

A Framework for Soil Microbial Ecology in Urban Environments

Andie Nugent¹ and Steven Allison²

¹UC Irvine

²University of California, Irvine

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Abstract

Urban ecosystems, although highly altered by humans, host diverse microbiomes that support vital ecosystem processes. While microbial ecologists are beginning to understand the drivers of microbial assembly and the link between community structure and function in many ecosystems, few of these advances have been applied to urban ecosystems. In this synthesis, we review research on the urban soil microbiome and develop a framework to integrate soil microbial communities with urban ecosystem function. We identify disturbance, altered resources, and heterogeneity as key drivers through which urbanization affects soils and soil microorganisms. Steep environmental gradients in many urban systems present a unique opportunity to address fundamental questions in microbial ecology, such as how microbes respond to stress and how biogeochemical rates relate to microbial diversity and composition. Answering such questions will help develop practical and equitable strategies for managing ecosystem benefits in cities where billions of people live.

Introduction

Urbanization has drastic impacts on geochemistry, climate, and biota, including diverse microbiomes. Although urban areas occupy less than 0.5% of global land area (Scheider *et al.*, 2009), urban land cover continues to expand, which could have substantial consequences for environmental health and sustainability (Seto *et al.*, 2012). Urbanization causes landscape fragmentation, which can reduce plant and animal biodiversity (Su *et al.*, 2012; Liang *et al.*, 2008; Delaney *et al.*, 2010). Urban light and sound pollution can alter animal behavior, disrupt species interactions, and cause shifts in species richness and composition (Longcore & Rich, 2004; Ciach & Fröhlich, 2017; Firebaugh & Haynes, 2016; Francis *et al.*, 2009). Soils in cities are often contaminated with organic pollutants and heavy metals. These contaminants can stress plants, contaminate plant tissues, impact soil and pollinator animal communities, and pose health risks for human residents (Fryzova *et al.*, 2017; Hernandez & Pastor, 2008; Pavao-Zuckerman & Coleman, 2007; Tauqueer *et al.*, 2013; Pan *et al.*, 2018; Wang *et al.*, 2013). The environmental impact of urban land use can reach far beyond city limits through greenhouse gas emissions (Pichler *et al.*, 2017), atmospheric nitrogen deposition (Fenn *et al.*, 2003), and water pollution (Russelet *et al.*, 2008; Overbo *et al.*, 2021; Wright *et al.*, 2010).

At the same time, urban environments sustain critical ecosystem processes. For example, sprawling urban areas continue to provide sufficient habitat, resources, and dispersal routes to support a high level of biodiversity (Wenzel *et al.*, 2020; Angold *et al.*, 2006). Insect pollinators can thrive in urban landscapes, which has made them a focus of urban conservation efforts (Baldock *et al.*, 2019; Hall *et al.*, 2016). Urban green spaces can help to offset impacts of urbanization by filtering air, regulating climate, and slowing runoff (Bolund & Hunhammar, 1999; McPhearson *et al.*, 2015). Urban soils support nutrient cycling processes and, with proper management, may be effective at sequestering carbon (Pouyat *et al.*, 2010; Brown *et al.*, 2011). While urban landscapes appear quite different from their natural counterparts, cities continue to support diverse and functional ecosystems. Understanding these novel urban ecosystems can help inform management strategies and maintain vital ecosystem processes that make cities more sustainable.

In addition to flora and fauna, soil microorganisms are essential for ecosystem functioning and can provide ecosystem services. However, soil microbial communities have been largely overlooked in urban ecology research. Only recently has there been a push to understand the impact of urbanization on the soil microbiome (Antwis *et al.*, 2017). This is a rapidly emerging area of research and, to our knowledge, there is not yet an overarching conceptual framework for effectively developing and answering critical questions about urban soil microbial communities.

In this paper we propose a new framework to advance research on urban soil microbial communities and their role in ecosystems. This framework combines and expands on previous advances in urban soils, urban ecology, and microbial ecology. We apply our framework to synthesize previous findings and discuss the implications of urban soil microbes for ecosystem and human health. We find that, strikingly, there has been very little work done to link microbial taxa to functioning in urban soils – information which could guide urban sustainability efforts and our fundamental understanding of microbial structure-function relationships. Finally, we offer recommendations for research priorities and practices to guide the field of urban microbial ecology in answering these crucial questions. We emphasize the need for collaboration between ecologists, biogeochemists, and social scientists to gain a holistic understanding of microbes and their interactions with humans in the urban environment.

Framework for Urban Soil Microbial Ecology

Many ecosystem processes depend on soil microbiomes that contain a diverse and abundant array of bacteria, fungi, and archaea (Reese *et al.*, 2016; Ramirez *et al.*, 2014; Wang *et al.*, 2018). Soil microbial communities drive the cycling of key nutrients including carbon, nitrogen, and phosphorus within ecosystems (Aislabe & Deslippe, 2013). Soil microbes also support primary producer growth and diversity, promote soil health by removing heavy metals and other contaminants, and regulate soil carbon storage. Microbiologists and microbial ecologists have therefore made an effort to understand how the environment drives microbial community activity in order to predict the direction and magnitude of microbial consequences for ecosystem function.

Our proposed framework (Figure 1) draws on previously published ideas but fills a knowledge gap by emphasizing the intersection between humans and microbial function in urban ecosystems. Humans create and intensively manage urban environments and are thus a key component of our framework. Human society, including economies, cultures/values, policies, technologies, and resources determine how the urban environment is structured and how it functions (Alberti, 1999; Byrne, 2007). However, these factors are difficult to capture quantitatively and are generally outside the wheelhouse of microbial ecologists. To address this challenge, we draw from Pickett and Cadenasso's (2009) analysis of altered resources, disturbance, and heterogeneity as the key mechanisms through which humans shape urban soils (Arrow A). Altered resources, disturbance, and heterogeneity are factors ecologists are already well-equipped to study and can be used to understand how complex societal dynamics ultimately change environmental drivers. These changes, particularly in soils, have consequences for microbial community composition and function (Arrow B), which will in turn cause shifts in environmental resource pools and fluxes (Arrow C) (Hall *et al.*, 2018). Finally, the environmental changes driven by microbial activity feed back to human society through the creation of environmental services or harms (Arrow D). Humans may adjust policy and behavior accordingly, which starts the cycle over again.

Our framework is useful because it synthesizes existing knowledge on urban ecology, microbial ecology, and urban soil science. Moreover, we elaborate on how disturbance, altered resources, and heterogeneity (Arrow A) influence urban ecosystem functioning through impacts on microbial communities (Arrows B and C). We then develop and discuss key questions to address knowledge gaps in our framework that limit fundamental understanding of urban microbial ecology and microbial ecology more broadly. Finally, we offer suggestions to facilitate collaboration needed among ecologists, biogeochemists, and social scientists to understand how the human-environment-microbe feedback loop plays out in cities around the world. Such collaboration will improve our decision-making and management strategies in urban spaces with the ultimate goals of sustainability and environmental justice.

Disturbance

Disturbance in the urban environment is practically unavoidable, especially during the initial land conversion. As land is developed, soil layers are removed, mixed, and replaced with backfill soil that often comes from other locations (Craul, 1985). This disturbance regime can result in altered soil horizons and chemistry compared with less-disturbed soils (Huot *et al.*, 2017). To our knowledge, no one has yet attempted to track the changes in soil microbial communities on the short-term time scale of pre- and post-development in order to determine the initial impacts. However, with a chronosequence of sites at different ages since development, we can assess how the soil and microbial communities may respond over time after the initial disturbance.

Yao *et al.* (2006) analyzed a chronosequence of turfgrass lawns ranging from 1-95 years of age. They found that microbial diversity was similar across all turfgrass ages and microbial function remained relatively consistent aside from some differences in preferred carbon substrate. This study indicates that microbial communities may be highly resilient and able to return to steady state rapidly after a major disturbance.

Other research, however, has shown that it may take 25 years or more for soil carbon and nitrogen storage to recover to pre-development levels (Golubiewski *et al.*, 2006). Scharenbroch *et al.* (2005) found that older urban soils have more abundant and active microbial communities and higher rates of carbon and nitrogen mineralization than new urban soils. The above-mentioned studies focused on differences in microbial communities based on urban soil age. Crucially, because few studies have compared microbial communities pre- and post-development, it is difficult to determine whether these communities have truly “recovered” or if they might be novel in composition and functioning. Thus, it is unclear how quickly microbial communities recover after disturbance to urban soils. Even if microbial communities bounce back quickly, there may be a substantial lag for the recovery of soil geochemical properties.

Soil bulk density may be one important factor driving response to disturbance. Bulk density of recently developed residential soils is significantly higher than old residential and park soils (Scharenbroch *et al.*, 2005). Edmondson *et al.* (2011) found urban soils to be least compacted under trees and most compacted under lawns. Dense soils limit the flow of oxygen, water, and nutrients through the soil matrix which in turn changes the resources to which microbes have access. Higher density soils may favor anaerobic bacteria, which correlate with higher denitrification potential (Linn & Doran, 1984). However, compacted soil has also been correlated with generally lower microbial abundance, enzyme activity, organic carbon and total nitrogen (Li *et al.*, 2002; Dick *et al.*, 1988). Therefore, bulk density may be important in explaining the reduced microbial abundance and activity observed in recently developed urban soils.

The initial development period is the most intense disturbance that urban soils likely experience, but many soils continue to experience smaller repeated disturbances. For example, athletic fields undergo frequent surface restoration which has been shown to inhibit carbon sequestration (Townsend-Small & Czimczik, 2010). This result is consistent with a study by Chen *et al.* (2013) which found that disturbance of urban soils resulted in greater carbon loss. Interestingly, their study found that microbial biomass in the top 10 centimeters did not differ between soil disturbance and rehabilitation treatments. It may be possible that although microbial biomass did not change, community functioning may be impacted by the disturbance. This possibility should be investigated. Likewise, Townsend-Small and Czimczik’s (2010) study left open the question of whether the microbial community continues to be abundant and active with turfgrass management, and what role microbes might play in patterns of carbon storage and loss.

Altered Resources and Soil Chemistry

The resources that microbial communities need to survive and grow may be altered in an urban setting (Figure 2). From non-urban systems, we know that a shift in resource availability, whether to the microbes’ benefit or detriment, will often cause microbial communities to change in activity, and this change can have ecosystem consequences (Malik *et al.*, 2020; Tieman & Billings, 2011; Chung *et al.*, 2007). Among the most important soil chemical characteristics and resources for microbial growth are pH, carbon, nitrogen, phosphorus, and water. In many urban soils, levels of these resources are considerably different from native rural or unmanaged soils. Urban landscapes are also exposed to higher heavy metal deposition, pesticides, and soil sealing. Here

we explore the impacts that these factors may have on the urban soil microbiome. Interactions between these variables make it challenging to predict their combined impact on microbial communities and activity. Teasing apart the individual and combined effects of these variables will be important in order to appropriately manage urban soils and promote healthy soil microbiomes.

pH – Due to the narrow optimal pH range for many taxa, soil pH is a strong driver of microbial community composition and function (Rousk *et al.*, 2010; Glassman *et al.*, 2017; Zhalnina *et al.*, 2015; Mukherjee *et al.*, 2014; Kaiser *et al.*, 2016; Pietri & Brookes, 2008). Generally, bacterial communities are more diverse and enzymatically active in neutral soils than more acidic soils (Fierer *et al.*, 2006; Liu *et al.*, 2014; Acosta-Martinez & Tabatabai, 2000). However, lower pH may promote some desirable microbial functions such as increased carbon storage (Malik *et al.*, 2018). While natural soils are generally neutral or slightly acidic, urban soils are often alkalized (Lorenz & Kandeler, 2006). This increased pH in urban soil has been associated with decreased microbial function (Caracava *et al.*, 2017). However, the role of pH in driving microbial community structure and function in urban soils is largely unknown and requires further study.

Carbon - Carbon content in urban soils is frequently altered. Particularly in urban turfgrass systems, frequent mowing and clipping may alter soil organic matter dynamics and microbial function (Thompson & Kao-Kniffen 2019). Mowing lawns and leaving the trimmings versus removing them can have consequences for nutrient cycling. Grass clipping can stimulate microbial activity by increasing root exudation. Returning the clippings to the soil can provide nutrients to soil microbes as the clippings decompose, reducing the need to fertilize. Removing the clippings, on the other hand, may cause microbes to rely more on existing SOM and decrease the soil's ability to act as a nitrogen sink. Removal of plant biomass has also been shown to decrease microbial biomass and respiration and cause microbes to rely on more recalcitrant forms of carbon, increasing the abundance of recalcitrant carbon and nitrogen cycling genes in the community (Wang *et al.*, 2011; Xue *et al.*, 2016).

Carbon availability in urban areas is also affected by the 'CO₂ dome', which is an area of increased atmospheric CO₂ concentration due to the local and concentrated burning of fossil fuels. Atmospheric CO₂ levels can impact soil microbes, mainly indirectly through changing plant inputs. Carney *et al.* (2007) found that doubling CO₂ levels resulted in higher activity of microbial carbon-degrading enzymes. Although CO₂ fertilization can be beneficial for plant growth, Carney *et al.* (2007) found that soils still lost carbon overall after long-term exposure to increased CO₂. Likewise, He *et al.* (2014) observed that CO₂ enrichment in soybean agricultural soil resulted in increased abundance of functional genes for carbon and nitrogen cycling, although this study did not look at the downstream impacts of these changes on soil carbon and nitrogen dynamics. Together, these two studies have implications for microbial carbon cycling in cities, with the concern that carbon loss could be accelerated in urban soils due to increased microbial enzyme activity, and nitrogen cycling may be altered. To our knowledge, though, no studies have specifically investigated the impact of urban CO₂ domes on microbial function. We recommend this topic as a priority for future studies.

Nitrogen – Nutrients such as nitrogen and phosphorus are often added directly to urban greenspaces as fertilizer or are unintentionally added from runoff and atmospheric deposition. These nitrogen inputs may be high enough to trigger symptoms of nitrogen saturation in urban soils (Chen *et al.*, 2010; Yang & Toor, 2016; Taylor *et al.*, 2005). In studies of non-urban systems, nitrogen amendments generally reduce microbial respiration, biomass, and extracellular enzyme activity while altering community composition (Ramirez *et al.*, 2012; Treseder, 2008). Consequently, nitrogen deposition may promote soil carbon storage, although the mechanisms for this observation are unclear (Zak *et al.*, 2016). What effect does added nitrogen have on urban soil microbes? Urban systems are capable of cycling nitrogen at rates comparable to non-urban systems (Reisinger *et al.*, 2016) and may have increased rates of nitrogen mineralization and nitrification (Reisinger *et al.*, 2016; Pouyat *et al.*, 1997; Enloe *et al.*, 2015). Microbial genes related to nitrogen-cycling are abundant in urban park soils (Wang *et al.*, 2018). These findings indicate that urban soil microbes are highly active in nitrogen cycling. Additionally, in an urban-rural gradient study, soil nitrogen was found to be a better predictor of microbial enzyme activity than carbon or pH (Cusack, 2013), adding further evidence that nitrogen is an important factor influencing microbial communities in urban soils.

Despite the high nitrogen cycling activity of their microbial communities, urban soils remain significant sources of nitrogen runoff (Yang & Toor, 2016; Taylor *et al.* , 2005) and nitrous oxide (van Delden *et al.* , 2016; Townsend-Small and Czimczik, 2010; Kaye *et al.* , 2004). Microbes may reach a stoichiometric limit to the amount of nitrogen they can take up. Bird and Bonnett (2018) found that additional nitrogen stimulated microbial extracellular enzyme activity related to carbon acquisition, indicating that carbon may be a more limiting nutrient once nitrogen is readily available. Therefore, to improve microbial denitrification and nitrogen uptake, it may be necessary to supplement fertilized soils with additional carbon sources.

Water – Variation in water availability may impact the activity and function of urban soil microbes. Many urban soils are irrigated, and some receive substantial irrigation in order to support lush greenery in an otherwise arid setting. Meanwhile, urban soils in more mesic regions tend to be drier due to increased runoff from features like impervious surfaces and drainage systems (Picket & Cadenasso 2009). Green and Oleksyszyn (2002) compared irrigated lawns, xeriscaped (reduced irrigation) lawns, and unmanaged desert patches and found that irrigated lawns showed the highest invertase and cellulase activities, indicating that irrigation promotes microbial breakdown of carbon sources. This result is consistent with Orchard and Cook’s (1983) findings that wetter soils contribute to higher microbial respiration and soil carbon loss. Irrigation also makes nitrogen more accessible to microbes, while drier soils decrease diffusion of substrates through the soil, limiting microbial activity (Stark & Firestone, 1995). The combination of irrigation and fertilization results in greater N₂O and NO fluxes from urban soils (Hall *et al.* , 2008; Kaye *et al.* , 2004). Balancing the combined use of fertilizer and irrigation may therefore be important for managing urban green spaces while minimizing greenhouse gas efflux (Bijoor *et al.* , 2008).

Heavy Metals – Heavy metal pollution is an unfortunate consequence of human activities such as smelting and fossil fuel combustion (Martín *et al.* , 2015; Luo *et al.* , 2015; Benin *et al.* , 1999). Roadsides and industrial areas are hotspots for heavy metal pollution in soils. As soil toxicity from heavy metals increases, microbial biomass and activity generally decrease (Azarbad *et al.* , 2013; Oliveira & Pampulha 2006; Papa *et al.* , 2010). Some microbial taxa are impacted more than others by heavy metals (Oliveira & Pampulha 2006). It will be important to determine whether the impacted taxa have consequences for ecosystem function and, if so, how we might reduce soil pollutants to restore vital microbial processes.

Pesticides - To maintain idyllic urban greenspaces and reduce damage from insects and weeds, pesticides (primarily herbicides and insecticides) are often applied to urban soils. There have been recent efforts to understand the impacts of these chemicals on soil health, including the functioning of soil microorganisms. Several reviews have found mixed effects of pesticides on microbial communities and their functions (Riah *et al.* , 2014; Imfeld & Vuilleumier, 2012; Kalia & Gosal, 2010). Depending on the pesticide, impacts on microbial biomass and enzyme activity may be negative, neutral, or positive. Effects may be short-lived or more long-term, and microbial interactions with pesticides may depend on other factors such as temperature, soil fertilization, and soil carbon content (Reedich, Millican & Koch, 2017; Munoz-Leoz *et al.* , 2012; Garcia-Delgado *et al.* , 2018). Additionally, because the majority of pesticide studies focused on agricultural systems or lab microcosms, little is known about how in situ urban microbial communities respond to pesticide application and what this may mean for soil health and function.

Impervious Surfaces - A considerable amount of urban land is covered by impervious surfaces such as buildings, roads, sidewalks, and other paved areas. Therefore, studies on open urban soils may not be sufficient to gain a comprehensive understanding of urban ecosystem functioning. Impervious surfaces serve as a barrier that alters or prevents the exchange of substances between the soil, surrounding environment, and atmosphere. Soils beneath impervious surfaces have been found to contain less carbon and nitrogen than open soils and have reduced microbial activity (Raciti *et al.* , 2012; Wei *et al.* , 2014; Lu *et al.* , 2020). Sealed soils may also have decreased microbial diversity and altered community structure (Hu *et al.* , 2018; Yu *et al.* , 2019). Sealed soils were largely ignored until recently, but now researchers are emphasizing the need to include them in overall urban carbon budgets and models of urban geochemical dynamics (e.g. Bae & Ryu, 2020; Hu *et al.* , 2018; Wei *et al.* , 2014).

Novel Plant Communities – As in non-urban systems, soil microbial communities in urban greenspaces

appear to be shaped, at least in part, by plant inputs and diversity (Hui *et al.*, 2017). Urban ecosystems are often home to novel plant communities, including many non-native plant species (Kowarik, 2011). Since plants can be major drivers of microbial community assembly, novel plant communities may foster microbial communities different from those typical in soils with native vegetation. Urbanization also facilitates the spread of invasive plant species (Skultety & Matthews, 2017; Santana Marques *et al.*, 2020; Lechuga-Lago *et al.*, 2017), and invasive plants have been shown to alter the soil microbiome, in turn impacting native plant survival and causing shifts in ecosystem processes (e.g. Batten *et al.*, 2006). Even non-invasive exotic plants can alter the soil microbiome, shifting microbial community structure and function (Kourtev *et al.*, 2002). More research should be done on the impact of common non-native and invasive urban plants compared to native plants on soil microbial communities and soil function. The impact of overall plant diversity on microbial communities should also be studied within urban systems.

Heterogeneity

At first glance, cities may appear to be a homogenous sea of concrete. However, the urban environment is composed of a highly diverse array of land-use types, ranging from parks and lawns dominated by turfgrass, to busy commercial centers with a mix of concrete and greenery, to large industrial complexes mainly characterized by impervious surfaces and polluted soils. These land use patches tend not to exist along a clear gradient, but are instead jumbled together to create a complex habitat mosaic (Figure 3) (Zhou *et al.*, 2018). Along with variation in land-use types, there is also heterogeneity of climate within urban spaces. Overall, cities tend to be hotter than their surrounding environment, a phenomenon known as the Urban Heat Island (e.g. Oke, 1995; Imhoff *et al.*, 2010; Li *et al.*, 2017). Within this heat island, a variety of micro-climates exist due to the position and size of buildings, density of trees and other green infrastructure, and other factors (Liao & Heo, 2018; Pincebourde *et al.*, 2016). Soils within a city can be trucked in from multiple non-local sources, and can vary in nutrient load, irrigation, heavy metal and pesticide pollution, and other characteristics depending on the management and development history of that land (De Kimpe & Morel, 2000; Zhiyanski *et al.*, 2017; Karim *et al.*, 2014; Ziter & Turner, 2018).

How does the heterogeneity of urban habitats impact soil microbial community assembly, dispersal, and function? Understanding the role of landscape heterogeneity for microbial communities has only recently become a priority in microbial ecology as a whole. There is evidence that microbial communities vary with habitat heterogeneity (Horner-Devine *et al.*, 2004). However, due to microorganisms' small size, their dispersal and survival may be constrained by different factors from macro-organisms (Martiny *et al.*, 2006) and therefore microbial response to habitat heterogeneity and patchiness, and the distance between patches, may not be predictable using our current theoretical frameworks based on macro-organism studies (Mony *et al.*, 2020). We do not know how the size of and distance between habitat patches in cities impact microbial communities, which should be a priority for future studies. However, there is some research suggesting that different urban land use types such as bioswales, parks, green roofs, and residential soils differ in microbial composition and diversity (Gill *et al.*, 2020; Wang *et al.*, 2018). Microbial litter decomposition also differs between urban soil types, indicating that microbial function may be affected by habitat type (Vauramo & Setälä, 2011). Heterogeneity likely has an impact on the assembly and function of urban microbial communities, and future studies should investigate how microbial communities respond to patch type, size, edginess, and distance between patches.

While cities may be highly heterogenous at small to medium scales, it is possible that cities reduce environmental variation at regional and global scales. The "Urban Convergence" hypothesis states that urban areas are more similar to each other than to their surrounding rural environments, and some studies have found evidence for this trend with biological, geochemical, soil, and microclimate variables (Kaye *et al.*, 2006; Hall *et al.*, 2016; Herrmann *et al.*, 2020; Polsky *et al.*, 2014; McKinney, 2006; Groffman *et al.*, 2017; Pearce *et al.*, 2016). However, no studies to our knowledge have investigated whether soil microbial communities converge in taxonomic identity or functioning across cities and, if so, what are the implications for ecosystem function. With a high degree of heterogeneity at neighborhood and city scales, and possible homogenization occurring at regional and global scales, it will be important to analyze urban soil microbial function at all

of these scales.

Priorities for Future Research and Recommended Approaches

There is a crucial need for sustainable and equitable design of urban spaces to benefit humans and the environment from local to global scales. To best harness the power of microbial communities to achieve this goal, we have identified the following essential questions in urban microbial ecology and biogeochemistry. Furthermore, addressing these questions will help advance these disciplines more broadly, including in non-urban ecosystems. We summarize the current research providing insight into these questions thus far, and recommend approaches for future research.

Are urban soil microbial communities taxonomically and/or functionally distinct from non-urban soil microbial communities, and how much variation exists within the urban environment?

Microbial phyla most commonly found in soils include: a-Proteobacteria, B-Protobacteria, Acidobacteria, Actinobacteria, Firmicutes, Planctomycetes, Bacteroidetes (Zhang, 2008; Fierer *et al.* 2007). At the phylum level, taxa dominating urban soils are consistent with those observed in non-urban soils (Lysak *et al.* 2018; Reese *et al.* 2016; Wang *et al.* , 2018; Huot *et al.* , 2017). However, relative abundances of these phyla differ within urban soils and along urban-rural gradients (Hui *et al.* 2017; Tan *et al.* , 2019; Stoma *et al.* , 2020). Overall diversity sometimes increases with urbanization (Tan *et al.*, 2019; Naylo, 2019), sometimes decreases (Rai *et al.* , 2018), and often remains the same but with shifts in composition (Reese *et al.* , 2016; Joyner *et al.* , 2019; Yao *et al.* , 2006; Huot *et al.*, 2017). Understanding how overall microbial diversity and community composition changes within urban soils is an important first step, but it is also important to understand what drives community assembly and the consequences of varying community composition for ecosystem function. Hence the next two questions.

If differences in microbial taxa and function exist, what are the associated drivers? (Arrows B and C, Fig. 1)

Although we are only just starting to determine which microbes reside in urban soils, it is becoming clear that there are differences between urban and rural communities, and soil communities within the urban matrix can also vary. What environmental variables are driving these differences? How do different taxa respond to these drivers? Answers to these questions are essential if we wish to manage soils to promote healthy and beneficial microbial communities. Urban microbes may be affected by the same environmental variables as non-urban microbes, but there may be differences in the magnitude of interactions between the drivers and the microbial taxa present.

Questions 1 and 2 can, and ideally should, be answered in conjunction. With careful sampling design, it is possible to characterize urban soil microbial communities while simultaneously identifying major drivers of community composition. One common approach has been to establish urban-rural gradients using factors like human population density, neighborhood income, and pollution levels (e.g. Azarbad *et al.* , 2013; Chen *et al.* , 2010; Xu *et al.* , 2013). This method allows identification of large-scale effects of urbanization on soil function. However, gradients may be less effective at fine-to-medium scales due to the high levels of heterogeneity and patchiness across the urban landscape.

A second major approach has been to focus on particular land use types within the urban matrix, e.g. soils along roads, under impervious surfaces, or beneath turfgrass lawns and parks (e.g. Hu *et al.* , 2018; Zhao *et al.* , 2012; Law & Patton, 2017; Yao *et al.* , 2006; Lorenz & Kandeler, 2006; Papa *et al.* , 2010). Since factors such as dominant plant cover, pH, moisture content, and nutrient content can be among the largest drivers of microbial community composition and may differ drastically across these sites, this approach may be helpful to link microbial taxa and functioning with multiple environmental factors. Focusing on particular land-use types may also enable researchers to generate more site-specific management recommendations to improve urban soil function.

How much does taxonomic composition vs. functional plasticity play a role in urban soil microbial community function? (Arrow C, Fig. 1)

A major topic of interest in microbial ecology is the link between taxonomic composition and function. If composition is sufficient to predict microbial community function, then sequencing communities and measuring microbial biomass would facilitate prediction of microbial community impacts on ecosystem dynamics. To an extent, metagenomic analysis has been useful for understanding and predicting a microbial community's functional roles (e.g. Fierer *et al.* , 2012; Graham *et al.* , 2016). While some functions are phylogenetically conserved, studies have also found that soil microbial communities exhibit functional plasticity and can shift ecological and resource acquisition strategies depending on pressures from the environment (Martiny *et al.* , 2015; Evans & Wallenstein, 2013; Morrissey *et al.* , 2017). Microbial taxa may also be redundant, where the loss of one taxon can be compensated by the function of another (Allison & Martiny, 2008). This research is still developing, and we do not yet understand the direct consequences of most microbial taxa in any ecosystem.

In urban soils, no research explicitly linking specific microbial taxa to functioning has been conducted to our knowledge. To manage urban soils and boost ecosystem services, it will be important to understand the functional limitations of the microbial communities currently inhabiting urban soils. This knowledge will have implications for how soil communities can be manipulated by managing environmental factors, or whether inoculation of the soil with novel microbes will be needed to achieve desirable results. Furthermore, urban soils can serve as model systems for studying fundamental questions about structure-function relationships in microbiomes.

There are other ways in which studies of urban microbiomes could enhance the understanding and societal relevance of ecological science as a whole (Foreman, 2016). Urban areas experience many environmental extremes within a small geographic area. This variation provides an opportunity to study how variables like pH, heavy metals, and precipitation impact organisms while controlling for other state factors like geography, elevation, and seasonality (Jenny, 2012). With many major research labs located in urban areas, there is scientific expertise and infrastructure available to set up local observational networks and sample more frequently to capture long-term urban ecosystem dynamics (Sparrow *et al.* , 2020; Wang *et al.* , 2021). Urban ecosystem health, including soil microbiome health, could also be monitored through partnerships with community organizations and volunteers (Bliss *et al.* , 2001). As part of this urban ecosystem monitoring effort, it would be feasible to combine field, common garden, and laboratory studies to more explicitly link microbial taxa to function and better understand how microbial communities respond to changes over time.

What consequences do soil microbial communities have for urban ecosystem function and human well-being? (Fig 1, Arrows C and D)

Urban microbial communities may have significant effects on urban ecosystem processes, including greenhouse gas fluxes, soil nutrient dynamics, and plant growth. However, it remains unclear to what extent microbial communities drive these processes as opposed to plants and other organisms. Studies that parse out the functions of soil microbes will help clarify where to invest management efforts to improve soil services.

Soil microbial communities drive ecosystem processes that in turn affect human populations. On regional and global scales, soil microbes have the potential to help mitigate or exacerbate the climate crisis by regulating soil carbon uptake and release (Cavicchioli *et al.* , 2019). On the scale of a city or a neighborhood, however, little is known about how soil microbes affect human communities. Some human health studies have recently found that exposure early in life to a diverse environmental microbiome can reduce asthma and allergy rates, and there has been a push to “rewild” cities with diverse plant- and soil-associated microbes (Sandifer *et al.* , 2015; Rook, 2013; Selway *et al.* , 2020; Mills *et al.* , 2020; Mills *et al.* , 2017). In cities, green spaces are generally the source of diverse environmental microbiomes. Green spaces are not evenly distributed throughout cities and tend to be more common in wealthier neighborhoods. On the other hand, urban soils can also house pathogenic microbes and may serve as reservoirs for antibiotic resistomes (Xiang *et al.* , 2018; Li *et al.* , 2018). Therefore, urban soil microbiomes have the potential to help or harm humans, and these benefits and burdens may not be evenly distributed across cities.

Microbiome services raise a question of environmental justice: are wealthier, often white, communities be-

nefitting more from access to green space microbiomes than low-income and minoritized communities? And are there other microbial community functions that benefit or harm some human communities over others? A recent analysis by Schell *et al.* (2020) found that a history of systemic racism in cities remains a strong determinant of how urban ecosystems are structured. The urban environment may have a patchy distribution of goods and harms that continue to correlate with race and income. Understanding how microbial functioning is different across the urban landscape and how that affects human communities should be a priority in urban microbial ecology. This research would benefit from collaborations with human geographers, social and environmental justice experts, city officials, and community members to identify impacts of urban soil microbiomes on human communities and develop ways to improve the urban environment through understanding of microbial functioning.

How might urban areas be better designed/managed to boost ecosystem services by soil microbial communities while minimizing harms? (Arrow A, Fig. 1)

Efforts are being made to improve ecosystem benefits in cities. Much of this work focuses on conserving or restoring native habitat (e.g. Marzluff & Ewing, 2008; De Sousa, 2003). While restoring urban land to a pre-development state may provide ecological benefits, there has been a recent push to investigate the ecological roles that novel urban ecosystems play and to consider whether they might also be providing important ecosystem services, acting as reservoirs for biodiversity, and conveying other environmental benefits (Klaus & Kiehl, 2021; Kowarik, 2011; Planchuelo *et al.*, 2019). Pavao-Zuckerman (2008) points out that urban soils can be deliberately manipulated as part of ecosystem management and restoration. While habitat restoration may be the preferred and conventional way to manage ecosystem processes in some locations, it is worth considering whether fostering a novel but more functionally beneficial ecosystem is a better use of management effort and resources.

Cities have already been taking advantage of novel ecosystems to improve sustainability and promote ecosystem services. For instance, green roofs have been designed to help cool buildings and reduce air conditioning needs (Takebayashi & Moriyama, 2007). Bioswales filter debris and pollution out of storm water and recharge groundwater sources (Li & Davis, 2009). Phytoremediation takes advantage of plant uptake of heavy metals in order to clean up polluted soils (e.g. Cheng, 2003; Ali *et al.*, 2013). Only recently has attention been paid to the role of microbes in these processes (e.g. Cui *et al.*, 2017; Hryniewicz & Baum, 2014), and a better understanding of microbial function could allow us to improve on green infrastructure technologies. It is possible that urban greenspace cover may be underestimated (Zhou *et al.*, 2018), so there might be opportunities to boost greenspace ecosystem services in cities.

While most green infrastructure has focused heavily on plants, microbes themselves may have the potential to reduce the negative impacts of urbanization, either independently or in conjunction with plants. For example, microbial communities in green roof soils help plants tolerate and recover from environmental stress (Hoch *et al.*, 2019; Fulthorpe *et al.*, 2018). Additionally, permeable reactive barriers have been designed to intercept and remove nitrates from groundwater by promoting microbial denitrification within the barriers (Vallino & Foreman, 2008). Soil microbes also influence the breakdown of pesticides, although the efficacy of this microbial degradation depends on community composition and environmental conditions (Reedich, Millican & Koch, 2017). Several studies have tracked and modeled microbial pesticide degradation to address and prevent pesticides and their harmful breakdown products from leaching into groundwater and aquatic systems (e.g. Yale *et al.*, 2017; Verma *et al.*, 2014; Soulas & Lagacherie, 2001). A more thorough understanding of microbial communities and their functions may allow us to “micromanage” microbial services (Peralta *et al.*, 2014) and develop new technologies, infrastructure, and land management practices to improve urban soil health and ecosystem processes.

Conclusion

We propose a new conceptual framework for urban microbial ecology that will help focus research questions and advance knowledge about urban microbial communities and ecosystem functioning. By identifying key drivers, we provide a path forward to link human actions with changes in the soil microbiome. Feedback

loops connect microbes back to human society through the provisioning of environmental goods and harms, which brings attention to microbial consequences for human wellbeing. We argue that microbial ecologists and biogeochemists should take advantage of urban ecosystems for future study. Not only do microbial communities represent convenient systems for fundamental research on urban biogeochemistry, microbiomes could also play a role in creating healthier and more sustainable cities. Overall, urban ecosystems deserve more attention from microbial ecologists, and urban ecology would benefit from a greater focus on microbes.

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