

PERSPECTIVE OPEN



Harnessing soil biodiversity to promote human health in cities

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Biodiversity is widely linked to human health, however, connections between human health and soil biodiversity in urban environments remain poorly understood. Here, we stress that reductions in urban soil biodiversity elevate risks to human health, but soil biodiversity can improve human health through pathways including suppressing pathogens, remediating soil, shaping a beneficial human microbiome and promoting immune fitness. We argue that targeted enhancement of urban soil biodiversity could support human health, in both outdoor and indoor settings. The potential of enhanced urban soil biodiversity to benefit human health reflects an important yet understudied field of fundamental and applied research.

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INTRODUCTION

Earth is rapidly being urbanized, with 70% of the human population expected to live in cities by 2050¹. Urban ecosystems provide major benefits to people, such as promoting social development and living convenience. However, high population densities in cities cause environmental impacts, such as losing natural habitats and increasing pollution and temperature. Together these factors threaten biodiversity (the variety of life, including eukaryotes, such as plants, animals, and fungi, and prokaryotes, such as bacteria and archaea), reduce ecosystem functioning, and impact human health and well-being². Nature-based solutions provide a promising avenue for mitigating the multifaceted challenge of managing the human health impacts caused by urbanization^{3,4}. For example, protecting and enhancing the existing, as well as creating new, biodiversity-friendly green spaces is just one nature-based solution that positively impacts human health^{5,6}. However, in addition to plants that act as the ‘greeners’ in the nature-based solutions, there is another hidden actor linked to human health in cities that remains unappreciated – the soil.

Soils represent one of the largest reservoirs of biological diversity on Earth, responsible for critical ecosystem functions such as nutrient cycling, organic matter decomposition, soil formation and plant performance⁷. Soil invertebrates enhance water infiltration and the retention and removal of pathogens, nutrients, heavy metals and other contaminants in urban areas⁸. Thereby, soil biodiversity and functioning affect human health through multiple pathways, including the provisioning of human and animal food, supply of genetic, medical and biochemical resources (e.g., antibiotics, pharmaceuticals), suppression of human, animal and plant pathogens, and the modulation of human immune responses^{9–15}. Unfortunately, urbanization-linked management practices, such as the removal or replacement of natural soil, surface-sealing, compaction, pollution, and above-ground vegetation changes affect soil biodiversity^{16–18}, with subsequent impacts on its functioning to support human health.

There are multiple factors that negatively impact soil biodiversity in cities, and these impacts often differ among degrading processes. For example, habitat fragmentation and management of water runoff are likely to influence soil biodiversity by changing their habitat and food resources^{19,20}. Further, cities are heat islands and consequently will influence soil biodiversity by increasing the metabolism of soil biota, which is likely to have flow-on impacts to community composition as well as food web structuring²¹. In addition, inadequate wastewater disposal impacts soil biodiversity through eutrophication of soils and by spreading of pathogens²². Accordingly, the links between soil biodiversity and human health—specifically in an urban context—remain poorly explored.

Here, we emphasise the importance of soil biodiversity and its functioning in urban environments, with a focus on its links with human health. We first provide an overview of soil biodiversity in urban ecosystems. We then highlight why soil biodiversity is key for human health in urban ecosystems by showing multiple links. We conclude with potential ways forward to advance human health in cities by enhancing soil biodiversity.

SOIL BIODIVERSITY IN URBAN ECOSYSTEMS

While the global biodiversity and functional importance of soil is increasingly recognized²³, knowledge on soil biodiversity in urban ecosystems lags behind, with only few notable exceptions. For example, studies both at the local (e.g., Central Park in New York City) and global scale suggest that soil microbial diversity in urban green spaces is similar to that in natural systems^{24,25}. The reservoir of soil biodiversity is not restricted to public urban green spaces as it includes all soil-associated systems, such as private yards, community gardens, road verges, foot paths, green roofs, green walls, as well as indoor potted plants and indoor and outdoor soil-derived aerobiomes (or dusts) (Fig. 1). Notably, from a human health perspective all these different urban green components

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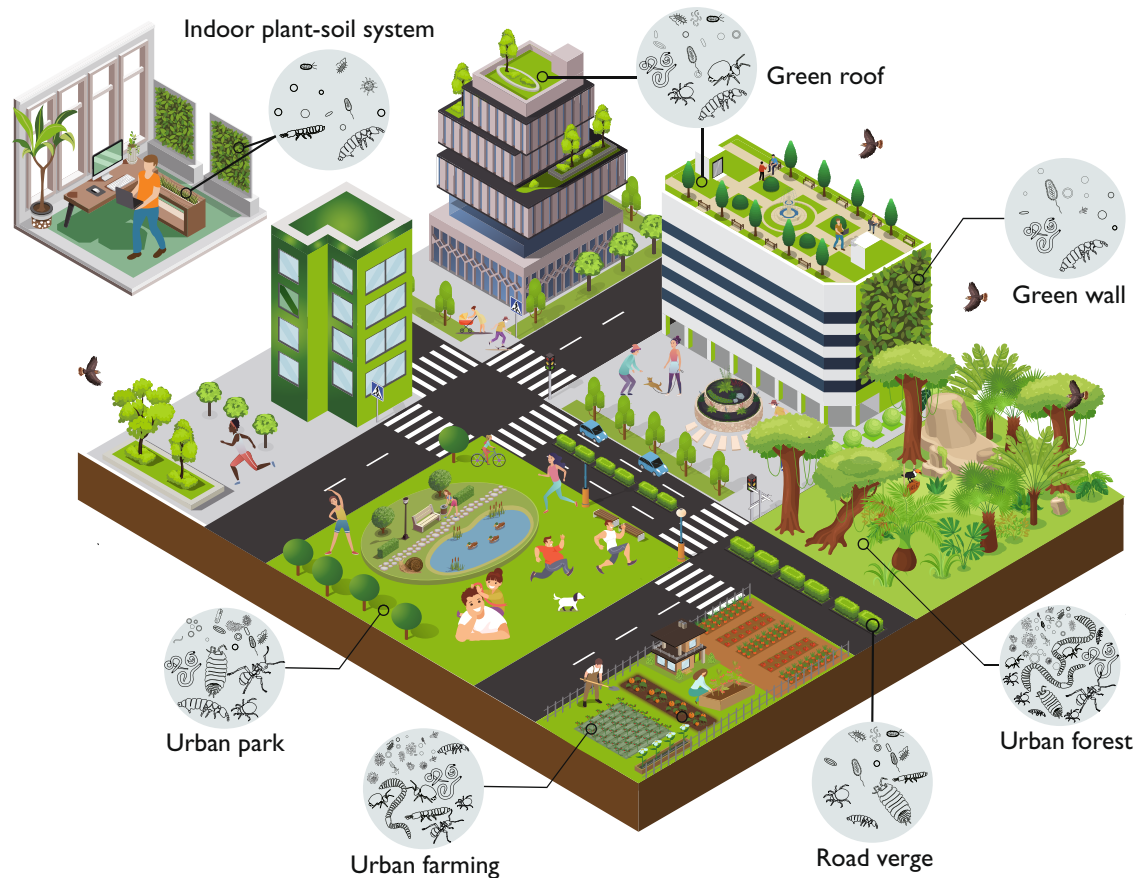


Fig. 1 Soil is a primary reservoir of biodiversity in urban ecosystems. Human-caused disturbance and loss of natural habitats greatly affect urban soil biodiversity. However, there are multiple mitigation options (e.g., green roofs and walls, indoor habitats, diversified and restored parks) to provide soil habitat to increase soil biodiversity in indoor and outdoor spaces.

vary greatly with the intensity and style of urban development, which also needs closer attention and consideration. For example, green roofs can provide habitat for many soil animals by providing suitable habitats and food resources²⁶. Urban farming and community vegetable gardens were shown to host a high soil biodiversity by enhancing the open- to sealed soil ratio and by promoting diverse plant communities^{27,28}. Also, soil-associated particles and microbiota typically comprise a major portion of airborne dust and aerobiomes generated from the surrounding environment^{29,30}.

Human-caused disturbance, resource changes, and loss of environmental heterogeneity in urban ecosystems are known to affect soil biodiversity, and cause the differences observed between urban and natural soil systems^{19,31}. For example, urban microbial biodiversity is repeatedly being reported to become homogenized across cities^{25,32}. This means that while alpha diversity of soil microbiota may be high at any particular urban location, the beta diversity, i.e., differences in microbiota community composition between sites, and hence the overall heterogeneity of microbiota to which human populations are exposed, is often reduced due to increasingly common anthropogenic and human-impacted habitats for microbes in urban environments. Similar to microbial diversity, nematodes in urban systems are at a global average equally abundant in urban than in non-urban systems (including natural ones), while their composition changes towards an increased dominance of fast-growing bacterivores and herbivores at the expense of larger omnivores in urban systems³³. This trend of more negative effects on larger organisms also applies to larger-sized soil invertebrate groups, such as earthworms, springtails, mites and ground beetles, that become

diminished in species richness and abundance in urban systems, likely due to their vulnerability to pollution and habitat loss (e.g., through soil-sealing and reduction of plant diversity)^{34–38}.

The changes in soil biodiversity in urban systems inevitably leads to shifts in the structure and functioning of food webs in urban soils. For example, the observed increase of fast-growing (opportunistic) taxa of bacteria, protists and nematodes in urban ecosystems is linked to increased nitrogen loss, reduced carbon sequestration and increased greenhouse gas emissions^{25,33,39}. Likewise, the reduction of tree-associated ectomycorrhizal fungi in urban systems is linked to increased nutrient leaching, reduced plant growth, health and overall system stability¹⁶. Also, diversity losses of macroinvertebrates in cities may increase CO₂ emissions through reduced carbon and nitrogen sequestration due to reduced litter decomposition and incorporation into the soil^{40–42}. Further, the loss of top predators (e.g., birds of prey) and altered habitat characteristics in urban ecosystems can result in functionally destabilised food-webs (including those in soil) and result in changes to trophic cascades that benefit certain soil biota groups, including termites, ants and snails that risk damaging buildings, reducing plant performance and transmitting human pathogens^{43–46}. As ecosystem health is intimately tied to human health through the provisioning of ecosystem services⁴⁷, changes in soil biodiversity will ultimately translate to human health impacts⁴⁸.

In the following sections, we provide details on the multiple lines of evidence that link urban soil biodiversity to human health. Negative links to human health include hosting of soil pathogens and drug-resistant bacteria, and potential for poorly-functioning soils to release stored greenhouse gasses. We focus primarily on human pathogens and largely do not include the more prevalent

examples of soil-borne plant pathogens as their importance for human health has been covered elsewhere^{23,49,50}. Positive links to human health include suppressing soil-borne pathogens of humans, remediating contaminated soil, and potential for enhancing immunoregulation and other microbiota-mediated links to human health.

NEGATIVE LINKS BETWEEN SOIL BIODIVERSITY AND HUMAN HEALTH

Soil pathogens and pests with direct and indirect links to human health

Urban ecosystems are incubators for emerging human diseases as they can, for example, accelerate the persistence and spread of soil-borne zoonotic pathogens that threaten human health⁵¹, especially in tropical regions. Pathogenic microorganisms often represent fast-growing, opportunistic and generalist feeding strategies, and microorganisms sharing these traits are generally more abundant in disturbed and degraded soil ecosystems that are common in urban ecosystems⁵². Therefore, a long list of human bacterial and fungal pathogens may be present in urban soils. This list includes *Clostridium tetani*, *Clostridium botulinum*, *Clostridium perfringens*, *Listeria monocytogenes* and *Blastomyces dermatitidis*, the biological agents causing serious human diseases such as tetanus, anthrax, botulism, gastrointestinal, wound, skin, and respiratory tract diseases⁵³. The large and widespread free-living soil protist *Acanthamoeba* spp. may cause serious human infections including corneal abrasions and fatal encephalitis⁵⁴. Additionally, *Acanthamoeba*-caused keratitis has increased in urban areas since this infection is often associated with contact lens contamination⁵⁵. Even some freshwater bacteria like *Legionella* spp. can survive in soil and subsequently infect humans to cause legionellosis disease⁵⁶.

Some human pathogens have also gained resistance against treatments, with the most notorious example being antibiotic resistant bacteria that are increasing through inappropriate use of antibiotics^{57–59}. These antibiotic resistant bacteria have been commonly found in urban environments, both outdoors (e.g., in urban park soils) and indoors (e.g., soil-derived dusts in public transport infrastructure, shopping malls, schools, and sports stadiums^{60,61}). Importantly, multidrug resistant human pathogenic bacteria that are now a common issue for hospitals mostly originate in soils²².

Many larger soil organisms can indirectly threaten human health as vectors of pathogens and antibiotic resistance genes^{22,62}. For example, the foodborne pathogen *Campylobacter jejuni* is a leading cause of human bacterial gastroenteritis, and can multiply and spread inside *Acanthamoeba* spp. and avoid human immune response when channeled into human hosts by the protist^{63,64}. The opportunistic pathogen *Klebsiella pneumoniae*, a common contaminant of animal and plant-based foods, has been cultured from the soil and feces in a wide range of agricultural and domestic animals, birds, insects and earthworms⁶⁵. Being a key vector of antimicrobial resistance genes, the soil-associated *K. pneumoniae* causes a range of acute infections and poses a serious risk to public health due to its role in introducing multidrug-resistant and hypervirulent strains into the human gut⁶⁶. These observations lead us to ask (as discussed later) whether the opportunistic growth-patterns and urban-associations of many pathogens such as those described above might be impeded by greater soil biodiversity.

Soils harbor many parasitic species that pose risks to human health, especially in crowded urban areas with poor sanitation⁵¹. For example, eggs of soil-transmitted helminthic worms can be deposited on soil via the feces of infected persons⁶⁷. Helminth infections present a major burden of parasitic diseases, especially in areas with warm and moist climates⁶⁸. Some soil arthropod

pests, such as red fire ants (*Solenopsis invicta*), species of Ixodoidea and Staphylinidae, are harmful to people through biting and spreading diseases^{69–71}. Moreover, pest or invasive termites that damage urban infrastructure can have substantial economic and ecological consequences⁷².

Sources of greenhouse gasses

Greenhouse gas accumulation is one of the main forcing agents driving climate change in urban ecosystems that greatly threatens human health⁷³. Soil biodiversity has a key role in the cycling of elements, particularly carbon and nitrogen⁷⁴. Differences in soil biodiversity in urban compared to non-urban soils suggests that elemental (or biogeochemical) cycling is also shifted. A recent global field survey showed that urban soils host a higher proportion of genes associated with archaeal methylophilic methanogenesis and denitrification processes than natural soils²⁵. This finding suggests that urban soils might have increased methane and nitrous oxide emissions and therefore represent important sources of greenhouse gas emissions than more natural ecosystems. Further, intensive management of urban green spaces, such as frequent mowing and plant removal, increases CO₂ emissions from soils compared to less intensive management⁷⁵. Reductions of soil animals in urban land likely impacts elemental cycling due to shifts in the decomposer microbiome⁷⁶.

POSITIVE LINKS BETWEEN SOIL BIODIVERSITY AND HUMAN HEALTH

Suppression of soil pathogens

An increase in the complexity of soil biota can effectively reduce soil-borne human pathogens⁷⁷. The suppression of pathogens by increased soil biodiversity has largely been shown in agricultural ecosystems for plant pathogens⁷⁸. For example, soils in natural systems with higher biodiversity can reduce the incidence of soil-borne plant diseases by inducing plant defense, producing antibiotics, competing with pathogens, and regulating plant immune systems^{79,80}. Indeed, biodiverse plant-soil systems appear to replace the opportunistic, fast-growing, generalist, and higher potential pathogenic character bacteria that are favored in disturbed and degraded ecosystems, with slower-growing, niche-adapted taxa⁵². While loss of soil microbial diversity exacerbates the invasiveness of bacterial pathogens and antibiotic resistance, maintaining high soil microbial diversity can act as a biological barrier to resist their spread^{57,81}. As such, a negative link between soil biodiversity and human pathogen abundance can be expected but requires further investigation.

Soil animals can control the community of pathogens through predation. Again, predation of soil animals on pathogens is mostly known for plant pathogens, such as Collembola preferably feeding on pathogenic fungi than on mycorrhizal fungi⁸². However, there is also evidence that human pathogens can be directly reduced by predation from soil animals. For example, studies in organic farms have shown that dung beetles suppress human pathogenic bacteria and decrease the persistence of human pathogens by accelerating the removal of dung⁸³. Earthworms were also reported to eliminate human pathogenic bacteria in dewatered sludge⁸⁴.

Remediation of contaminated soil

People living in cities, especially industrial cities, often are being exposed to contaminants via inhalation, dermal contact and ingestion of soil, and food grown in urban soil. Since urban soils are a potential repository for contaminants of organic and inorganic pollutants, this exposure imposes high risks to human health^{85,86}. Microorganisms in soil can help remove soil pollutants through degradation and transformation⁸⁷. The remediation

potential of soil microorganisms associated with plants has been addressed elsewhere, especially for heavy metals, although largely in agriculture systems⁸⁸. A long-term study showed that microorganisms decreased the concentration of free aqueous polycyclic aromatic compounds in polluted urban soil⁸⁹. Protists are reported to have close interactions with pollutants in soil through accumulation and transformation of microplastics, organic pollutants and heavy metals, but the potential role of protists in soil remediation is still little explored⁹⁰. Furthermore, larger soil animals can enrich heavy metals through their own absorption to reduce the amount in the soil and subsequently promote the accumulation of heavy metals by plants through their feeding activities in soil⁹¹. For example, earthworm inoculation can reduce the concentration of most metal elements and antibiotic resistance genes in urban soils^{92,93}.

Enhancing human immunoregulation

Living in cities comes with reduced exposure to biodiversity and may subsequently lead to the human immune system being poorly trained and over-sensitive to normally innocuous agents (e.g., dust particles, pollen)^{30,94}. There is increasing evidence that biodiverse green spaces—and their soils in particular—can enhance human health by exposing people to diverse beneficial environmental microbiota^{30,95–98}. Exposure to natural soil biodiversity may help build up immune fitness and promote human health via multiple pathways, including improved immunoregulation, anxiety reduction, provisioning of key metabolites (e.g., short chain fatty acids), and supporting metabolic health via a balanced functional profile of gut microbiota^{99–101}. Previous studies have shown reduced frequency of allergies and atopic sensitization in children that grow up on farms, compared to suburban areas, due to greater immune system exposure to a greater variety of environmental microorganisms¹⁰². Moreover, the immune fitness benefits are even greater in people that employ traditional farming methods involving more intimate contact with soils and farmyard manures compared to populations employing more industrial farming methods¹⁰³. A recent long-term study in Finnish urban daycare children demonstrated that a biodiversity intervention, via introducing plant and soil materials into daycare yards, enhanced immune biomarkers and health-associated commensal microbiota in exposed children, while decreasing the relative abundance of potential pathogenic bacteria^{97,104}. Generally, more diverse plant communities support a greater diversity of soil microbiota than low diversity plant communities, which could be harnessed to enhance the immune-boosting properties of soil biodiversity^{28,105}.

Indoor soil biodiversity is of increasing interest as a place for enhancing human health as urban residents spend more than 90% of their time indoors^{106,107}. In fact, indoor microorganisms strongly affect human health^{108,109}, where, for example, airborne infectious pathogenic bacteria can impact human health with increasing incidence of asthma and allergies in developed countries¹¹⁰. Therefore, bringing biodiverse soils into indoor environments might help to mitigate negative effects induced by these pathogens via (a) direct suppression through competition for space reducing some pathogenic bacteria, and (b) indirect effects through enhancing human immune fitness which may offer more longer-term health benefits. For example, indoor plant-soil systems may serve as an effective way to manipulate airborne bacteria towards communities that support human health^{105,111,112}. Indeed, a recent study demonstrated that introducing farm-like indoor microbiota in non-farm homes reduced asthma development in children¹¹³.

Improving the human microbiome

Functionally important gut bacteria may be lost in people due to poor diet, lifestyle and exposure to antibiotics, and then

subsequently lead to human metabolic health and disease^{114,115}. As one of the richest and most abundant reservoirs of environmental microbiota, soils are of particular interest for supplementing the human microbiota¹¹⁶. In fact, the human microbiota can be supplemented from the outdoor soil environment via multiple pathways, such as direct contact with soil⁹⁶, ambient dust transfer^{30,95,117}, contact with household pets¹¹⁸, and interactions with household dust¹¹². Interestingly, certain health-promoting spore-forming bacteria that dominate human guts may even be promoted within biodiverse soil systems¹¹⁹. Therefore, exposure to healthy urban soils might provide the basis for natural diversification of the gut microbiome and result in improved human health outcomes.

HARNESSING SOIL BIODIVERSITY FOR MANAGING HUMAN HEALTH IN CITIES

Ecosystem restoration in urban ecosystems and the renewal of biodiverse plant-soil systems represents a promising strategy for improving soil biodiversity to the benefit of human health^{120,121}. Conserving and restoring soil biodiversity in cities should be prioritised to reduce the risk of immune-mediated diseases and improve human health via reducing pathogens, purifying soil pollutants, as well as enhancing human immunoregulation and modulating the human microbiome (Fig. 2). Moreover, this will simultaneously benefit the supporting and cultural services associated with soil biodiversity (e.g., sustaining soil-based urban ecosystems, such as parks, gardens, forests, and urban-agriculture), which should improve the quality of the environments in which people live and have positive implications for human health. Therefore, assessing the role of exposure pathways when considering environmental factors such as soil biodiversity is important. Unfortunately, little is known on how to integrate soil biodiversity to harness the benefits they bring, especially in relation to human health in current urban restoration and management systems, calling for more investigations in future.

In urban settings where paved/sealed surfaces and poor-quality soils with low plant and soil biodiversity, we believe the potential human health benefits (and risks) associated with enhancing soil biodiversity with appropriate exposure pathways can be readily conceptualized and warrants further research. There are several possible ways forward to advance human health via modulating urban soil biodiversity, for example: (1) preservation, enhancement and expansion of biodiverse green spaces and elimination of soil sealing in and around cities wherever possible, to protect the habitats of diverse soil biotas and to enhance biodiversity at regional scales^{23,122}; (2) maintain and/or transplant habitat that supports soil biotas to provide them suitable living conditions, such as retaining leaf litter in urban parks which may help support litter transformers and decomposers (e.g., isopods, springtails, mites, ground beetles), which will not only increase soil biodiversity but also help controlling soil pathogens via predation^{123,124}; (3) establish more green infrastructure for the built environment (e.g., green roofs, green walls, urban farming, community gardens, compact parks), and manage the green infrastructure to incorporate higher vegetation diversity and complexity providing more habitats and food resources for soil biotas and decreasing soil pathogens via biota interactions^{28,125}; (4) establish more biodiverse indoor plant-soil systems (e.g., indoor green walls with soil substrates, potted plants) to increase people's exposure to soil and its biodiversity, while improving biodiversity in the environment that will benefit human immunoregulation^{98,109,113}. These suggestions provide a practical basis for integrating soil biodiversity with the aim of harnessing its benefits for human health and sustainable urban settlement, and should be further considered with multiple stakeholder groups across public health, urban planning, environmental sustainability, and biodiversity management.

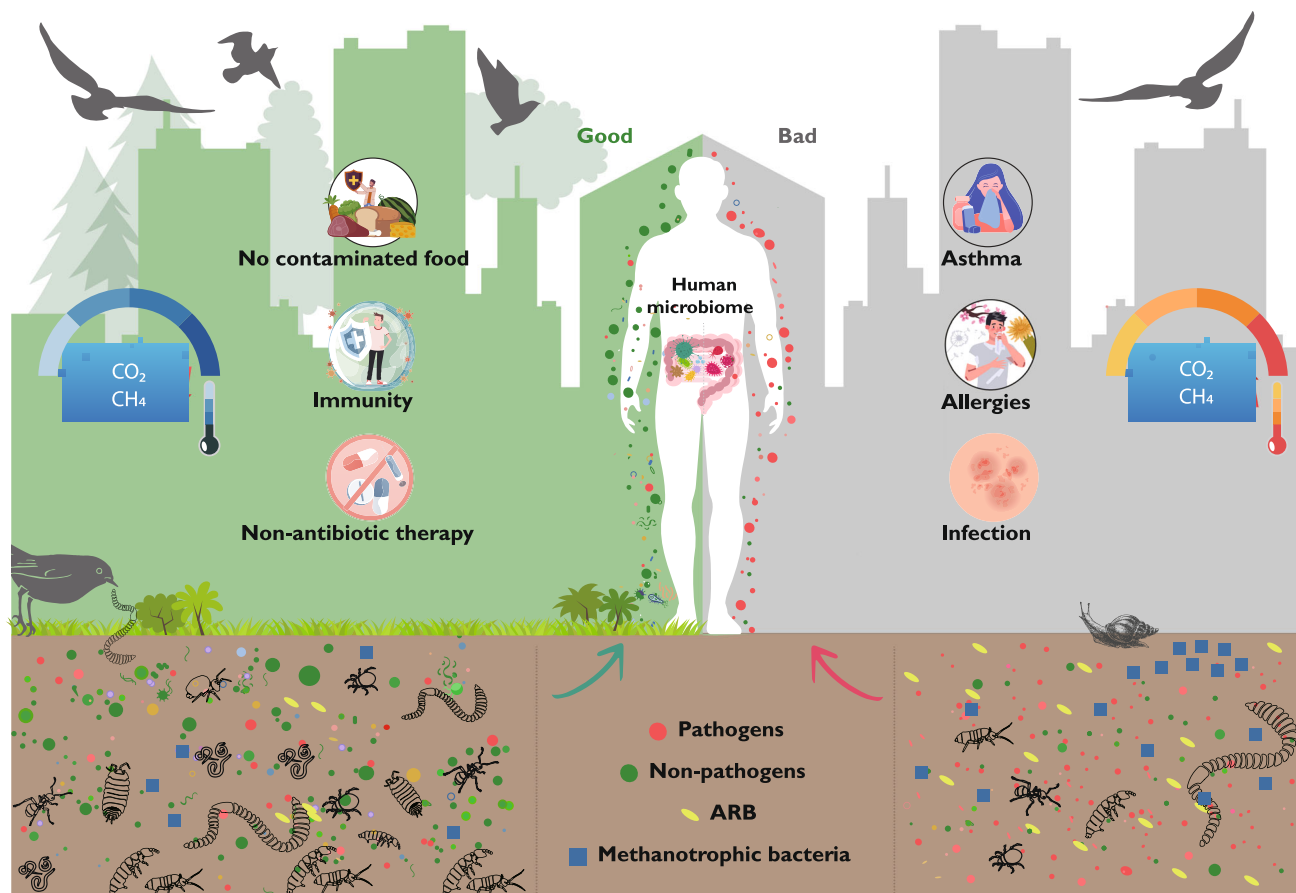


Fig. 2 Harnessing soil biodiversity for advancing human health in cities. Conserving biodiverse green spaces and establishing more green infrastructure benefit the maintenance of soil health by increasing soil biodiversity, suppressing soil pathogens and antibiotic resistance bacteria (ARB), and reducing the amount of the microorganisms that increase rates of methane and nitrous oxide emissions. Appropriate management of soil biodiversity in cities can reduce the risk of immune-mediated diseases and improve human health in cities via reducing pathogens, purifying soil pollutants, as well as enhancing the human immunoregulation, and modulating the human microbiome.

To achieve these goals, more studies focusing on soil biodiversity in cities are needed, especially those comparing urban and adjacent non-urban soils. A wide range of taxa should be investigated including their adaptations to urban environments. Furthermore, restoring soil biodiversity will also require considering the size of cities and the number of inhabitants, although there are likely to be consistent negative impacts on soil biodiversity in cities across the world that affect human health^{18,25}. In addition, further evidence is needed to determine which soil biodiversity interventions have the greatest benefit to human health. Therefore, harnessing soil biodiversity for managing human health in cities could be a compelling area for interdisciplinary research, integrating sociological knowledge of barriers to outdoor access and enjoyment, and a call for collaboration to link soil ecology with medical and sociological sciences is urgently needed.

CONCLUDING REMARKS

Soil biodiversity is a key ecosystem component that supports ecosystem and human health. Here we provide insights into urban soil biodiversity that is lagging behind knowledge on above-ground ecosystems. The functional importance of soil biodiversity in supporting human health in an urban context is largely unrecognised, despite knowledge of the general importance of soil biodiversity in driving multiple ecosystem functions in non-urban habitats. Therefore, we offer strategies to promote soil biodiversity with the aim of benefiting human health. In our view,

there is a pressing need to better understand and apply urban soil biodiversity as a promising option to enhance human health. Harnessing urban soil biodiversity to promote human health will provide a new perspective on nature-based solutions that helps meet the rising challenges of biodiversity loss, climate change and the growing burden of disease in human populations in cities.

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this article.

DATA AVAILABILITY

No datasets were generated or analysed during the current study.

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AUTHOR CONTRIBUTIONS

Y.G.Z. conceived the study and provided input across all sections from an urban soil perspective. X.S., S.G. and M.F.B. conceptualized the structure and content of the manuscript. X.S. wrote an initial draft with the help of B.W., C.Y.L., Y.Y.Z. and Z.P.L. in literature and data searching. S.G., C.L., A.T., M.F.B., S.S. and Y.G.Z. expanded upon the ideas contained within the draft and helped edit the manuscript. Y.Y.Z. and X.S. designed the figures.

COMPETING INTERESTS

The authors declare no competing interests.

ADDITIONAL INFORMATION

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