

Beneath the Pavement: Understanding mycorrhizal fungi in urban ecosystems and the path forward

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Societal Impact Statement

Mycorrhizal fungi form beneficial partnerships with most plants, supporting soil health and ecosystem function globally. Yet we know little about how these fungi respond to urbanization—the fastest-growing land-use change worldwide. Evidence shows that mycorrhizal fungi persist in cities, but community composition shifts under urban pressures. Most studies focus on temperate, northern cities and rarely consider seasonal dynamics, limiting global insight. Everyday management of greenspaces by residents, such as adding or removing organic matter, can scale up to shape urban soil health. Expanding research across climates will clarify how mycorrhiza fungi sustain biodiversity, ecosystem services, and human well-being in cities.

Summary

Urban expansion is reshaping ecosystems worldwide, yet the responses of mycorrhizal fungi—key mediators of plant–soil interactions—remain poorly understood. In this review, we synthesize current knowledge on the environmental and ecological factors shaping mycorrhizal fungal diversity, distribution, and function in cities. We highlight how greenspace and landscape features—including plant community composition, site size and connectivity, and soil properties—interact with fungal dispersal limitations to structure communities under urban-specific stressors. Our synthesis identifies critical knowledge gaps. Research is geographically biased toward temperate, northern cities and often overlooks seasonal dynamics, constraining understanding of urban mycorrhizal ecology across climates and cultural contexts. Ectomycorrhizal fungi are particularly sensitive to habitat loss and fragmentation, emphasizing that maintaining large, connected greenspaces is crucial for conserving their diversity and ecosystem contributions. Socio-cultural influences on urban fungal communities remain largely unexplored, and experimental, trait-based, and molecular approaches are underutilized. We propose interdisciplinary research directions that link fungal ecology with urban planning and community engagement. By framing cities as coupled human–natural systems, this review provides a framework for integrating mycorrhizal fungi into urban biodiversity, ecosystem service, and public health agendas. Such integration can guide the design of resilient, biodiverse, and health-promoting greenspaces, while fostering local stewardship and inclusive decision-making.

Keywords: Mycorrhizal fungi, Plant–soil interactions, Socio-ecological processes, Urban ecology, Urban resilience

Introduction

Cities are often imagined as biological deserts, yet beneath sidewalks, parks, and street trees lies an immense and largely unseen world of organisms sustaining urban life. Among these hidden communities, soil microbial assemblages—and in particular, mycorrhizal fungi—quietly shape how plants, people, and ecosystems adapt to the challenges of urbanization. Urban areas currently house approximately 55% of the world's population, a figure projected to rise to nearly 70% by 2050 (Kundu, 2020).

Urbanization—the transformation of natural ecosystems into densely built environments with high human populations—drives profound changes in biodiversity and ecosystem function that extend far beyond city boundaries (Abrego et al., 2020; Alberti et al., 2003). These effects often interact with other global change drivers, including climate change and social inequities in urban planning, to amplify their impacts on regional biota and ecosystem processes (Alberti et al., 2003; Kundzewicz et al., 2014; Poulton Kamakura et al., 2024; Schell et al., 2020; Walker et al., 2024a; Walker et al., 2024b). The interplay of natural and human factors in cities creates complex, multi-scale dynamics that challenge our understanding of how to maintain urban ecosystem health.

One key strategy for supporting biodiversity and ecosystem function in cities is the design and management of greenspaces. Urban greenspaces provide habitat for plants and wildlife, promote human health and well-being, and deliver essential ecosystem services such as moderating heat island effects, reducing flooding, and filtering air pollutants (Amini et al., 2020; Fan et al., 2023; Hoover and Hopton, 2019; Turner-Skoff and Cavender, 2019). While the visible, aboveground communities of plants and animals have received substantial attention, the hidden microbial networks that underpin these ecosystems are equally crucial. Belowground microbial assemblages, including those associated with plant roots, influence soil structure, nutrient cycling, and even human health (Banerjee and Van Der Heijden, 2023; Fan et al., 2023; O'Riordan et al., 2021; Stewart et al., 2024; Sun et al., 2023). Yet among these microbes, mycorrhizal fungi—the symbiotic partners of most land plants—remain particularly understudied in urban environments.

Mycorrhizal fungi are essential components of the soil microbiome, forming obligate associations with the roots of most plant species and regulating key biogeochemical processes (Brundrett and Tedersoo, 2018). Their symbiotic roles and ecological functions depend on the type of association they form—arbuscular mycorrhizal (AM) or ectomycorrhizal (EM) (Figure 1). Both types enhance host plant nutrient and water uptake and increase resilience to pathogens, pollutants, drought, and heat stress (Anthony et al., 2022; Bahadur et al., 2019; Veresoglou and Rillig, 2012; Wang et al., 2021). These benefits are especially critical in urban ecosystems, where resources fluctuate and stressors are intense

(Scharenbroch et al., 2005; Stewart et al., 2024; Watson et al., 2014). Mycorrhizal fungi also mediate carbon and nutrient cycling—processes frequently disrupted by disturbance and management in cities (Anthony et al., 2022; Mohan et al., 2014; Phillips et al., 2014; Tatsumi et al., 2023).

The colonization of roots by mycorrhizal fungi, as well as their community diversity, abundance, and composition, show variable responses to urbanization. EM fungi appear particularly sensitive: regional and global analyses indicate that urbanization has reduced EM fungal diversity and abundance more sharply than in bacteria, archaea, or other fungal guilds such as saprotrophs and pathogens (Arnolds, 1999; Delgado-Baquerizo et al., 2021; Epp Schmidt et al., 2017; Hui et al., 2017; Korneykora et al., 2022; Ochimaru and Fukuda, 2007; Scholier et al., 2023). This sensitivity is reflected in the growing number of EM fungal taxa now listed as threatened in the International Union for Conservation of Nature’s Red List (IUCN, 2025; Mueller et al., 2022), including species such as *Cortinarius pavelkii*, which require protection from urban encroachment (Castellano et al., 2015). Yet not all mycorrhizal fungi decline in cities. Certain EM fungal genera—including *Inocybe*, *Laccaria*, and *Scleroderma*—tolerate frequent disturbance and persist in urban greenspaces (Csizmár et al., 2023; Hui et al., 2017; Louise et al., 2024; Sanchez-Tello and Corrales, 2024; Shen et al., 2022). In some cases, these greenspaces even harbor rare or Red-Listed EM fungal species, highlighting the context-dependent nature of urbanization effects (Purahong et al., 2022). Likewise, several AM fungal taxa tolerate harsh urban conditions and remain abundant under similar stressors (Buil et al., 2021; Carrenho and Gomes-da-Costa, 2011). However, because AM fungi remain less studied in urban settings—and none are currently recognized on the IUCN Red List—their ecology in cities is still poorly understood.

Despite these emerging insights, the community dynamics and functional roles of mycorrhizal fungi across diverse urban ecosystems remain underexplored (Stewart, 2025). In this review, we synthesize current knowledge of mycorrhizal fungal communities in urban environments, emphasizing the soil and site characteristics that shape them. We examine how greenspace and landscape features, and biotic and chemical stressors influence mycorrhizal diversity and function. We then explore how broader socio-cultural processes—including governance, inequality, and human–plant–mycorrhizal relationships—mediate these patterns across cities. Finally, we identify key research gaps and propose future directions for integrating social and ecological perspectives in the study of urban mycorrhizal fungi. Together, these approaches can advance a more inclusive, interdisciplinary understanding of how urban symbioses sustain life beneath our feet.

Impacts of greenspace and landscape features on the distribution of mycorrhizal fungal communities in cities

Plant community composition, abundance, and green infrastructure

Rapid cycles of urban development, ownership, and changing land-use priorities create a mosaic of heterogeneous greenspaces within cities, each maintained for varying social and ecological functions (Figure 1). Although the effects of greenspace and landscape features—such as plant community composition, site size, habitat edges, and connectivity—on urban biodiversity are increasingly studied (Ossola et al., 2019; Hopkins et al., 2021), their influence on urban mycorrhizal fungi has been largely ignored.

Plant community composition is one of the strongest predictors of mycorrhizal fungal community structure and can fluctuate over time due to management or successional processes (Hopkins et al., 2021; Hui et al., 2017; Whitehead et al., 2022). EM fungal assemblages are tightly linked to host tree species and are often more abundant in evergreen than in deciduous urban parks (Hui et al., 2017; Whitehead et al., 2022). In contrast, AM fungi exhibit lower host specificity, which likely explains their high colonization rates across diverse urban habitats, including associations with ruderal, invasive, and non-native hosts (Buil et al., 2021; Gupta et al., 2018; Hoch et al., 2019; Lin et al., 2021). Often these AM-associated plants have traits that categorize them as pioneer species allowing them to thrive in disturbed and confined spaces such as pots, balconies, gardens, and small green patches better than long-lived perennials and trees. As a result, woody species in cities often experience stress, short lifespans (~10 years), and distinct, less diverse mycorrhizal communities (Alzetta et al., 2011; Olchowik et al., 2021; Salisbury et al., 2022).

Host plant abundance and the integration of built elements through green infrastructure also shape urban mycorrhizal diversity. EM fungal richness increases with tree basal area (Ochimaru and Fukuda, 2007) but declines in turf-dominated or ruderal greenspaces (Epp Schmidt et al., 2017). Similarly, AM fungal diversity and abundance rise with host cover (Pärtel et al., 2017; Whitehead et al., 2022). Semi-natural infrastructures—such as green roofs, stormwater biofilters, and planter boxes—serve as novel habitats for mycorrhizal fungi (Figure 1). AM colonization on green roofs can match levels found in natural soils and increases with plant diversity (Chaudhary et al., 2019; Hoch et al., 2019; Metzler et al., 2024). In stormwater biofilters, however, AM colonization remains comparatively low despite strong links to plant composition (Brodsky et al., 2019; Winfrey et al., 2017). Because host identity, health, and abundance so strongly influence mycorrhizal fungal communities, urban soil restoration efforts should emphasize post-establishment plant maintenance and regular health monitoring—especially for long-lived woody

hosts.

Fragmentation impacts on greenspace size, habitat edges, and connectivity

Natural disturbance regimes such as fire and flooding are largely suppressed in cities, yet human-driven disturbances occur more frequently and often more intensively than in other land-use types. These anthropogenic disturbances range from nutrient enrichment through fertilizer use to the continual fragmentation of greenspaces and creation of new habitat edges (Drinnan, 2005; Tatsumi et al., 2023). Fragmentation and reduced greenspace size are associated with lower AM colonization, decreased seedling survival, and reduced EM fungal diversity and abundance, particularly in patches smaller than 2 ha (Drinnan, 2005; Rusterholz et al., 2020). Remnant greenspaces can recover biodiversity over time—either passively, through reduced disturbance, or actively, through management—mirroring the island biogeography patterns observed in long-established urban parks (Nielsen et al., 2014). Whether such recovery dynamics apply to mycorrhizal fungi remains uncertain, as most estimates of fungal diversity and abundance across greenspace sizes rely solely on sporocarp surveys. Sporocarp surveys substantially underestimate community change because many species lack visible fruiting bodies, and those that do often vary in production across seasons and years (Pinna et al., 2010; Straatsma et al., 2001). To more accurately assess how greenspace size shapes mycorrhizal communities, future research should integrate eDNA sampling of roots, soils, and air across multiple time points each year to identify critical greenspace size thresholds below which mycorrhizal diversity and abundance decline—information vital for urban planners and land managers.

Fragmentation also increases habitat edges, altering microclimate, soil chemistry, and the composition of microbial and plant communities (Dickie and Reich, 2005). Edge effects reduce EM and AM fungal colonization, diversity, and mycelial network connectivity, but can also increase AM spore abundance relative to undisturbed locations (Abrego et al., 2020; Carrenho and Gomes-da-Costa, 2011; Tatsumi et al., 2023). Although both EM and AM fungi are sensitive to fragmentation and edge formation, their responses differ in scale and mechanism. For instance, even though EM mycelia can extend meters from host roots, seedling colonization declines sharply with increasing distance from forest edges. This pattern suggests that EM fungi depend on well-connected greenspaces and proximal host trees to sustain belowground mycelial networks (Abrego et al., 2020; Peay et al., 2012). In contrast, AM fungal hyphae typically explore only a few centimeters of soil around host roots (< 3 cm; Mai et al., 2019), yet their propagules can disperse independently of plants and even along roadsides aided by aboveground dispersal through a remarkably diverse pool of spores—a process likely mirrored by EM fungi, though untested in urban contexts (Chaudhary et al., 2020; Clavel et al., 2025). The combination of efficient dispersal

pathways and a broader host range likely enables AM fungi to occupy a greater number of habitat “islands” across the urban matrix (Davison et al., 2018). Future research should characterize fungal communities along disturbance transects—such as park trails or property boundaries—and test how greenspace connectivity influences their persistence and function.

Mycorrhizal fungal dispersal across urban landscapes

Dispersal processes influence mycorrhizal fungal distribution locally, regionally, and globally, but fungal dispersal in urban ecosystems remains understudied (Abrego et al., 2020; Abrego et al., 2024; Chaudhary et al., 2020; Peay et al., 2012). In fact, urban ecosystems have been entirely excluded from recent global efforts to map mycorrhizal biodiversity, likely due in part to a lack of data on mycorrhiza in urban ecosystems for most cities on Earth (Figure 2), and a clear bias towards temperate ecosystems (Figure 3; see Mikryukov et al., 2023 and Van Nuland et al. 2025 for recent global studies on global soil fungal diversity). Fungi disperse through propagules like spores, sclerotia, colonized root tips, and hyphal fragments, that are transported by wind, water, and animal vectors, or spread through mycelial growth within the soil (Chaudhary et al., 2020; Claridge and Trappe, 2005). Across urban-rural gradients globally, aerial samples of mycorrhizal fungi show particularly dramatic declines in diversity and abundance when compared to less specialized fungi like soil saprotrophs (Abrego et al., 2020). However, city aerial samples are not uniformly devoid of mycorrhizal fungal propagules, and diverse and abundant communities of AM fungi have been collected on green roofs (Chaudhary et al., 2020). In addition, there is evidence of AM propagule dispersal between green roofs and surrounding greenspaces (Droz et al. 2022). Although the above studies provide vital insight into the community composition of mycorrhizal fungal propagule pools in cities, dispersed propagules may not be viable, reactive, or suited to the given site conditions to successfully establish (Bever et al., 1996; Chaudhary et al., 2020; Metzler et al., 2024; Oehl et al., 2009; also see Nara, 2009 and Peay et al., 2012 for examples in EM fungi). Therefore, studies investigating the dispersal *and* establishment process of various AM and EM propagule types are needed in urban ecosystems (Bueno and Moora, 2019; Chaudhary et al., 2020; Correia et al., 2019).

Dispersal and establishment of mycorrhizal fungi are impacted by fungal spore and reproductive characteristics. For instance, AM fungal spores collected on green roofs were smaller than the average spore size of all species currently described in the AM group (i.e., Glomeromycota), and species composition of spores also varied seasonally (Chaudhary et al., 2020). Comparable studies of EM spores have yet to be deployed in urban systems, but forest and global studies report that EM fungal species’ differences in spore sizes, reactivity, and seasonality also influences community composition (Abrego et al., 2024; Bruns et al., 2009; Gardes and Bruns, 1996; Kausered et al., 2011; Nara, 2009; Peay and Bruns,

2014). Further, EM fungi exhibit a wide diversity in sporocarp and spore morphologies adapted to different climatic conditions and dispersal mechanisms (Halbwachs et al., 2015), but how these variations in morphology impact dispersal in urban landscapes have not been addressed. One research gap worth addressing is how the distribution of EM species producing above versus belowground sporocarps varies across local greenspaces.

Another way to investigate mycorrhizal fungal dispersal and establishment in urban ecosystems is to study the impacts of urbanization on animal and human vectors. Long-term effects of urban fragmentation include the loss of many of the mammals, birds, and soil fauna (e.g., mites, springtails, slugs, etc.) that are critical for mycorrhizal fungal propagule dispersal across the landscape (Correia et al., 2019; Lamont et al., 1985; Nugent and Allison, 2022; Vašutová et al. 2019; Yates and Hobbs, 1997). For example, urban Australian bandicoots are important vectors of EM spores, but the diversity and abundance of EM communities they dispersed decreased with decreasing greenspace size (Hopkins et al., 2021). Humans also act as vectors for mycorrhizal fungi in cities by both the intentional inoculation of soil, garden plants, and trees, and the unintentional transport of mycorrhizal fungal propagules on clothing or translocated plant materials (Maltz and Treseder, 2015; Metzler et al., 2024; Stewart et al., 2024). However, how these human activities impact mycorrhizal community structure within and across cities is not often considered (but see Metzler et al., 2024) and should be investigated further.

Urban soil properties and processes that structure mycorrhizal fungal communities

Urban soils are generally classified as anthrosols or technosols, reflecting extensive human modification through the removal, addition, and mixing of soil horizons or the incorporation of artifacts and construction materials (Lehmann and Stahr, 2007). Within these broad categories, soil properties—such as texture, drainage, chemistry, and organic matter content—vary widely among cities and greenspace types (Hui et al., 2017; Lehmann and Stahr, 2007; Whitehead et al., 2021). Despite this diversity, extensive soil sealing for roads, buildings, and other infrastructure often leads to compaction, alkalinity, and altered soil-atmosphere interactions and horizon formation (Schmidt et al., 2017; Tatsumi et al., 2023; Zhang et al., 2023). Urban soils also tend to accumulate high concentrations of fertilizers, heavy metals, and persistent organic pollutants compared to rural soils (Cachada et al., 2012; Karliński et al., 2014; Korneykora et al., 2022; Schmidt et al., 2017; Tarvainen et al., 2003). Together, these properties broadly influence plant growth and microbial activity, yet their specific effects on mycorrhizal fungi remain poorly understood (Arnfield, 2003; Dou and Chen, 2021; Grzesiak, 2009; Weisskopf et al., 2010).

Soil sealing

Soil sealing—where soils are covered by impermeable materials—disrupts soil-atmosphere interactions and is one of the most pervasive processes shaping urban function. By physically separating above- and belowground compartments and compacting soils during construction, sealing reduces water and gas infiltration, pore volume, and aggregation, while increasing heat absorption and pH. In the short term, these changes suppress biological functions such as root growth, soil respiration, nitrification, and carbon mineralization, thereby altering microbial activity, diversity, and host plant responses (Arnfield, 2003; Dou and Chen, 2021; Grzesiak, 2009; Weisskopf et al., 2010; Zhang et al., 2023). Over longer time scales, soil sealing disrupts pedogenesis and the formation of distinct soil horizons, which may particularly affect mycorrhizal fungi adapted to specific soil layers (Bahram et al., 2015; Dickie et al., 2002; Hui et al., 2017). Empirical studies report declines in both AM and EM fungal colonization and diversity under sealed or compacted soils, alongside community shifts toward drought- and heat-tolerant taxa such as *Sclerocystis* (Grassi et al., 2023; Martinová et al., 2016). These community shifts are also influenced by host tree species or cultivar, with some hosts maintaining higher AM fungal colonization and abundance than others (Grassi et al., 2023; Torppa et al., 2023).

To disentangle host versus fungal responses, long-term studies incorporating diverse host plant species are needed. Furthermore, testing a range of semi-permeable sealing materials near walkways, medians, and parkways could guide city planners in improving infiltration, soil health, and mycorrhizal abundance.

Soil pH and nutrient levels

Across both global and urban contexts, soil pH is a key determinant of fungal community composition (Davison et al., 2021; Fernandez and See, 2025; Schmidt et al., 2017; Scholier et al., 2022). Urban soils tend to be neutral to alkaline due to topsoil removal and residues from construction materials. Elevated pH is often associated with reduced AM and EM colonization (Karpati et al., 2011; Wiseman and Wells, 2005), although some studies report no effect on AM fungi (Karliński et al., 2014). High-pH urban soils also show declines in mycorrhizal diversity and distinct community shifts compared to rural or forest soils (Karpati et al., 2011; Korneykova et al., 2022; Martinová et al., 2016; Olchowik et al., 2021; Timonen and Kauppinen, 2008; Sanchez-Tello and Corrales, 2024). Similarly, EM sporocarp diversity and richness decrease with increasing soil pH across urban and suburban sites (Ochimaru and Fukuda, 2007).

Beyond pH, nutrient dynamics such as nitrogen and phosphorus availability exert equally important but often contrasting effects on mycorrhizal communities. Nitrogen is frequently added to urban soils through fertilization, runoff, and atmospheric deposition from fossil fuel combustion. Although nitrogen can

increase fine root and mycelial production, it often weakens symbiotic efficiency and drives community shifts toward nitrophilic taxa (Treseder, 2004). Long-term European surveys attribute severe EM fungal declines to nitrogen deposition (Arnolds, 1991), and similar patterns are observed in cities (Baxter et al., 1999; Markkola et al., 1995; Ochimaru and Fukuda, 2007; Schmidt et al., 2017; Tarvainen et al., 2003; Tatsumi et al., 2023; Timonen and Kauppinen, 2008). For AM fungi, nitrogen also structures community composition (Guo et al., 2025), though responses vary with host identity (Xue et al., 2025) and city biome (Yu et al., 2022).

Phosphorus and soil organic matter (SOM) also vary widely across urban soils, often due to sewage inputs, runoff, or management practices. High phosphorus levels generally suppress mycorrhizal colonization and diversity (Karpatai et al., 2011; Martinová et al., 2016; Timonen and Kauppinen, 2008; Wiseman and Wells, 2005), though exceptions occur (Karliński et al., 2014; Tonn and Ibáñez, 2017; Whitehead et al., 2022). SOM strongly reflects management intensity and greenspace age and is positively associated with mycorrhizal diversity and colonization (Karpatai et al., 2011; Korneykova et al., 2022; Martinová et al., 2016; Scharenbroch et al., 2005). Low SOM typically coincides with lower fungal diversity, especially in temperate cities, although some high-latitude urban greenspaces maintain higher soil carbon than nearby rural forests (Korneykova et al., 2022). Collectively, the variable effects of nitrogen, phosphorus, and SOM highlight the need for broader sampling across underrepresented biomes that are driven by different nutrient limitations (see Figures 2 and 3).

Soil pollutants

Heavy metals enter urban soils primarily through industrial waste and traffic emissions, with variable consequences for mycorrhizal fungi and hosts. High metal concentrations generally reduce EM colonization and diversity (Baxter et al., 1999; Olchowik et al., 2021; Timonen and Kauppinen, 2008), yet may increase AM fungal diversity and abundance (Karliński et al., 2014; Whitehead et al., 2022). Some AM and EM fungi tolerate or accumulate metals, or increase the uptake of their hosts, enabling mycoremediation or phytoremediation applications (Blaudez et al., 2000; Bompadre et al., 2020; Demasi et al., 2018; Kafil et al., 2019; Karimi et al., 2011; Kokkoris et al., 2019; Rineau et al., 2010). Conversely, other mycorrhizal fungal taxa can reduce host metal uptake or induce physiological tolerance (Hachani et al., 2020; Riaz et al., 2021), underscoring the importance of selecting species suited to desired ecosystem services.

In addition to heavy metals, urban soil salinization represents another widespread chemical stressor with major implications for mycorrhizal associations. Elevated salinity typically decreases mycorrhizal

colonization and diversity (Dastogeer et al., 2020; Guerrero-Galán et al., 2009). Nonetheless, some mycorrhizal fungi confer salt tolerance to hosts by improving nutrient uptake and regulating ionic balance (Calvo Polanco et al., 2008; Dastogeer et al., 2020; Guerrero-Galán et al., 2009; Zwiazek et al., 2019). In cold cities where salinity is a recurring issue because of deicing agents, inoculating plants with locally adapted EM communities enhances seedling biomass and stress tolerance (Zwiazek et al., 2019; Thiem et al., 2018). These findings, along with the variable success of commercial inoculants (Koziol et al., 2024), emphasize the potential of developing locally sourced inocula for urban plant health and greenspace restoration. Future research should investigate whether mycorrhizal communities in arid climates can confer similar benefits to hosts irrigated with saline water sources.

Socio-cultural factors influencing resident engagement, relations, and access to mycorrhizal fungi in cities

Broad urbanization processes and contexts

Social and power dynamics broadly shape city development, including the distribution and quality of urban greenspaces (Poulton Kamakura et al., 2024; Walker et al., 2024a). Current studies often focus on aboveground patterns of habitat quality using publicly documented social metrics such as income or housing policy, but belowground characteristics—including those related to mycorrhizal fungi—remain largely unexplored (Alberti et al., 2003). For instance, correlations between tree cover and plant diversity with median income have been termed ‘luxury effects’ (Leong et al., 2018). While not universal (Kuras et al., 2020), such effects on mycorrhizal fungi are likely mediated by both individual and municipal capacity to manage greenspaces (Barak et al., 2020). Poulton Kamakura et al. (2024) developed the POSE framework (social Power, Objectives, Social context, Effort) to explain interdisciplinary questions about social factors and habitat quality in cities, and this approach could also illuminate patterns in urban soil and mycorrhizal biogeography.

Broad urbanization processes, including historical policies such as redlining and patterns of urban spread, further shape urban soils and greenspaces. Urban redlining disproportionately affects neighborhoods with high proportions of racial and ethnic minority residents by diverting investment, contributing to unequal soil pollution (Watson et al., 2022), water runoff (Hobbie et al., 2023), food access (Li and Yuan, 2022), tree cover (Locke et al., 2021), and overall biodiversity (Burghardt et al., 2022; Schell et al., 2020). Similar patterns likely influence mycorrhizal fungal reservoirs, but empirical data are scarce. Further, cities’ growth patterns influence the geometry of roads (Chen et al., 2024) and remaining greenspaces, affecting both soil sealing and habitat connectivity with implications for mycorrhizal dispersal. Future research should test hypotheses regarding differential impacts on EM and AM fungal diversity,

abundance, and dispersal, mediated by urban greenspace type along socio-economic gradients and between neighborhoods.

Income–biodiversity patterns are evident at multiple scales, down to tree size and age (Burghardt et al., 2022), highlighting the importance of management and jurisdiction. Tree care often occurs at individual residential scales, whereas new plantings for urban greening are typically managed at municipal levels. These multi-scale social processes likely influence mycorrhizal communities, as diverse host plant care supports mycorrhizal specificity (Leimar and McNamara, 2023; Steidinger and Bever, 2014; Bachelot and Lee, 2018). Practitioner tree selection also shapes EM and AM fungal distributions, indirectly influencing soil fertility (City of Chicago Bureau of Forestry, 2023; Zak et al., 2019). Understanding these multi-level social dynamics is essential for urban mycorrhizal research and for maximizing tree lifespan and ecosystem benefits (Salisbury et al., 2022; Stewart et al., 2024).

Human-plant-mycorrhizal interactions

There is growing interest in “les villes nourricières” (nourishing cities), where urban agriculture enhances local food production. Mycorrhizal fungi could support these goals through improved plant growth and health. Given that urban soils are often polluted with heavy metals, identifying mycorrhizal fungal–host plant pairs that minimize contaminant accumulation is critical. For example, AM fungi inoculated into carrots and leeks increased antimony accumulation but kept levels below national safety guidelines (Pierart et al., 2018). Future research should monitor commonly cultivated urban food plants to better understand mycorrhizal effects on growth, yield, and contaminant uptake (Baum et al., 2015).

Foraging for edible and medicinal sporocarps provides another important avenue for human–fungi interaction but is frequently overlooked by planners and researchers (Shackleton et al., 2017). Foraging can alleviate food insecurity, reduce waste, supplement income, support medicinal autonomy, and strengthen social and cultural connections (Marquina et al., 2021). It can also directly and indirectly influence fungal community structure through collective greenspace management—e.g., adding or removing mulch, leaves, or compost—which often has stronger effects than broader urbanization drivers such as temperature increases or nitrogen deposition (Schmidt et al., 2017). This highlights the importance of small-scale human interventions in structuring mycorrhizal communities and underscores residents’ potential to make meaningful ecological contributions. Accordingly, urban residents and researchers should better characterize city macrofungal (sporocarp-producing) communities for cultural, recreational, and biodiversity purposes, and assess sporocarp pollutant concentrations and toxicity to ensure safe foraging (Azeem et al., 2020; Kokkoris et al., 2019).

Collaborative biodiversity surveys and online citizen science platforms provide additional opportunities for environmental education and engagement. Events like BioBlitzes combine expert guidance with public participation to generate actionable insights into mycorrhizal ecosystems (Tiago et al., 2024). Platforms such as iNaturalist and Mushroom Observer document and expand knowledge of fungal biodiversity, including commonly foraged urban species (<https://fun-dive.eu/en/get-involved/current-projects/mission-urban-mushrooms/>). By enabling broader-scale, publicly accessible assessments, these initiatives foster stronger connections to urban biodiversity (Haelewaters et al., 2024; Shumskaya et al., 2023). Expanding participation is critical for filling knowledge gaps and developing localized, mycorrhizal-focused conservation projects (Haelewaters et al., 2024).

Addressing current limitations in urban mycorrhizal studies and sowing the spores for future research

Urban mycorrhizal fungal research has expanded in recent years, yet several methodological limitations continue to constrain synthesis and progress (Figures 2, 3, and 5). Vague site descriptions, strong geographical and bioclimatic biases, and a lack of repeat sampling or experimental designs all hinder comparability and reproducibility across studies. Site information ranges from minimal (e.g., Csizmár et al., 2023) to highly detailed (e.g., Guo et al., 2025), with most research concentrated in northern temperate and woodland/shrubland biomes (Dyson et al., 2023; Figures 2–3). This uneven coverage risks overrepresenting certain ecological patterns while obscuring others. More consistent, transparent reporting of site characteristics—including site access methods, vegetation type, and soil management—would improve the interpretability of urban datasets. Supporting researchers in underrepresented regions and biomes is also critical for addressing global knowledge gaps. In addition, roughly three-quarters of urban mycorrhizal studies are based on single time-point sampling, overlooking strong temporal variation in community composition, abundance, and function (Ávila et al., 2021; Jumpponen et al., 2010; Tyburska et al., 2013). Establishing multi-season or long-term datasets will be essential for capturing the dynamics of fungal communities in cities. Finally, the literature remains overwhelmingly descriptive—88 % of studies versus 12 % experimental (Figure 5). Expanding controlled and field-based experiments, particularly in nurseries or green infrastructure test sites, will allow researchers to identify the key abiotic and biotic drivers of fungal composition and function (e.g., Grassi et al., 2023).

Beyond methodological improvements, there is a need to conceptually reframe how we study mycorrhizal

fungi in urban ecosystems. Future research should integrate socio-cultural dimensions alongside biophysical processes to better understand how urban form, management, and inequality shape belowground biodiversity (Figures 4 and 6). Frameworks such as the POSE model (Poulton Kamakura et al., 2024), originally developed for aboveground urban biodiversity, could help explain how social power, objectives, and context influence soil quality and fungal communities. Exploring how these socio-cultural gradients affect mycorrhizal dispersal, growth, and mutualistic outcomes would connect urban ecological and social theory in meaningful new ways. This includes expanding sampling to underrepresented greenspace types—such as low-income neighborhoods, residential planters, and commercial planting areas—where management intensity, plant composition, and resource inputs differ markedly from urban parks or forests (Gadsen et al., 2023).

Finally, advancing the field requires a sharper focus on mycorrhizal function across spatial scales. Key unknowns include whether fungal networks can persist and disperse beneath pavement, how sporocarp production and sporulation respond to fragmentation, and which environmental or management factors promote specific ecosystem services. Experimental work could test functions such as soil aggregation, nutrient and water transfer, plant stress tolerance, and pathogen resistance under varying soil and host conditions. Understanding these processes will enable researchers to provide evidence-based recommendations to city planners, landscape professionals, and residents, helping to align local soil management with broader ecological and social goals. Cultivating such integrative approaches will ultimately empower communities to design and sustain resilient, biodiverse urban soils.

Conclusions

Here, we highlight key gaps in the scientific understanding of mycorrhizal fungal communities and their roles in urban ecosystems. This review synthesizes the main environmental and social factors shaping urban mycorrhizal fungi, including host plant composition and distribution, greenspace configuration, fungal dispersal, and soil properties such as pH, nutrient availability, and pollutant concentrations. We also emphasize how socio-cultural processes—governing urban development, resource allocation, and greenspace management—influence human–plant–mycorrhizal relationships.

Persistent limitations in the current literature constrain progress in this field. Researchers should provide more detailed site descriptions, clarify land access and management histories, and expand studies to include southern hemisphere cities and underrepresented biomes. Increased temporal resolution through higher-frequency and longer-term sampling will help capture community dynamics across seasons and disturbance gradients. Moreover, experimental studies are critically needed to test mycelial growth

beneath pavements, dispersal, quantify fungal contributions to host nutrient uptake and stress tolerance, and assess enzyme production and substrate utilization relevant to soil remediation.

Finally, advancing urban mycorrhizal research requires integrating biophysical and socio-cultural perspectives. Environmental drivers and biological interactions in cities unfold within the broader social and political contexts that shape land use, accessibility, and ecological stewardship. Understanding how these intertwined processes influence mycorrhizal fungi—the unseen foundation of many urban ecosystems—is essential for designing resilient greenspaces. Greater attention to these fungi will enhance the capacity of cities to sustain multifunctional green infrastructure and foster coexistence among people, plants, and microbes.

Acknowledgements

This work was funded with grants from the Jeremy and Hannelore Grantham Environmental Trust, Paul, Allen Family Foundation, Bezos Earth Fund, Schmidt Family Foundation (JDS, ETK), NWO Gravity Grant MICROP [024.004.014] (JDS, ETK), NWO-VICI [202.012] (ETK), an Ammodo grant (ETK), SPINOZA (ETK), and a US Department of Energy award #DE-SC0023480 (MLM).

Author Contributions

KP and CD compiled and analyzed studies on urban mycorrhizal fungi. KP drafted the initial manuscript and NM, NR, JS, AC, VBC, TK, MG, MLM, and CD. contributed substantive revisions and comments. NM, NR, JS, and AC each authored and revised subsections within the socio-ecological section. Figures were prepared by KP and JD.

Data Availability Statement

Data used in this study are derived from resources in the public domain. A list of all studies compiled along with citations are available in SI Table 1.

Conflict of Interest Statement

The authors declare no conflict, financial or otherwise, that might be perceived as influencing the objectivity of this work.

Figures and legends begin on next page

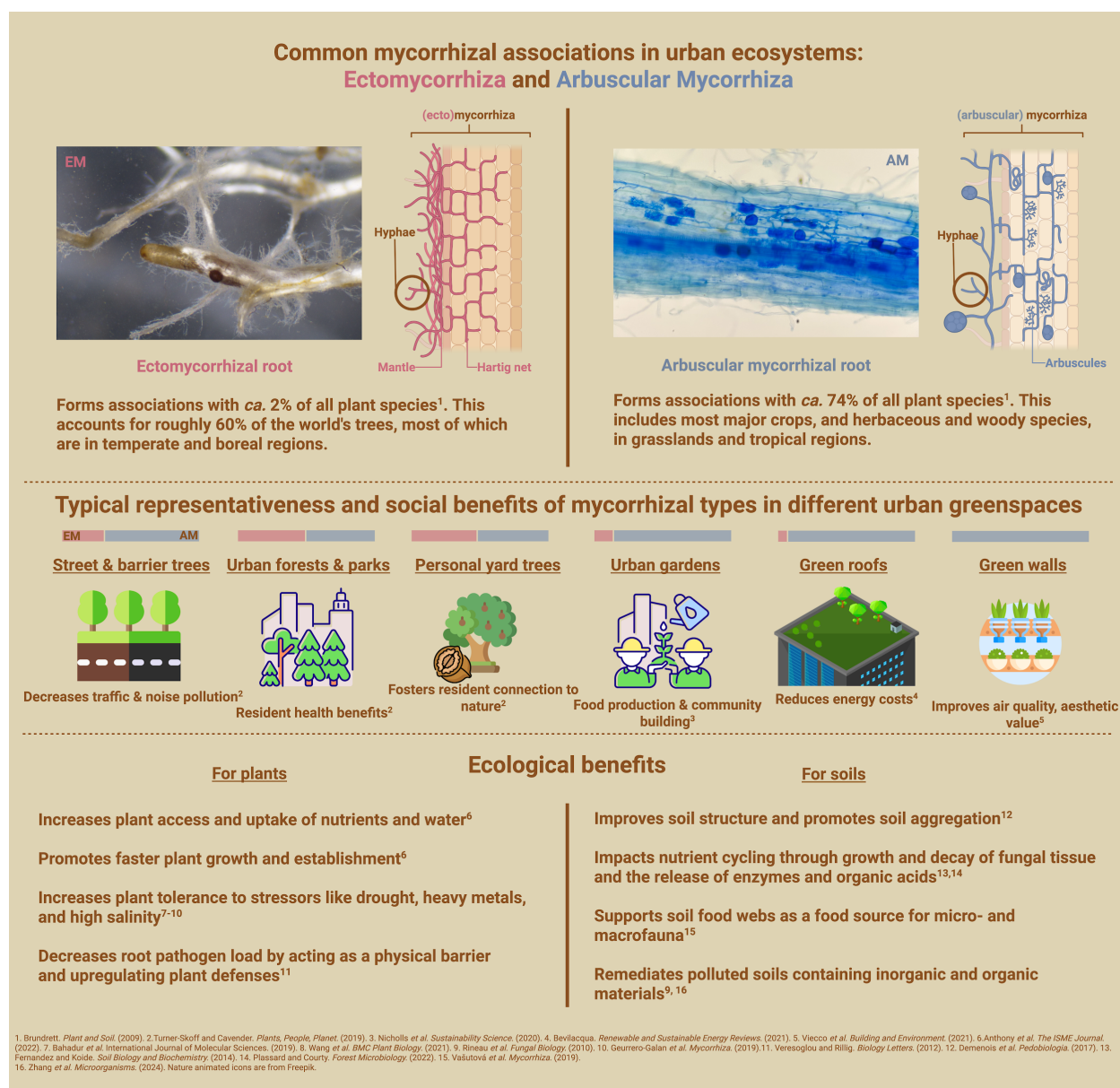


Figure 1. The two main types of mycorrhizal fungi associated with plants in urban ecosystems and their respective benefits across greenspaces. Ectomycorrhizal (pink) associations occur primarily in greenspaces dominated by woody plants, whereas arbuscular mycorrhizal (blue) associations are widespread across urban landscapes. Ratio bars above each greenspace indicate the typical relative abundance of each mycorrhizal type, which is largely shaped by planting choices (e.g. plant species that associate with arbuscular mycorrhizal fungi are often selected for street trees, gardens, and green roofs). Ratios are estimated from the literature and represent general trends rather than exact proportions. Social benefits of both mycorrhizal types are shown below the greenspaces, and ecological benefits for plants (left) and soils (right) are listed at the bottom of the figure.

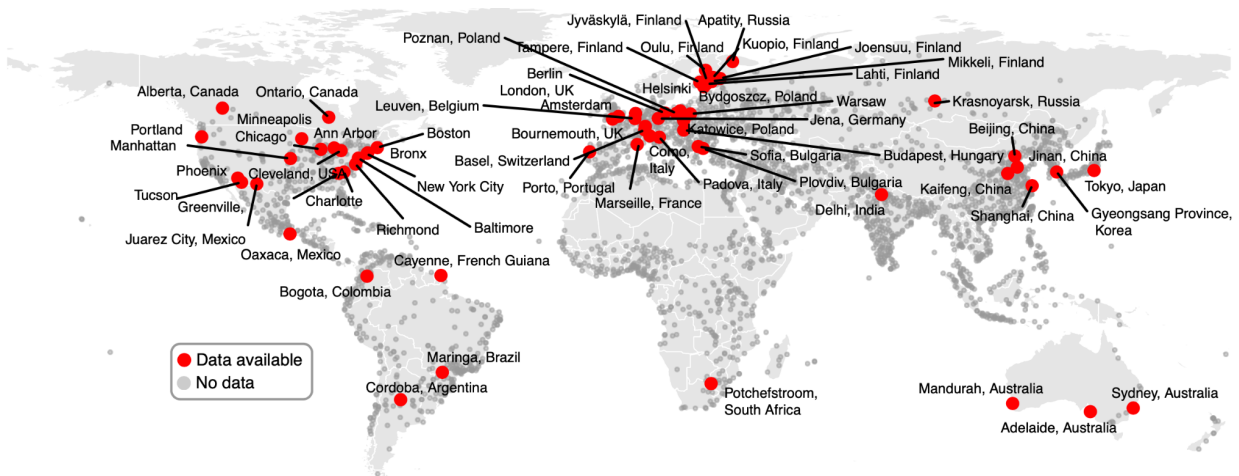


Figure 2. Global distribution of urban areas where mycorrhizal fungi have been studied. Red points indicate cities with existing surveys ($n = 72$; Table S1), while grey points represent cities with populations exceeding 100,000 that remain unstudied ($n = 7,342$). A subset of selected study locations are shown with text labels to highlight geographic spread; the full list is available in Table S1. The map was produced using the *rNaturalEarth* database in R (v4.2).

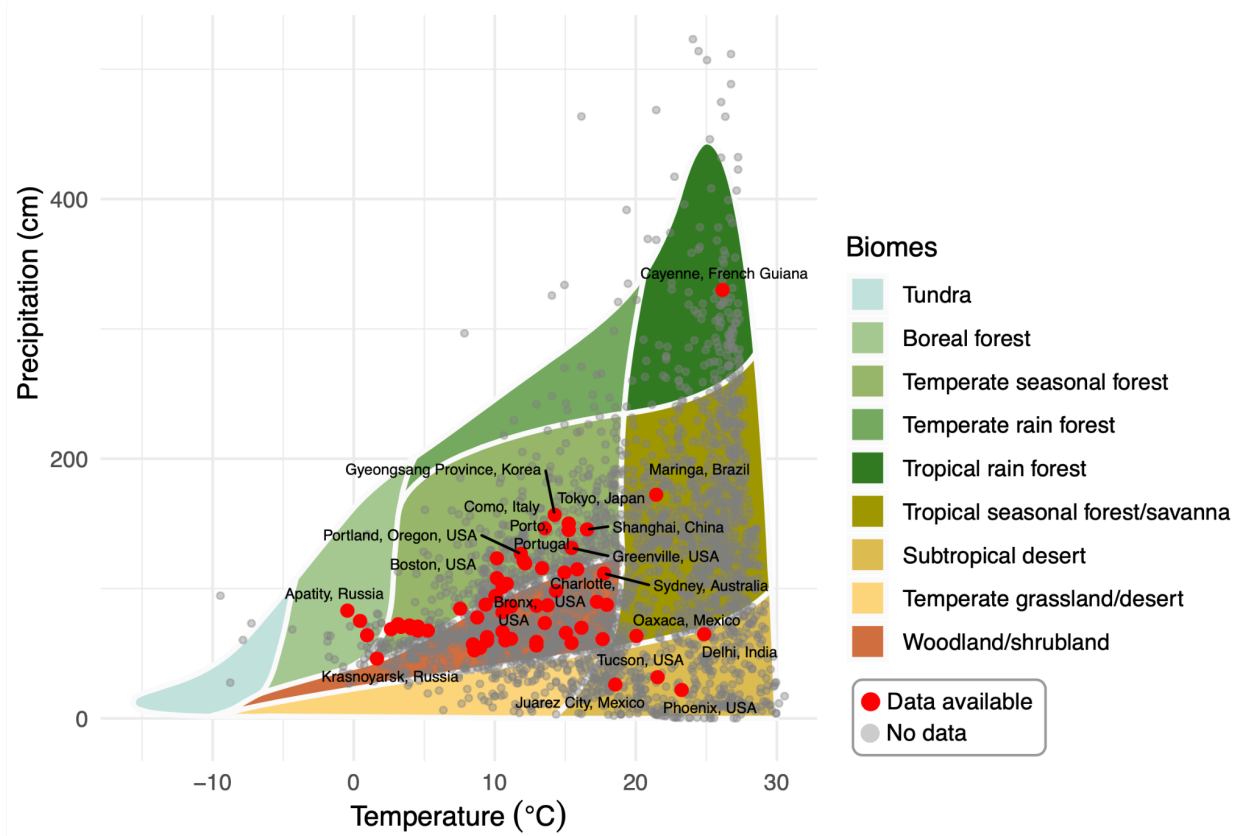


Figure 3: Bioclimatic distribution of cities studied for mycorrhizal fungi. Background colors represent Whittaker's biome classification. Red points mark cities with available mycorrhizal data (Table S1; sixteen of the 72 are labeled for illustration), while grey points denote global cities with populations above 100,000 lacking such data ($n = 7,342$). Axes show mean annual temperature ($^{\circ}\text{C}$, x-axis) and annual precipitation (mm, y-axis). Climatic data were obtained from the CHELSA dataset, and city locations from the *rNaturalEarth* database.

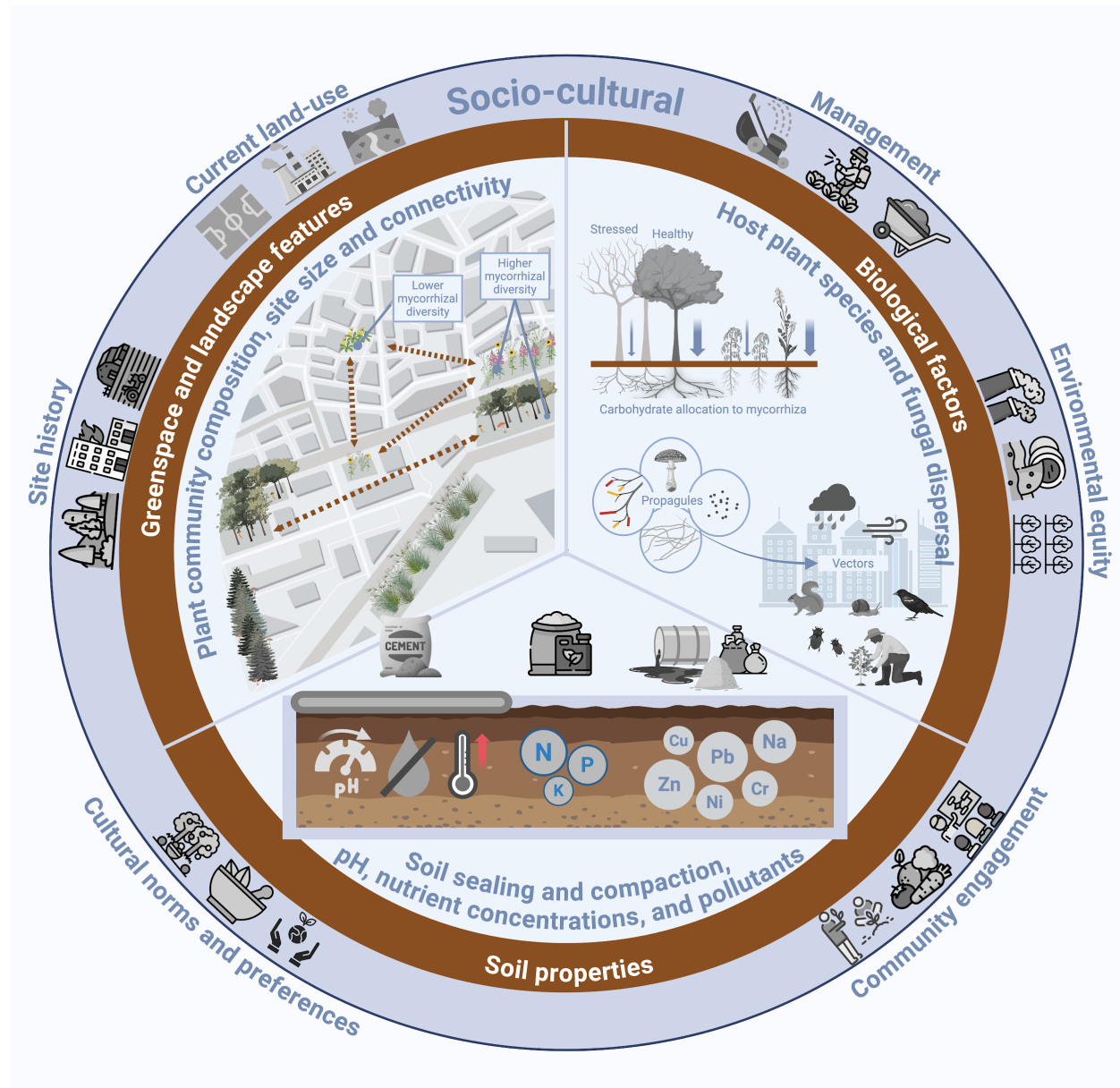


Figure 4. Socio-cultural factors interacting with greenspace characteristics, biological traits, and soil properties to shape mycorrhizal fungal communities in urban ecosystems. Key socio-cultural influences include site history (e.g. disturbance intensity and frequency), current land use or greenspace type, and environmental equity (e.g., distribution of biodiversity and pollutants). Additional influences involve management resources and practices, cultural norms and preferences (e.g. plant selection, aesthetics, ethnobotanical practices, and values surrounding nature and stewardship), and public engagement with greenspaces (e.g. community tree planting, urban gardening, and ecology education). These factors drive patterns of urban development that affect plant community composition and the size and connectivity of greenspaces. Larger patches often support greater plant and fungal diversity but tend to be more isolated

(dashed arrows, upper left). Biological factors include host plant tolerance to urban stressors and fungal dispersal. Poorly adapted hosts typically exhibit lower mycorrhizal diversity and colonization, likely due to reduced carbon allocation to roots and fungal partners (blue arrows, upper right). Dispersal occurs via spores, root fragments, hyphae, and sporocarps that are transported by water, wind, animals, and humans—vectors whose behavior and distributions are altered by urban infrastructure, heat islands, and habitat fragmentation. The effects of these changes on fungal dispersal remain poorly understood. Urban soils are modified by sealing, chemical inputs, and pollutants, leading to higher pH, temperature, nutrient loads, and heavy metal concentrations, alongside reduced moisture and gas exchange. These changes generally reduce mycorrhizal colonization, diversity, and abundance, though impacts vary by site, underscoring the need for context-specific assessment in research, design, and management.

STUDIES ON MYCORRHIZAL FUNGI IN URBAN ECOSYSTEMS

SAMPLING FREQUENCY

Studies that sampled across more than a single time period.



25%
18/72 studies

STUDY DESIGN

Studies that designed experiments testing mycorrhizal fungal responses within urban ecosystems or to urban stressors.



13%
9/72 studies

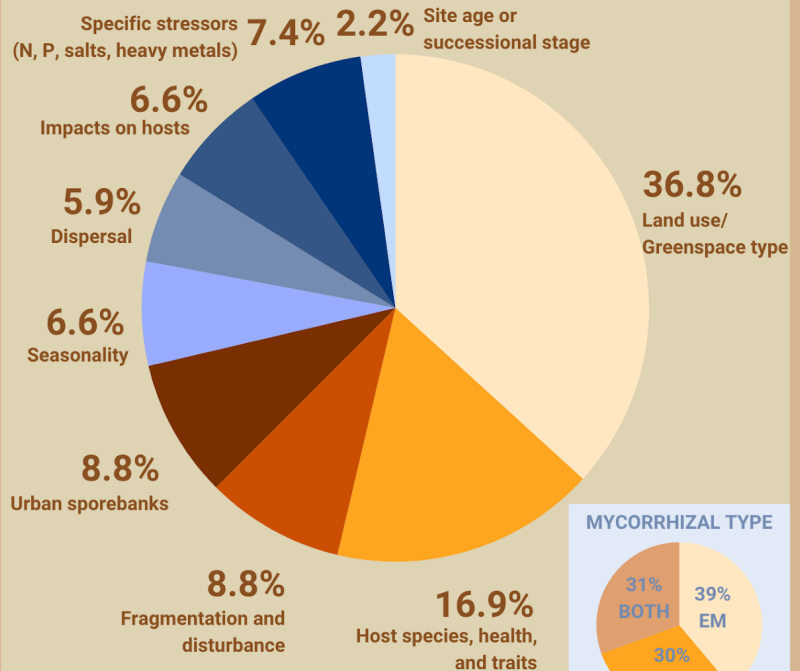
COMMUNITY SHIFTS

Studies that compared mycorrhizal communities between urban and rural sites, or between greenspace types.

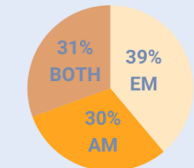


68%
49/72 studies

STUDY FOCI



MYCORRHIZAL TYPE



Studies most often report decreases in colonization, abundance, and richness when comparing urban sites with rural reference sites, though the magnitude of reductions can vary across site ages, host species, and cities.

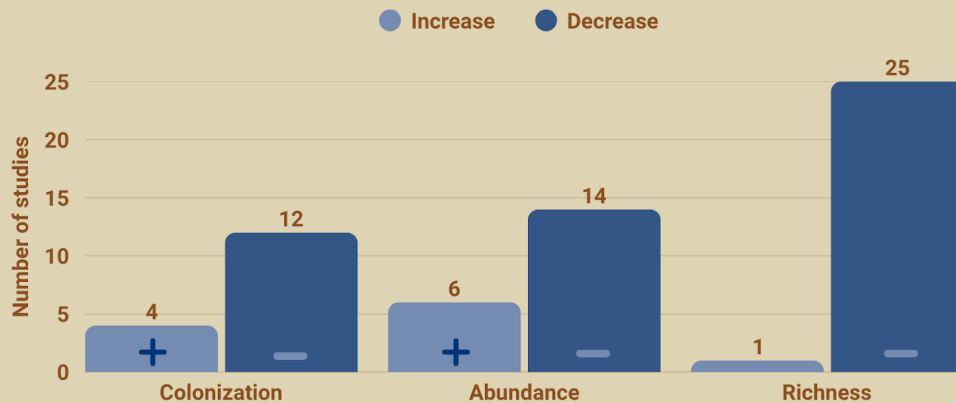


Figure 5. Summary of studies on mycorrhizal fungi in urban ecosystems: study designs, main foci, and findings. Sampling frequency, study design, and community shifts — Percentages of studies that sampled across multiple time points, conducted experiments (vs. descriptive surveys), and compared community composition or shifts between sites (n = 72; see Table S1). Study foci — Percentages of studies addressing nine common themes: land use/greenspace type; host plant species, health, and traits; fragmentation and disturbance; urban sporebanks; seasonality; dispersal; impacts on host plants; specific urban stressors; and site age or successional stage. Some studies appear under multiple categories due to overlapping aims. Mycorrhizal type — Percentages of studies focusing on different mycorrhizal associations. Findings — The bar chart (bottom) shows numbers of studies reporting increases (light blue, “+”) or decreases (dark blue, “–”) in mycorrhizal colonization, abundance, or richness in urban versus non-urban sites.

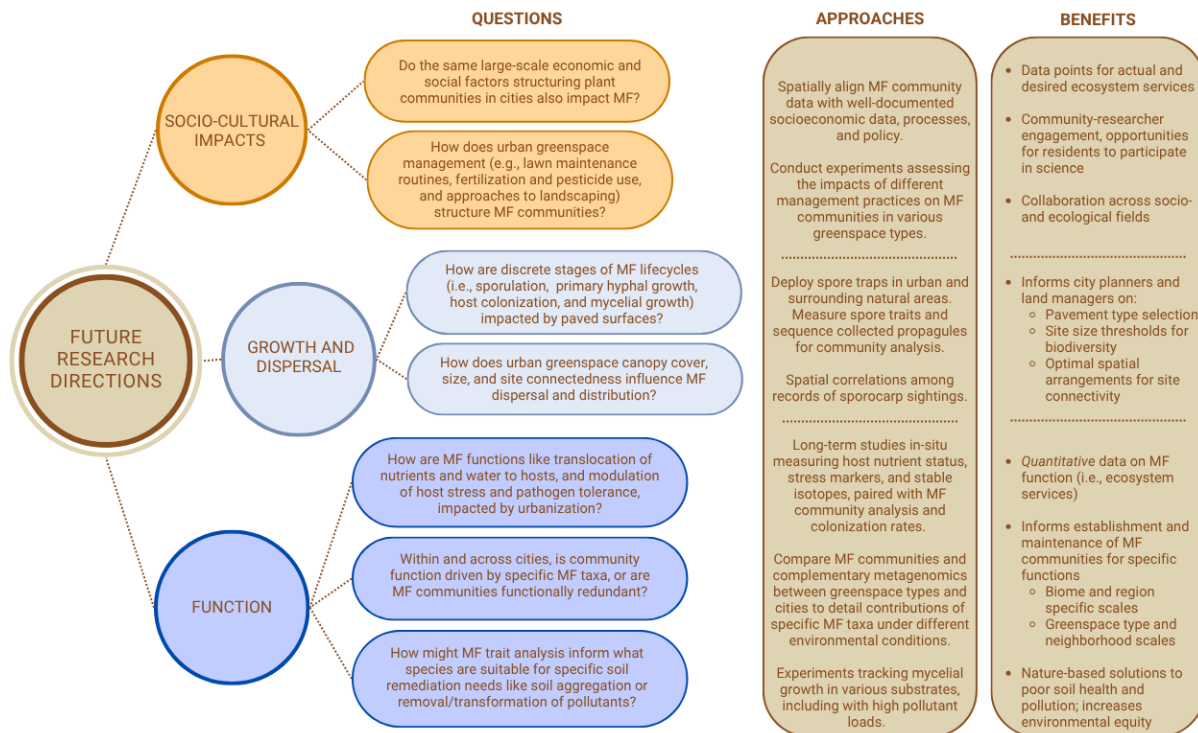


Figure 6. Future research directions, approaches, and anticipated benefits for studying mycorrhizal fungi (MF) in urban ecosystems. Research priorities include socio-cultural impacts, growth and dispersal, and functional roles of MF. These themes intersect, and projects can integrate questions (colored ovals) across multiple areas. Each research question aligns with specific approaches (left column) and expected benefits (right column). Approaches include spatial mapping of MF communities alongside resident demographic and site data; sampling fungal propagules and sporocarps; physiological measurements of nutrient and water exchange and host plant health (e.g. stable isotope tracing, nutrient assays, and biomass metrics); and molecular analyses such as metagenomics. Anticipated benefits include improved understanding of fungal contributions to cultural and ecological ecosystem services, greater environmental equity through enhanced plant and soil health, and expanded opportunities for community–researcher collaboration and interdisciplinary work. Findings will support urban planning and land management practices while deepening knowledge of MF community ecology and functioning in urban ecosystems.

Supporting Information Table 1. *Summary of 72 studies on mycorrhizal fungi in urban ecosystems reviewed in this article.* For each study, the table lists the lead author and publication year, study location, mycorrhizal (Myc) type, sample type, methods, hypotheses, and main findings. Studies marked with a section sign (§) collected samples at multiple time points. Mycorrhizal type is categorized as arbuscular (AM), ectomycorrhizal (EM), or both. Sample type indicates the fungal tissue or substrate analyzed (root, soil, sporocarp, spore, mycelium, or scat). Methodological approaches and summarized hypotheses are provided for context. In the Findings column: “–/+” denotes a decrease or increase, respectively, in community richness (R), abundance (A), or colonization (C). Shifts in community composition are indicated with an obelisk (†), and shifts toward specific taxa are marked with a double dagger (‡). Studies that did not report R, A, C, or composition data are denoted as “NA.” Table included in supplementary data.

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