreover, when microbes are given any consideration at all, it is often in the context of disease rather than in the benefits they provide. The fact that microbes rarely act as individual populations, but rather act as groups of populations in complex communities, or assemblages, has also been largely unappreciated outside of the discipline of microbial ecology. Many such communities harbor hundreds to thousands of populations that constitute interacting and interdependent networks (Allison and Martiny, 2008). These networks and the services they provide for humans are sensitive to both natural and anthropogenic disturbances, which result in responses that depend on variables such as community composition, species richness and evenness (Yeager *et al.*, 2005; Wittebolle *et al.*, 2009). Identifying and understanding the dynamics of microbial communities in urban environments is thus essential for managing microbes beneficially in the context of urban sustainability.

Microbiome definition and examples

The term “microbial community” has been used traditionally when referring to assemblages of microbes, but the term “microbiome” has become synonymous with microbial assemblages associated with macroorganisms. In particular, “microbiome” usually refers to Bacteria and Archaea associated with organs (e.g., gut), surfaces of organisms (e.g., epithelia), or organisms as a whole. Joshua Lederberg, a 1958 Nobel Laureate in Physiology or Medicine who described the intimate relationships between humans and microbes, has been credited with using microbiome in its contemporary context (Relman *et al.*, 2009).

During the last 10 years, emphasis on the human microbiome has established biogeographic maps of microbial communities on and within humans of different age, ethnicity, gender, and geographic location (Sears, 2005; Gill *et al.*, 2006; Diaz *et al.*, 2012; Fierer *et al.*, 2012; Faith *et al.*, 2013). Many additional studies have established strong linkages between microbiome composition and activity, and a variety of diseases (Armougom *et al.*, 2009; Larsen *et al.*, 2010; Hu *et al.*, 2011). Yet other studies have shown that some members of the human microbiome contribute beneficially to health in a variety of ways (Fierer *et al.*, 2012).

A large number of studies have also examined microbial associations with plants and animals (Rawls *et al.*, 2004; Thompson *et al.*, 2010; Kelley and Dobler, 2011; Yashiro *et al.*, 2011; King *et al.*, 2012). Some of these have contributed to the design and interpretation of human studies. Together, they have helped transform our understanding of organismal biology by revealing the extent to which multicellular organisms depend on bacterial associates or symbionts for optimal function.

Microbiome research has also addressed assemblages of microbes that are resident on or in a variety of the inanimate objects with which specific organisms come into contact.

Thus, cleaning sponge, shower curtain, kitchen and bathroom surface, cell phone, and computer microbiomes have all been described in an effort to better understand the microbial populations with which humans interact (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). These studies have revealed the presence of pathogens in sometimes surprising contexts (Feazel *et al.*, 2009), and documented a surprising level of diversity.

The microbiome concept is extended even further here to the urban scales that define the geographic boundaries within which most people currently spend their time. The urban scale is increasingly important due to the ongoing urbanization of human populations, and concerns about urban sustainability. Extension of the microbiome concept to this scale draws from diverse studies that have recognized urban environments as distinct, complex ecosystems that 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).

Urban microbiomes

What are urban microbiomes? Why do they matter? What do we need to know about them? In the past, methodological and conceptual constraints limited studies on urban microbes mostly to pathogens, pathogen indicators, bio-threat agents and waste treatment systems (Werner *et al.*, 2011; Dobrowski *et al.*, 2014). Some exceptional studies have addressed biogeochemical processes in urban settings (Milesi *et al.*, 2005; Groffman and Pouyat, 2009; Harrison *et al.*, 2011; Bettez and Groffman, 2012), including the role of microbes in the degradation of culturally valuable artifacts 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 studies have emphasized individual populations and their effects, and only a few can be considered integrative (Braun *et al.*, 2006; Knapp *et al.*, 2009; Hou *et al.*, 2013).

At present, the majority of observations on urban microbes emphasize building interiors. Regardless, urban microbiomes include microbial assemblages outside of as well as within buildings. Microbiomes occur in associations with building surfaces, roads, streets and other passages; surface and subsurface soils; the phyllosphere of plants; animal and human waste; water distribution systems, streams, drainage systems and other aquatic habitats (Fig. 1).

The urban atmosphere also harbors microbes, even though its populations are transient (Brodie *et al.*, 2007); it acts as both a source and a sink for microbes, and thus contributes to the urban microbiome as a whole (Fig. 1). In addition, the atmosphere provides a “teleconnection” for exchange of microbes between urban and rural systems, and a pathway for the introduction of microbes from distant systems (Bowers *et al.*, 2011). For example, dust and its associated microbes from China’s Gobi Desert have been deposited more than 10,000 km away Los Angeles, California. The impacts of such events on urban microbiomes are essentially unknown, but introductions of pathogens along with beneficial taxa are among them.

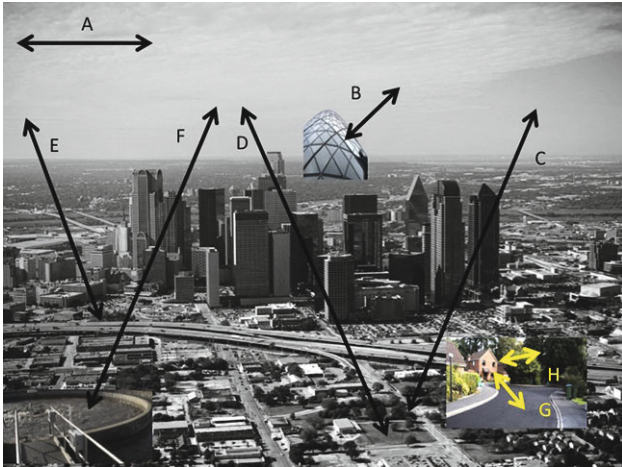


Fig. 1. Conceptual image of an urban microbiome showing some of its many reservoirs of microbes: A, the urban atmosphere and its surroundings as a reservoir of microbes transported into and out of urban systems, with long-distance teleconnections; B, building surfaces; C, vegetation; D, open grounds; E, streets and roadways; F, waste treatment systems; G, H connections between indoor and exterior microbiomes.

Thus, urban microbiomes can be defined very simply as the vast and diverse assemblages of resident and transient microbes that occur on or within the numerous habitats that comprise urban systems. Detailed characterizations of these assemblages are now conceivable using “next-generation” approaches for metagenetic and metagenomic sequencing. However, this capability begs several 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, e.g., urban agriculture?

Urban microbiomes: why do they matter?

The significance of urban microbiomes derives from many factors, some of which involve human wellbeing directly (Barnes *et al.*, 2011). For example, microbial communities in waste treatment systems have contributed greatly to the substantial gains in public health that have occurred since about 1900. Indeed, modern urban communities are inconceivable without advanced microbial waste treatment.

Urban microbiomes also affect human wellbeing indirectly. For instance, some microbes in urban environments produce greenhouse gases (e.g., nitrous oxide, N_2O , and nitric oxide, NO) that contribute to global warming and tropospheric ozone formation, both of which affect health adversely (Kaye *et al.*, 2004; Townsend-Small *et al.*, 2011), while other microbes contribute to pollutant detoxification (Kolvenbach *et al.*, 2014). Human life in urban systems is therefore inextricably linked to microbes, the importance of which is summarized briefly below with several examples.

Microbial biomass and diversity

In undisturbed terrestrial systems, soil microbial biomass typically accounts for a substantial fraction of total non-

plant biomass (Tate, 2000). Although inventories have not yet been reported for urban systems, the relatively small amount of exposed soil surface in them suggests that microbial biomass might be modest at best, and distributed very differently than in undisturbed systems. The potential consequences of different distributions are unknown; likewise the extent to which soil beneath built surfaces contributes to the biogeochemical “footprint” of urban systems is also unknown.

Nonetheless, microbes undoubtedly constitute the greatest reservoir of urban species and genetic biodiversity, exceeding the diversity of all urban plants and animals combined, with thousands of microbial species per gram of soil, and this does not even consider microbes that colonize or are otherwise associated with plants and animals themselves. The diversity of urban microbes includes species that provide major 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 and should be developed using the power of next-generation sequencing platforms, along with analyses of microbiome variability in space and time.

Microbes and biogeochemical transformations

Like their counterparts in unmanaged systems, microbes mediate numerous biogeochemical processes that affect mass and energy flows within urban systems, and mass and energy exchanges between urban systems and their surroundings. Many of these processes occur during waste treatment, which exploits a wide range of microbes to transform trace metals and pollutants, along with carbon-, nitrogen-, and phosphorous-containing compounds, in systems designed to promote human and environmental health (Bitton, 2011). Waste treatment systems have typically focused on microbes and microbial processes that reduce organic carbon concentrations through hydrolysis, fermentation and respiration, and eliminate fixed nitrogen from effluents, often with coupled systems for nitrification and denitrification (Bitton, 2011). In some cases, waste treatment also optimizes production and recovery of biogenic methane or bioelectricity as renewable sources of energy (McCarty *et al.*, 2011), and there is a growing need to optimize phosphorus recovery during waste treatment, since phosphorus limitation for fertilizer use is a serious emerging global-scale problem (Cordell *et al.*, 2008). Bacteria, including members of the genus *Accumulibacter*, play important roles in phosphorous removal during waste treatment (Seviour *et al.*, 2003; Peterson *et al.*, 2008), and could prove particularly important for phosphorous management in the future.

Other important microbial processes occur in urban soils, riparian systems and structures engineered for controlling water movement (e.g., storm runoff; Arango *et al.*, 2008; Cadenasso *et al.*, 2008; Harrison *et al.*, 2011; Li *et al.*, 2014). Denitrification is particularly significant, because it can limit exports to receiving systems (e.g., inland and coastal waters) of nitrate arising from nitrogen mismanagement and pollution (Klockner *et al.*, 2009; Harrison *et al.*, 2011). However,

denitrification also forms N_2O , which leads to an increase in the global warming “footprint” of urban systems. While rigorous management of nitrogen use in urban systems might represent the primary mechanism for controlling N_2O emissions, a deeper understanding of the relevant microbial populations, their activities and controls is also essential.

Microbes and water distribution systems

Microbial communities in water distribution systems have become a focal point for increased research, since “premise plumbing” systems (i.e., the water distribution systems of buildings) are now known to harbor distinct microbiomes (Wang *et al.*, 2013). Numerous opportunistic pathogens, including various mycobacteria, *Pseudomonas*, *Legionella* and protozoans such as *Acanthamoeba*, occur in premise plumbing, from which they can contribute to outbreaks of waterborne diseases. For example, the protozoa *Naegleria fowleri*, which causes a typically fatal primary amebic meningoencephalitis, has recently been found in premise plumbing in Louisiana, USA, even though its principle habitats have been open, warm surface waters.

Although much remains unknown about the microbiomes of premise plumbing, Wang *et al.* (2013) have suggested that they might be manipulated using a form of probiotic treatment to limit opportunistic pathogens. To accomplish this successfully will require new research programs leading to a level of understanding comparable to that currently emerging for the human gut microbiome. Success will also depend on greater recognition of the integral roles that microbes play in all built systems, as well as recognition of our routine and intimate associations with those microbes.

Exposures to microbes and consequences

Humans-microbe interactions, both direct and indirect, occur routinely in urban environments due to the ubiquity of microbes. Typically such interactions have no obvious consequences. However, exposures to some airborne microbes might have beneficial consequences for immunological fitness based on recent research results. In particular, lower incidences of asthma have been associated with exposures to microbes in rural rather than urban atmospheres (Riedler *et al.*, 2001; Ege *et al.*, 2011; Illi *et al.*, 2012). This outcome might be due to many factors, including the concentration and diversity of airborne microbes and durations of exposure. Regardless, the results indicate that increased urbanization could be associated with future increases in asthma if protective antigen exposures decrease. Interestingly, the protective benefits of rural atmospheres have been attributed to farm environments and activities. This suggests that urban agriculture might provide protective benefits if agricultural activity is incorporated appropriately within urban systems that promote human exposure to suitable suites of antigens.

Microbial interactions with plants

Soil microbes play profoundly important roles in plant production, and thus must be considered in initiatives to develop sustainable urban agriculture. Soil microbes compete with plants for nitrogen and other nutrients, but they can also promote growth by facilitating nutrient uptake through

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 defenses against disease by regulating some plant pathogens 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).

In addition, urban soils are usually degraded relative to agricultural and natural soils due to the presence of toxic metals and organics (e.g., copper, lead, polycyclic aromatic hydrocarbons), which can limit plant productivity. In some cases, soil microbes have been successfully used 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 and other 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.

Urban microbiomes: what do we need to know?

Analyses of urban microbiomes have only just begun. Recent studies have characterized urban atmospheres, waste treatment systems and building interiors (Brodie *et al.*, 2007; Cai *et al.*, 2014; Kembel *et al.*, 2014), yielding new and unanticipated insights about the composition and distributions of bacteria, including possibilities for improving health outcomes through microbiome-informed building design (Kembel *et al.*, 2014). However, these studies clearly represent only the first stages of much larger efforts to define the unique characteristics of urban ecosystems as well as characteristics they share with unmanaged systems. Some of the knowledge gaps and emerging questions about urban microbiomes are summarized below.

- A. 1. *Where in urban systems are microbes most abundant (e.g., the atmosphere, plants, soils, humans, and other animals, waste treatment systems, exteriors and interiors of buildings) and how does the relative importance of microbial reservoirs vary with space and time within and among urban systems?*
2. *How do the individual populations within urban microbiomes interact over space and time?*

The compositions and dynamics of urban microbiomes have not yet been explored in detail, and thus represent large knowledge gaps. Soils might represent the greatest concentration of genetic and functional diversity in urban microbiomes, but this assumption has not been evaluated empirically, and might not prove true across and among

cityscapes as soil distributions and masses change. Although interactions through the atmosphere of indoor and outdoor microbiomes are now being explored, there are likely other modes for interaction; identifying and analyzing such interactions is essential for developing explanatory and predictive models of microbial distributions and determining the factors that contribute to changes in them.

B. 1. For what important biological, ecological and biogeochemical functions are urban microbiomes responsible? How do they differ from the functions of microbiomes in 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 managed to control deterioration or weathering, or to promote pollutant remediation?

While some inferences can be derived from species composition inventories, in general little is known about urban microbiome biogeochemical functions. A few important functions (e.g., denitrification and methane oxidation) have been documented in some specific cases using targeted assays, but at present functions are often based on the presence of phylogenetic marker genes (e.g., 16S rRNA genes) that provide only broad indications of potential, and that have proven unreliable for detailed predictions involving specific taxa. Thus, the possibility of manipulating microbiomes or their functions to achieve particular goals, e.g., to control deterioration of building materials, remains a somewhat distant goal. Nonetheless, rapid gains in high throughput sequencing along with lower costs and improvements in sequence data analysis suggest that urban microbiome function can be addressed using the omics toolkit along with other targeted assays. Implementation of these studies could be profitably integrated with parallel studies on the use of nanomaterials to produce pollutant degrading building surfaces (Chen and Poon, 2009; Quagliarini *et al.*, 2012), a topic for which there is considerable interest. Do surface biofilms impede the performance of such materials? Are they inhibitory to microbial colonization? Can one be manipulated to affect performance of the other? Clearly there are many unanswered questions and numerous research opportunities.

C. 1. How do urban microbiomes interact with the microbiomes of surrounding regions, and what mechanisms are involved?

Neither urban systems nor their microbiomes exist in isolation. Exchanges between urban systems and the surroundings in which they are embedded obviously can occur via the atmosphere. Indeed, the importance of short- and long-range atmospheric transport for microbe dispersal is well documented. However, other transport mechanisms also disperse microbes, though their relative significance is unknown, and they likely vary among urban systems and for

specific microbial groups. Riverine transport, for instance, might be important as a source of some bacteria in some urban systems (e.g., Busan, Chungju, and Seoul), but play smaller roles in others (e.g., Cheongju, Daejeon, and Suwon). 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 many cases.

D. 1. 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?

Asthma is a growing problem in Korea as it is elsewhere (Cho *et al.*, 2006). Although not fully understood, a number of recent observations suggest that the incidence of asthma can be reduced by exposure to microbes present in rural atmospheres, particularly those that are associated with agriculture, and especially animal production. Whether or not such exposures and their potential health benefits can be reproduced in urban environments is unknown at present. However, with rising interest in Korean cities for urban agriculture, including “vertical farming” (http://www.hani.co.kr/arti/english_edition/e_national/588995.html), it might be possible to recreate some of the beneficial exposures that occur in rural systems, thereby adding a new dimension to urban food production. Recreating beneficial exposures will require a significant and multidisciplinary research effort, but it is worth recalling that urbanization is a recent phenomenon in human history, and that human immunological systems evolved in a very different context with exposures to different suites of antigens than occur in urban environments. Reproducing some of those exposures could contribute to improved urban health outcomes and promote urban sustainability.

Summary

Microbes are both the foundation and fabric of all life including human life. 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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