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A framework for soil microbial ecology in urban ecosystems

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Abstract

Nearly all ecosystems host diverse microbiomes that support vital ecosystem processes. At the same time, these ecosystems and their microbiomes are increasingly altered by human activities, particularly in highly managed urban environments. 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 human activities including urban development affect soils and their resident 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. Soil microbiomes in cities also provide ecosystem services and harms, making it crucial to understand how human activity drives those functions and the consequences for environmental and human health. We argue that much-needed integration across disturbance ecology, urban ecology, and microbial ecology will help generate practical and equitable strategies for managing ecosystem benefits in cities where most humans now live.

KEYWORDS
biogeochemistry, carbon cycling, ecosystem services, microbial ecology, microbiome, soil, urbanization

INTRODUCTION

Human impacts on the environment range in type, intensity, and scale. The effects of agriculture, mining practices, heavy metal pollution, and climate change on ecosystem structure and function have been thoroughly studied over the past several decades. Initially, plants and animals were the organisms of focus. Recently, microorganisms have gained more attention as key drivers of ecosystem processes. Yet even as microbiomes and their responses to human disturbances have come into greater focus, one major type of human impact has been largely overlooked: urbanization. Microbially driven processes such as carbon and nitrogen transformations have been studied in urban soils. However, we lack research linking these processes directly to microbial community membership and activity. Given that they lie along a steep human impact gradient, more focus on urban ecosystems would bolster fundamental understanding of microbial and ecosystem responses to disturbance (Figure 1).

Urbanization has drastic impacts on geochemistry, climate, and biota, including diverse microbiomes. Although urban areas currently occupy less than 0.5% of global land area (Schneider 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 (Delaney et al., 2010; Liang et al., 2008; Su et al., 2011). Urban light and sound pollution can alter animal behavior, disrupt species interactions, and cause shifts in species richness and composition (Ciach & Fröhlich, 2017; Firebaugh & Haynes, 2016; Francis et al., 2009; Longcore & Rich, 2004). 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 (Hernández & Pastor, 2008; Pan et al., 2018; Pavao-Zuckerman & Coleman, 2007; 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 (Overbo et al., 2021; Wright et al., 2011).

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 (Angold et al., 2006; Wenzel et al., 2020). Insect pollinators can thrive in urban landscapes, which has made them a focus of urban conservation efforts (Baldock et al., 2019; Hall et al., 2017). 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 (Brown et al., 2012; Pouyat et al., 2009). 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 services. While urban microbial research has a long history (e.g., Blaschke-hellmessen, 1969; Passarelli et al., 1949), only in the last decade or two have funding opportunities, cross-disciplinary interest, and technological advances positioned the field to grow rapidly. Within the recent wave of microbial ecology studies, the vast majority address human impacts such as climate change and pollution outside of urban systems. Although there has been extensive work on soil microbiomes in agricultural systems, if we want to understand how humans drive microbial community structure and function, we need to extend microbial ecology beyond “natural” and agricultural lands. Only recently has there been a push to understand the impact of urbanization on the soil microbiome (Antwis et al., 2017), and we do not yet know how insights from natural and agricultural systems apply to urban soils. A comparative approach is potentially useful (Figure 1); both urban and agricultural systems experience physical disturbance of surface soils, altered water regimes, high nutrient inputs, and introduction of novel plant communities. As with agricultural ecosystems, a deeper scientific understanding of urban ecosystems will become increasingly relevant as the human population expands.

Urban soils have been defined by the World Reference Base as Technosols, which are soils whose properties have been largely determined through human activity and often contain materials that would not be

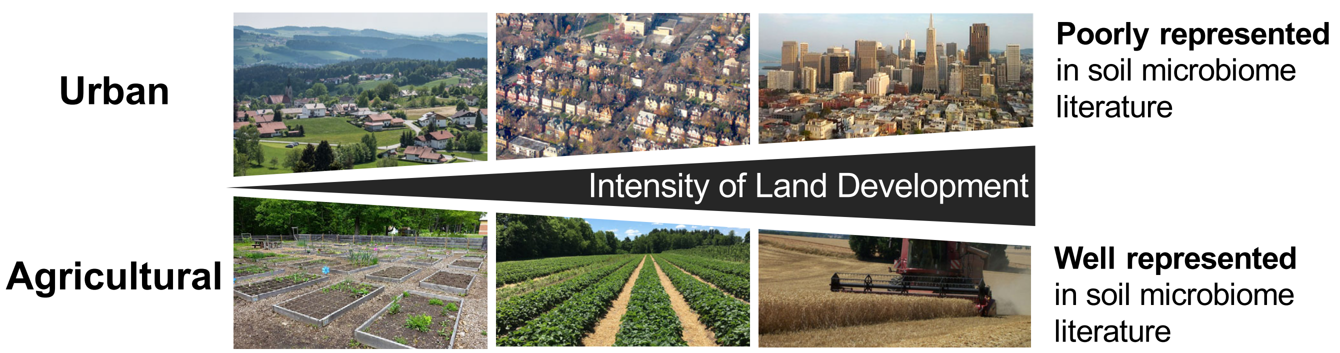

FIGURE 1 Comparison of human impact through land development on urban and agricultural ecosystems. Soil microbiomes in rural and agricultural landscapes have been well studied, while those in more urban landscapes have been largely overlooked

present without human intervention (Rossiter, 2007). Here, we define urban soils more broadly as any soil affected by or created through land development for human housing, commercial spaces, and workplaces. This definition encompasses rural towns and major cities. Urban soil may be new or old, and may be closely managed (e.g., park soil) or generally unmanaged (e.g., soil beneath parking lots). Urban soils may also be endemic or could be trucked in from other locations and may experience few or repeated disturbances. Thus, urban development creates a highly heterogenous soil matrix across both space and time. However, this heterogeneity and extreme disturbance regime present excellent opportunities to understand microbial functioning under changing conditions.

There is a growing body of work investigating microbial communities and their functions in the built environment, such as within air conditioning systems and on hospital surfaces (e.g., Bonetta et al., 2010; Chaoui et al., 2019). Additionally, there is ongoing research addressing microbial function in urban aquatic systems (e.g., Calderón et al., 2017; Chaudhary et al., 2018). Still, urban waterways do not include all the heterogeneity driving microbial communities within urban ecosystems. Soils have only recently gained attention as crucial habitat for microorganisms in cities, despite the long-established importance of soil microbiomes in other ecosystems. Microorganisms can contribute to urban soil genesis and nutrient availability by breaking down minerals and organic matter and fixing nitrogen, shaping the soils upon which people live (Kaviya et al., 2019). These soil–microbe feedbacks are 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 ecosystem functions. 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 that could guide urban sustainability efforts and improve 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 many experts and stakeholders, including ecologists, biogeochemists, urban planners, landowners, engineers, landscapers, and social scientists to gain a holistic understanding of microbes and their interactions with humans in the urban environment (Aronson et al., 2017; Shifflett et al., 2019).

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; Wang et al., 2018). Soil microbial communities drive the cycling of key nutrients including carbon, nitrogen, and phosphorus within ecosystems (Aislabie et al., 2013), thereby supporting primary producer growth and diversity. The soil microbiome additionally affects soil health by immobilizing heavy metals, degrading organic pollutants, and altering physical soil structure (Kaviya et al., 2019). Microbiologists and microbial ecologists have therefore tried to understand how the environment drives microbial community activity to predict the direction and magnitude of microbial consequences for soil and ecosystem function.

Our proposed framework (Figure 2) 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, determines how the urban environment is structured and how it functions (Alberti, 1999; Byrne, 2009). 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). Ecologists are already well-equipped to study these mechanisms, which have consequences for microbial community composition and function (Arrow B) and in turn cause shifts in environmental resource pools and fluxes (Arrow C) (Hall et al., 2018). Finally, the environmental changes driven by microbial activity feedback 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 disturbance ecology, urban ecology, and microbial ecology. We 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. We also

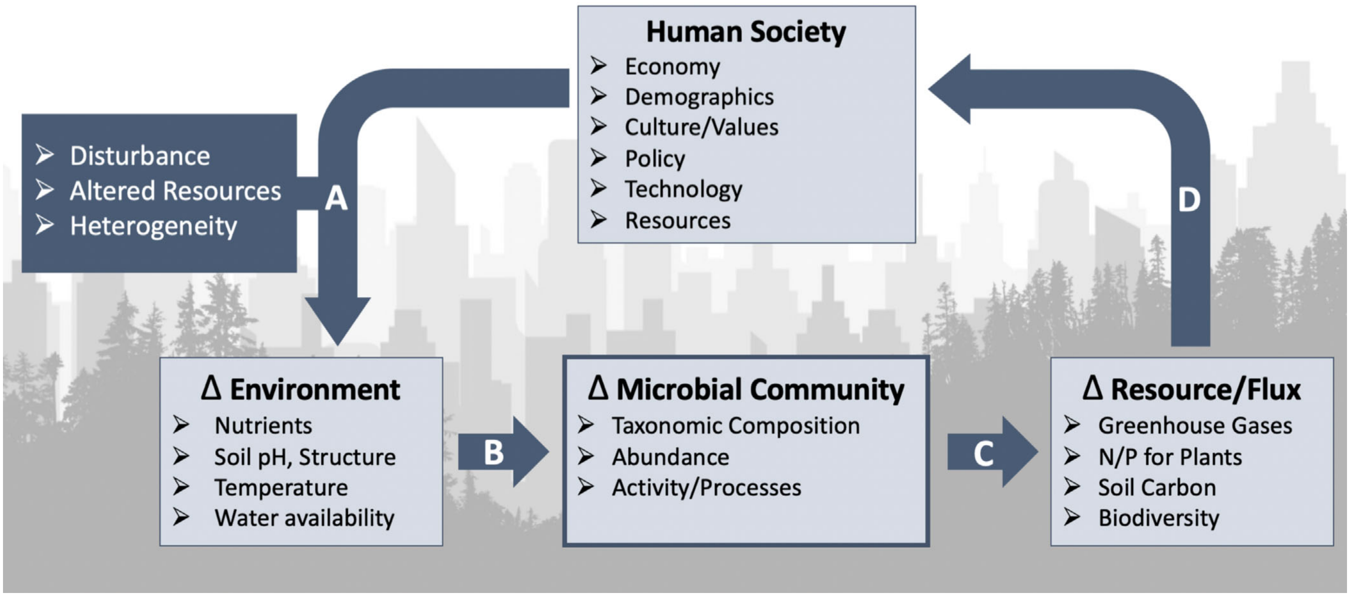

FIGURE 2 Authors' framework for studying soil microbial communities in human-impacted environments

emphasize the need for collaboration 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 goal of promoting sustainability and environmental justice.

DISTURBANCE

Disturbance in the urban environment is practically unavoidable, especially during initial land conversion. As land is developed, soil layers are removed, mixed, and sometimes entirely replaced with soil from other locations (Craul, 1985). This disturbance can result in altered soil horizons, mineral composition, and chemistry (Huot et al., 2017). In other cases, soils may be sealed under concrete with little soil mixing resulting in not only less physical disturbance but also reduced interactions between soil and air. The nature, frequency, and scale of soil disturbances vary widely across urban soils, which presents a challenge for retroactively defining baseline soil conditions and determining postdisturbance impacts. Urban soils may be more or less functional compared with their predisturbance state (Graham et al., 2021).

Using chronosequences of urban sites at different ages since land conversion, we can begin to assess how soil and soil microbial communities respond over time to disturbance. Microbial diversity may remain consistent across soil ages, indicating some resilience to disturbance (Yao et al., 2006). However, older soils have more abundant and active microbial communities and higher rates of C and N mineralization than newer urban soils (Scharenbroch et al., 2005). Golubiewski (2006) additionally found that it may take several decades for soil carbon and nitrogen storage to recover to predevelopment levels. Therefore, microbial function may be resilient on longer timescales than expected.

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 postdevelopment in a single location, it is difficult to determine whether these communities have truly "recovered" or whether 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 in the recovery of soil geochemical properties, which may have implications for soil management. Rather than attempting to restore urban soils to an uncertain predevelopment state, it may be more practical to accept them as fundamentally altered and prescribe management techniques aimed at achieving realistic soil health benchmarks (Simenstad et al., 2006).

Soil bulk density may be one important factor driving response to disturbance. The bulk density of recently developed residential soils is significantly higher than old residential and park soils (Scharenbroch et al., 2005).

Additionally, soils under turfgrass lawns are more compacted than soils under trees (Edmondson et al., 2011). 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 (Chamindu Deepagoda et al., 2019; Hartmann et al., 2014; Longepierre et al., 2021). Heavily compacted soils have also been associated with increased CO_2 and methane emissions (Hartmann et al., 2014). On the contrary, compacted soils generally have lower microbial abundance, enzyme activity, organic carbon, and total nitrogen (Li et al., 2011; Pengthamkeerati et al., 2011; Torbert & Wood, 1992; Zhong et al., 2019). Therefore, high bulk density may help explain the reduced microbial abundance and activity observed in recently developed urban soils. In an agricultural system, a negative response to soil compaction was observed across bacterial phyla, rather than impacting only particular taxa (Longepierre et al., 2021). In urban soils, compaction may likewise have a widely distributed impact on the microbial community and consequently its function.

Compaction is a known problem for urban soils, and therefore, heavily trafficked urban green spaces such as athletic fields are frequently aerated and resurfaced to loosen soil and promote air and water flow. However, this frequent disturbance regime, much like agricultural tilling, can reduce soil carbon sequestration by disrupting soil structure and exposing soil organic matter (SOM) to microbial decomposition (Balesdent et al., 2000; Townsend-Small & Czimczik, 2010). Therefore, it may be important to aerate soils enough to combat severe compaction while allowing enough time between disturbances to re-sequester the carbon lost after each aeration event. Understanding how disturbance regimes impact soil health will better enable land developers and managers to prevent unnecessary soil damage and accelerate recovery.

ALTERED RESOURCES AND SOIL CHEMISTRY

Urbanization may alter the resources that microbial communities need to survive and grow. From nonurban 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 (Chung et al., 2007; Malik et al., 2020; Tiemann & Billings, 2011). Among the most important soil chemical characteristics and resources for microbial growth are pH, carbon, nitrogen, and water. In many urban soils, levels of these resources are considerably different from rural or unmanaged soils. Urban landscapes are also exposed to heavy metal deposition, organic pollutants, soil sealing, and novel plant communities. Here, we explore the impacts of these factors 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 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 (Aciego Pietri & Brookes, 2008; Glassman et al., 2017; Rousk et al., 2010; Zhalnina et al., 2015). Generally, bacterial communities are more diverse and enzymatically active in neutral than in acidic soils (Acosta-Martínez & Tabatabai, 2000; Fierer & Jackson, 2006; Liu et al., 2014). However, lower pH may promote some desirable microbial functions such as increased carbon storage (Malik et al., 2018). While natural soils range in pH from acidic to neutral, urban soils are often alkalized (Lorenz & Kandeler, 2006). Urban soil alkalinity is primarily attributed to the leaching of calcareous substances from construction materials such as concrete (Yang & Zhang, 2015). Increased pH in urban soil has been associated with decreased microbial function (Caravaca 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 and nutrients

Carbon content in urban soils often changes following initial land conversion and may depend on ongoing land management methods. Particularly in urban turfgrass systems, frequent mowing and clipping may alter SOM dynamics and microbial function (Thompson & Kao-Kniffin, 2019). 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 with nitrogen. Removing the clippings, on the contrary, 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, indicated by an increase in recalcitrant carbon and nitrogen cycling genes in the community (Wang et al., 2011; Xue et al., 2016).

Nutrients such as nitrogen and phosphorus are often added directly to urban green spaces as fertilizer or are unintentionally added from runoff and atmospheric deposition. These inputs may be high enough to trigger symptoms of nitrogen saturation in urban soils (Chen et al., 2010; Taylor et al., 2005; Yang & Toor, 2016). In studies of nonurban 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., 2017). On the contrary, nitrogen deposition can also promote carbon loss from low-nutrient environments (Koceja et al., 2021). Therefore, soil type can have a strong impact on microbial response to nitrogen inputs.

At the watershed scale and within parks and lawns, we know that urban systems are capable of cycling nitrogen at rates comparable to or greater than nonurban systems (Enloe et al., 2015; Pouyat et al., 1997; Reisinger et al., 2016). The microbial contribution to urban nitrogen transformations has been less studied. Microbial genes related to nitrogen cycling are abundant in urban park soils (Wang et al., 2018), indicating that urban soil microbes are highly active in nitrogen cycling. Wang, Marshall, et al. (2017) presented one of the first studies to identify relative nitrogen cycling activity among microbial taxa in urban soils. They found that ammonia-oxidizing archaea may play a greater role in nitrification within urban soils than in rural soils. Additionally, they found a high abundance of microbes containing the nosZ clade II gene, which has been negatively correlated with soil N_2O emissions (Xu et al., 2020). This may present opportunities for managing urban microbial communities to reduce greenhouse gas emissions from soil.

In concert with the high nitrogen cycling activity of their microbial communities, urban soils remain significant sources of nitrogen runoff (Taylor et al., 2005; Yang & Toor, 2016) and nitrous oxide (N_2O) (Kaye et al., 2004; Townsend-Small & Czimczik, 2010; van Delden et al., 2016). Microbes may reach a stoichiometric limit to the amount of nitrogen they can take up. Birt and Bonnett (2018) found that additional nitrogen stimulated microbial extracellular enzyme activity related to carbon acquisition, indicating that carbon may become a limiting resource if nitrogen is readily available. Therefore, if ecosystem management goals include increasing microbial denitrification rates and soil nitrogen uptake, it may be necessary to supplement fertilized soils with additional carbon sources.

Atmospheric CO_2

Carbon availability in urban areas is affected by the "CO_2 dome," an area of increased atmospheric CO_2 due to the local and concentrated burning of fossil fuels. With CO_2 levels rising globally, many researchers have investigated the impact of CO_2 enrichment on soil communities. For instance, He et al. (2014) and Yu et al. (2018) observed that CO_2 enrichment stimulated microbial functional genes involved in carbon and nitrogen cycling. Carney et al. (2007) found that doubling CO_2 levels resulted in higher activity of microbial carbon-degrading enzymes leading to an overall loss of soil carbon despite potential CO_2 benefits for plant growth. Increased CO_2 may also alter community composition and diversity (Jia et al., 2020; Jin et al., 2020; Wang, Marsh, et al., 2017). These impacts of CO_2 on microbial community structure and function are likely occurring indirectly through changes in plant inputs, nitrogen availability, soil pH, and moisture (Deltedesco et al., 2020; Gao et al., 2020; Wu et al., 2021).

Together, these 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. Carbon losses may be exacerbated in soils exposed to warming and irrigation (Carrillo et al., 2018; Thakur et al., 2019; Yu et al., 2021), potentially leading to interactions between CO_2 enrichment and urban management strategies such as irrigation and temperature regulation. To our knowledge, though, no studies have specifically investigated the impact of CO_2 domes on urban soil microbiome function. We recommend this topic as a priority for future studies.

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 to support lush greenery in arid regions. Meanwhile, urban soils in more mesic regions tend to be drier due to increased runoff from features such as impervious surfaces and drainage systems (Pickett & 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 in arid climates. This result is consistent with Orchard and Cook's (1983) findings that wetter soils contribute to higher microbial respiration and soil carbon loss, potentially offsetting the carbon sequestration benefits of increased plant biomass in irrigated urban spaces. 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 N_2O 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 (Benin et al., 1999; Luo et al., 2015; Rodríguez Martín et al., 2015). 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, with consequences for soil greenhouse gas emissions (Ma et al., 2021; Oliveira & Pampulha, 2006). It will be important to further study the impacts of heavy metal pollution on soil communities and consequently on ecosystem functions, allowing us to explore new ways to reduce soil pollutants and restore vital microbial processes.

Organic pollutants

To maintain idyllic urban green spaces and reduce damage from insects and weeds, pesticides 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 (Imfeld & Vuilleumier, 2012; Kalia & Gosal, 2011; Riah et al., 2014). 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 (García-Delgado et al., 2018; Muñoz-Leoz et al., 2012; Reedich et al., 2017). Additionally, because most pesticide studies focused on agricultural systems or laboratory microcosms, little is known about how in situ urban microbial communities respond to pesticide application and what the response means for soil health and function.

Persistent organic pollutants (POPs) are also present in many urban soils and can have profound effects on ecosystem health. Such pollutants include polycyclic aromatic hydrocarbons, polychlorinated biphenols, and polybrominated biphenyl ethers, which can originate from e-waste processing, vehicle emissions, electronic insulation, lubricants, and other industrial sources. Although the use of these hazardous compounds is regulated and has generally decreased over time, their persistence in the environment still poses a tremendous challenge. These pollutants alter soil microbiome structure and favor taxa, which can tolerate and break down POPs (Girardot et al., 2020; Wu et al., 2020; Zhang et al., 2010). Heavily polluted urban sites such as brownfields can continue to host diverse, active microbial communities that mitigate pollutants. However, it remains unclear whether there is a trade-off between POP tolerance and other ecosystem-relevant functions. The ability of microbes to break down POPs may also depend on temperature, salinity, and nutrient availability, providing an opportunity to optimize soil conditions to promote bioremediation (Varjani & Upasani, 2017).

Soil sealing

A considerable amount of urban soil is sealed under impervious surfaces such as buildings, roads, sidewalks, and pavement. As of 2011, around 4.4% of the land area of European Union nations was artificially covered, half of which was sealed beneath impervious surfaces (Prokop et al., 2011). Within the United States, impervious surfaces cover 17.5% of urban land area, and this fraction can be much higher in particularly dense cities (Nowak & Greenfield, 2012). Soil sealing rates may be outpacing population growth in many regions (Munafo et al., 2010; Prokop et al., 2011). As urban soil sealing continues, studies limited to open urban soils may not be sufficient to gain a comprehensive understanding of urban ecosystem functioning.

Impervious surfaces create a barrier that inhibits the exchange of substances between the soil, surrounding environment, and atmosphere. The resulting sealed soils contain less carbon and nitrogen than open soils and have reduced microbial activity (Lu et al., 2020; Raciti et al., 2012; Wei et al., 2014). Sealed soils may also have decreased microbial diversity and altered community structure (Hu et al., 2018; Yu et al., 2019). The impact of soil sealing on ecosystem function had been largely ignored until recently, but now researchers are emphasizing the need to include sealed soils 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 nonurban systems, soil microbial communities in urban green spaces 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 (Lechuga-Lago et al., 2017; Marques et al., 2020; Skultety & Matthews, 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 noninvasive exotic plants can alter the soil microbiome, shifting microbial community structure and function (Kourtev et al., 2002). More research should be done on how soil microbial communities and functioning respond to common exotic or invasive plants versus native plants. 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. It may be important to distinguish between these land uses to more wholly understand microbial function in cities and devise appropriate soil management approaches.

These land-use patches tend not to exist along a clear gradient but are instead jumbled together to create a complex habitat mosaic, which may create a novel context for studies of microbial biogeography and dispersal (Figure 3; Zhou et al., 2018). Along with variation in land-use types, there is also heterogeneity of climate within urban spaces. Cities tend to be hotter than their surrounding environment, a phenomenon known as the urban heat island (e.g., Imhoff et al., 2010; Li et al., 2017; Oke, 1995). Within this heat island, a variety of microclimates exist due to the position and size of buildings, density of trees, and green infrastructure (Liao & Heo, 2018; Pincebourde et al., 2016). Soils within a city can be trucked in from multiple nonlocal 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; Karim et al., 2014; Zhiyanski et al., 2017; 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. 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 macroorganisms (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 macroorganism studies (Mony et al., 2020). In urban ecosystems, altered hydrology and foot and vehicle traffic may facilitate microbial dispersal at a more rapid rate and over greater distances than is typical in natural environments. On the contrary, vast swathes of impervious surfaces between green spaces may create a barrier to dispersal. No studies to our knowledge have investigated mechanisms of dispersal between soil patches in cities; this should be a focus in future studies.

While dispersal of urban microbial communities is poorly understood at this time, research has characterized communities within urban habitats such as bioswales, parks, green roofs, and residential soils. In general, these studies found differences in microbial composition and diversity by habitat (Gill et al., 2020; Wang et al., 2018). Microbial litter decomposition also differs between urban soils, 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.

It will also be important to track the impacts of temporal variation in environmental variables. In nonurban systems, microbial activity often varies with seasonality, rain pulses, or ecological succession (e.g., Cong et al., 2015; Deng et al., 2017; Tomar & Baishya, 2020). Several studies have found that soil respiration in cities

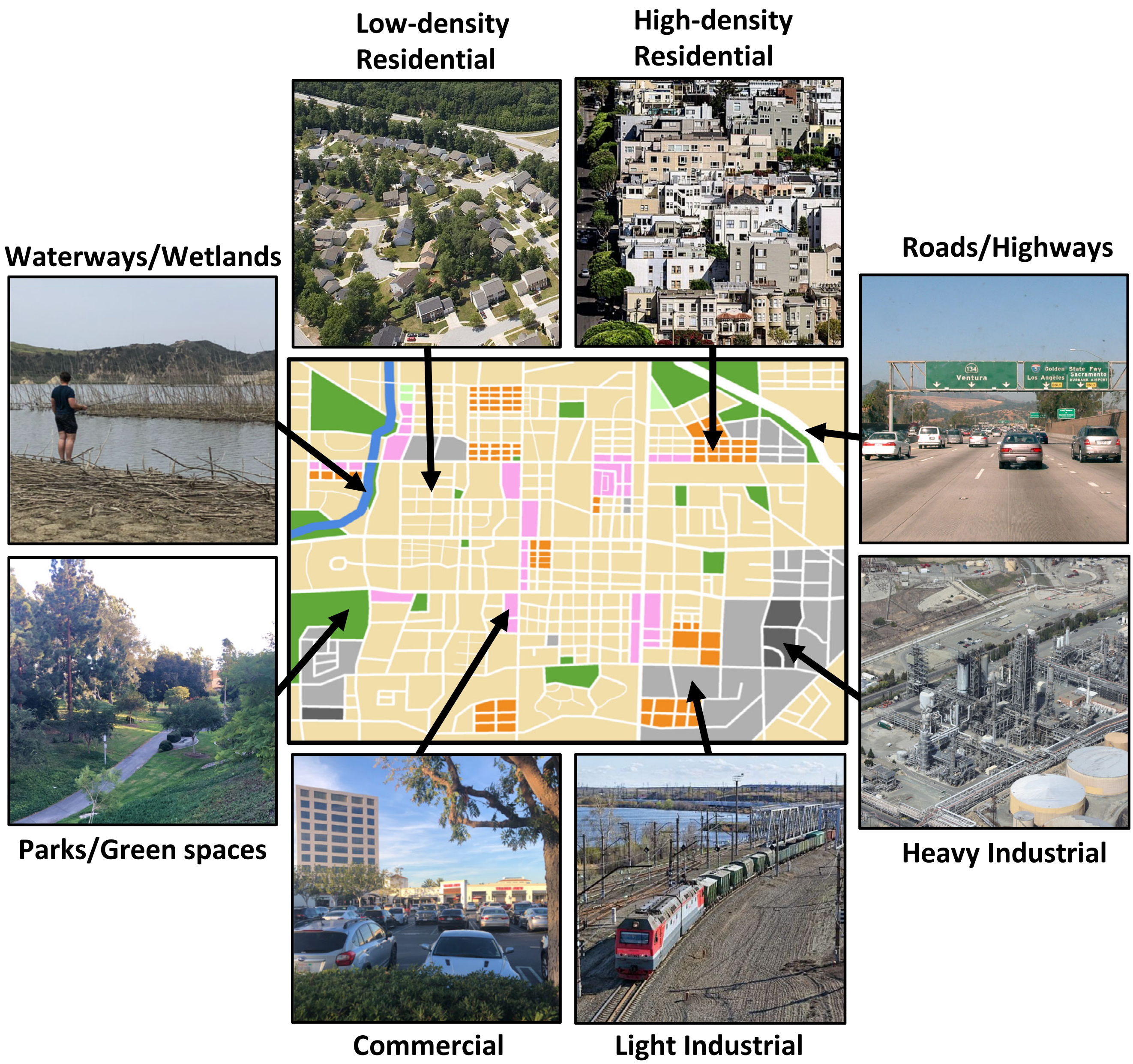

FIGURE 3 Conceptual diagram of an urban matrix, based on a zoning map of Santa Ana, CA. Colors indicate major land-use types

likewise follows seasonal trends, with higher respiration in warmer, wetter months (e.g., Decina et al., 2016; Goncharova et al., 2017; Tao et al., 2016). As summarized in "Disturbance" section, there is also evidence of some microbial functional succession after initial land conversion. Still, it is unclear how the altered resources and disturbance regimes in cities interact with seasonality, heat waves, or extremes in precipitation to drive microbial community structure and function. This interaction should be explored in future work.

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. Some studies have found evidence for this trend with biological, geochemical, soil, and microclimate variables, as well as in urban streams and waterways (Booth et al., 2016; Groffman et al., 2017; Hall et al., 2016; Herrmann et al., 2020; Kaye et al., 2006; McKinney, 2006; Pearse et al., 2016; Polsky et al., 2014). Recently, Delgado-Baquerizo et al. (2021) found evidence for the homogenization of soil microbial taxa and functional genes in urban green spaces across the globe. Homogenization of soil communities was related to economic metrics, climate, and land management practices. This work used metagenomic data to draw conclusions about community function. Moving forward, it will be important to validate these conclusions with complementary methods such as transcriptomics, proteomics, and extracellular enzyme assays that can reveal the in situ consequences of community homogenization for soil processes and ecosystem health. With a high degree of heterogeneity at neighborhood and city scales, and homogenization likely occurring at regional and global scales, urban soil microbial function should be analyzed at all 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 nonurban ecosystems. We summarize the current research providing insight into these questions thus far and recommend approaches for future research.

1. *Are urban soil microbial communities taxonomically and/or functionally distinct from nonurban soil microbial communities, and how much variation exists within the urban environment?*

Microbial phyla most found in soils include the following: α-Proteobacteria, β-Proteobacteria, Acidobacteria, Actinobacteria, Firmicutes, Planctomycetes, and Bacteroidetes (Fierer et al., 2007; Zhang & Xu, 2008). At the phylum level, taxa dominating soils from parks, schoolyards, gardens, road medians, and other urban green spaces are consistent with those observed in nonurban soils (Huot et al., 2017; Lysak & Lapygina, 2018; Reese et al., 2016; Wang et al., 2018). However, relative abundances of these phyla differ within urban soils and along urban–rural gradients (Hui et al., 2017; Stephanou et al., 2021; Stoma et al., 2020; Tan et al., 2019). Overall, diversity sometimes increases with urbanization (Naylo et al., 2019; Tan et al., 2019), sometimes decreases (Rai et al., 2018), and often remains the same but with shifts in composition (Huot et al., 2017; Joyner et al., 2019; Reese et al., 2016; Yao et al., 2006). Additionally, there is tremendous diversity within these major phyla, which can influence community function. Understanding how microbial diversity and community composition change 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.

2. *If differences in microbial taxa and function exist, what are the associated drivers?* (Figure 2, Arrows B and C)

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, as well as among soil communities within the urban matrix. What environmental variables are driving these differences? How do different taxa respond to these drivers? Answers to these questions are essential to manage for healthy and beneficial microbial communities. Urban microbes may be affected by the same environmental variables as nonurban microbes, but there may be differences in the intensity of these factors and 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 such as human population density, neighborhood income, and pollution levels (e.g., Azarbad et al., 2013; Chen et al., 2010; Zhao & Guo, 2010). This method allows the 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. Temporal trends in temperature and precipitation should also be considered as microbial drivers both among and within cities.

A second major approach has been to focus on particular land-use types within the urban matrix, for example, soils along roads, under impervious surfaces, or beneath turfgrass lawns and parks (e.g., Hu et al., 2018; Law & Patton, 2017; Lorenz & Kandeler, 2006; Papa et al., 2010; Yao et al., 2006; Zhao et al., 2013). 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.

3. *How much does taxonomic composition* versus *functional plasticity play a role in urban soil microbial community function?* (Figure 2, Arrow C)

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 the prediction of microbial community impacts on ecosystem dynamics. To an extent, metagenomic analysis has been useful for understanding and predicting microbial community's functional roles (e.g., Fierer et al., 2012; Graham et al., 2016, Amend 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 (Evans & Wallenstein, 2014; Martiny et al., 2015; 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, studies explicitly linking specific microbial taxa to function have only recently been conducted. Research on urban microbial communities has been limited primarily to describing composition and functional gene abundance, without directly linking community genetics to in situ ecosystem variables. Bledsoe et al. (2020) and Bonetti et al. (2021) recently used urban constructed wetlands to link microbial community structure to greenhouse gas emissions and quantify microbial contributions to ecosystem services. To manage urban soils and boost ecosystem services, it will be important to understand the functional roles and limitations of the microbial communities in a wider variety of 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.

Studies of urban microbiomes could enhance the understanding and societal relevance of ecological science (Forman, 2016). Urban areas experience many environmental extremes within a small geographic area. This variation provides an opportunity to study how variables such as pH, heavy metals, and precipitation impact organisms while controlling for other state factors such as geography, elevation, and seasonality (Jenny, 2012). With many major research laboratories located in urban areas, there is scientific expertise and infrastructure available to set up local observational networks and reveal long-term 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 might 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.

4. *What consequences do soil microbial communities have for urban ecosystem function and human well-being?* (Figure 2, Arrows C and D)

Urban microbial communities may have significant effects on urban ecosystem processes, including soil genesis, 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 (Mills et al., 2017, 2020; Rook, 2013; Sandifer et al., 2015; Selway et al., 2020). 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 contrary, urban soils can also house pathogenic microbes and may serve as reservoirs for antibiotic resistance (Li et al., 2018; Xiang 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 benefitting 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 people and develop ways to improve the urban environment through better understanding and valuing of microbial services.

5. *How might urban areas be better designed/managed to boost ecosystem services by soil microbial communities while minimizing harms?* (Figure 2, Arrow A)

Efforts are being made to improve ecosystem benefits in cities. Much of this work focuses on conserving or restoring native habitat (e.g., De Sousa, 2003; Marzluff & Ewing, 2008). While restoring urban land to a predevelopment 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 provide important ecosystem services, act as reservoirs for biodiversity, and convey 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 may be unfeasible in urban ecosystems, and fostering a novel but more functionally beneficial ecosystem might be a better use of management effort and resources. To this end, it will be important to form multidisciplinary collaborations with conservationists, city planners, landscape architects, and engineers when managing urban soils.

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 stormwater 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., Ali et al., 2013; Cheng, 2003). Only recently has attention been paid to the role of microbes in these processes (e.g., Cui et al., 2017; Hrynkiewicz & Baum, 2014), and a better understanding of microbial function could allow us to improve on green infrastructure technologies. It is possible that urban green space cover is underestimated (Zhou et al., 2018), so there might be more opportunity than expected to boost ecosystem services in cities. A study of three Swedish cities found that 22.5% of urban area was covered in turfgrass lawns (Hedblom et al., 2017). In addition to that already substantial area of green space, Rupprecht and Byrne (2014) estimated that "informal" green spaces such as vacant lots, brownfields, and road verges made up between 4.8% and 6.3% of cities, presenting additional and undervalued land area that can be utilized to improve urban sustainability.

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 (Fulthorpe et al., 2018; Hoch et al., 2019). 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 et al., 2017). Several studies have tracked and modeled microbial pesticide degradation to prevent pesticides and their harmful breakdown products from leaching into groundwater and aquatic systems (e.g., Soulas & Lagacherie, 2001; Verma et al., 2014; Yale et al., 2017). 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 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 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 well-being. We argue that microbial ecologists and biogeochemists should take advantage of the heterogeneity and sharp environmental gradients in 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 healthy, equitable, and 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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CONFLICT OF INTEREST
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