Harnessing Soil Microbiomes for Creating Healthy and Functional Urban Landscapes

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Abstract

Urban soil microbiomes are attractive interventional targets for creating healthy and functional urban landscapes. In this chapter, we introduce molecular meta-omics techniques that can be used to study the composition and functioning of such microbiomes in a high-throughput and culture-independent manner. We highlight studies in which such approaches have been applied to soil microbiomes in both natural and managed ecosystems. We then discuss how data from such approaches can be interpreted using ecological frameworks and discuss how such information can in turn be used to develop sustainable solutions for managing urban landscapes and increasing the productivity of urban agroecosystems.

Keywords

Soil · Soil microbiome · Urban landscapes · Sustainability · Multi-omics

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17.1 Introduction

By 2050, more than two-thirds of the world's population will reside in urban areas (United Nations 2014). Creating healthy and functional urban landscapes capable of supporting such a population is therefore a global priority. A vast majority of urban landscapes have soils as their foundational basis which in turn are extensively modified and actively managed to provide a multitude of services for urbanites. They support infrastructure, green cover, cycle nutrients, regulate runoff and act as a sink for pollutants (Wall et al. 2012). In recent years, efforts have renewed to utilize urban soils for developing sustainable urban agroecosystems to produce fresh and nutritious vegetables for local consumption (Toju et al. 2018). Yet, we understand little about the biological diversity that underpin the provision of most such services. This is in part due to the widely held assumption that urban soils have been modified to such an extent that they lack the ability to support species-rich biological communities. However, studies in recent years have convincingly shown that urban soils support complex communities of macroorganisms (such as plants and insects) and microorganisms (such as bacteria, archaea, and fungi) that actively interact to drive ecological processes (McGuire et al. 2013; Ramirez et al. 2014). This observation has prompted scientists and policy makers alike to analyze how such communities function and in turn how such information can be leveraged to manage and manipulate entire biological communities for applicable benefits.

Typically, microorganisms vastly outnumber macroorganisms in most ecosystems and exist as complex communities termed as microbiomes (Flemming and Wuertz 2019). In natural ecosystems, soil microbiomes have been shown to possess the requisite genetic machinery to regulate soil carbon stocks, cycle essential plant-nutrients, confer resistance to plants from invasive pathogenic microorganisms, and degrade pollutants (Bell et al. 2016; Fierer 2017; Schimel and Schaeffer 2012; Van Der Heijden et al. 2008). Pioneering efforts have revealed that urban soil microbiomes can be highly diverse and can comprise several novel microorganisms (Ramirez et al. 2014). In addition to being species-rich, molecular surveys have shown that urban soils harbor genetic novelty of medical and biotechnological relevance not found in other ecosystems (Charlop-Powers et al. 2016). Although these observations highlight the tremendous potential of soil microbiomes as interventional targets, they remain to be systematically explored across different urban landscapes.

Here, we outline strategies for studying different facets of species-rich urban soils and discuss scientific challenges specific to the molecular investigation of entire soil microbiomes. We then highlight how such information can be leveraged to manage microbiomes in urban landscapes with a view to optimize the provision of microbiome-mediated ecosystem services and for developing novel microbial solutions that can increase the productivity of urban agroecosystems in a sustainable manner.

17.2 Disentangling Soil Microbiomes Using Molecular Meta-Omics

The highly diverse nature of soil microbiomes in general and our current inability to culture the vast majority of its members mean that we require approaches that enable us to study them at a high resolution and in a culture-independent manner. Molecular meta-omics approaches allow us to do this and encompass a wide range of techniques that can be used to study different facets of entire microbiomes. Typically, such techniques involve the extraction of biomolecular fractions (DNA, RNA, proteins, and metabolites) directly from environmental samples and profiling them using either high-throughput sequencers or mass spectrometers (Franzosa et al. 2015).

While, such techniques have been successfully applied to study diverse environmental and host-associated microbiomes, their efficacy is often limited when it comes to examining soil microbiomes. For example, the activity of ribonucleases—enzymes that degrade nucleic acids—are often elevated in soils in comparison to other systems (Keown and Greenfield 2004) which in turn prohibit a representative fraction of DNA or RNA from being obtained under standard sampling and laboratory working conditions. Similarly, the co-extraction of such enzymes and a milieu of other chemicals present in the soil matrix can limit downstream steps such as PCR amplification (Schrader et al. 2012) or analyte separation using liquid chromatography (Bundy et al. 2009). In addition to such analytical challenges, the amount of data required to capture the diversity of soil microbiomes is often large which in turn necessitates high-end computational infrastructure (Kyrpides et al. 2016) that is not commonly available to the vast majority of scientists. Addressing these issues requires new considerations when using individual techniques as well as designing studies that integrate multiple techniques. In the following sections, we outline the utility of such techniques for studying different aspects of the urban soil microbiome and also highlight challenges specific to each technique.

17.3 Quantifying Microbiome Composition and Function Using Metagenomics and Metatranscriptomics

Characterizing microbiome composition (identities of resident microorganisms and their relative abundance within the community) is typically the first step in any study that seeks to either understand the role of microbiomes under a given context or how they can be managed for applicable benefits. This can be accomplished using a technique termed metagenomics which involves the direct recovery of DNA from samples, fragmenting them into short pieces and profiling millions of such fragments in a random fashion using high-throughput sequencers (Fig. 17.1). The identity of different microorganisms is inferred by matching the nucleotide sequences of these fragments to sequences in reference databases. The relative abundance of the different microorganisms can then be deduced by calculating the number of times

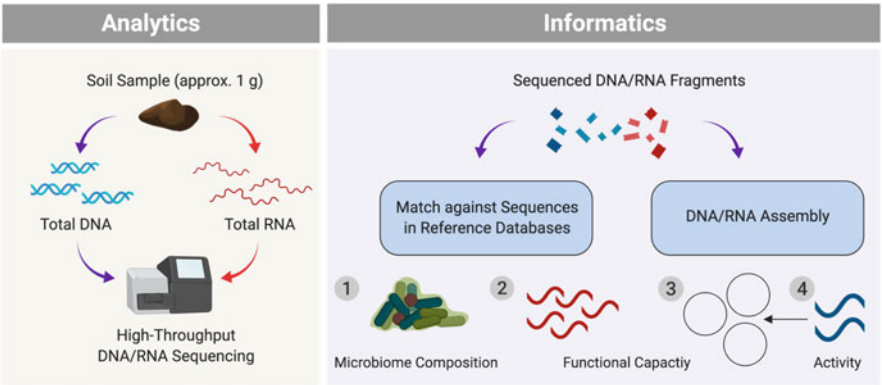

Fig. 17.1 Analytical and informatics workflow for metagenomics and metatranscriptomics. Total DNA/RNA is recovered from soil samples, fragmented, and characterized using high-throughput sequencing. Sequenced fragments are processed in two ways. By matching DNA fragments to sequences in reference databases, information of microbiome composition (*1*) and collection of genes (*2*) can be obtained. Collection of transcripts (*2*) can be obtained in a similar fashion. By assembling DNA fragments and binning them, one can obtain a collection of genomes (*3*), often termed metagenome assembled genomes (MAGs). In a similar fashion, entire transcripts can be assembled (*4*) and mapped back to MAGs to infer organismal origin

each fragment assigned to a particular microorganism occurs within the dataset. In addition to providing information on the identities of the different microorganisms, nucleotide sequences also provide information about the entire collection of genes that exist within the microbiome under study.

Examining collections of genes is not necessarily the objective of studies which seek to examine only the composition of microbiomes, in which case, sequencing single genes or regions of such genes which can act as a reliable molecular marker for different microorganisms can be pursued. In the case of microbiomes, this marker is typically the gene encoding for the small sub-unit of the 16S/18S rRNA. Entire genes or regions of such genes are selectively amplified from a sample's DNA pool (in its entirety) prior to sequencing. Identities of different microorganisms and their abundances are inferred in a manner similar to the one outlined earlier. Since this approach only involves the sequencing of amplified targets, it should not be confused with metagenomics. However, it is frequently included under the umbrella of metagenomic techniques as a way to examine microbiome composition. Using this approach, the earth microbiome project, one of the largest scientific collaborative efforts in recent times to catalogue the earth's microbial diversity revealed that soils around the world are highly diverse and are largely composed of oligotrophic microorganisms. By correlating microbial community diversity with environmental factors such as pH and temperature, this work also highlighted that soil diversity is highest in regions with a relatively low mean temperature (about 10 °C) and at near neutral pH (around 7) (Thompson et al. 2017). Therefore, in addition to revealing microbial community composition, the utility of this approach can be expanded by

coupling it with associative statistical modeling to reveal environmental markers that structure such communities.

As noted previously, metagenomic techniques also provide information about the entire collection of genes which exist within the microbiome under examination. Gene identities and abundances can provide insights into a microbiome's collective functional capacity. For example, soil microbiomes in New York's central park were shown to harbor several novel gene clusters encoding for natural products of biotechnological relevance through a targeted metagenomics approach (Charlop-Powers et al. 2016). However, a more powerful approach comprises the assembly of short DNA fragments into longer ones termed contigs which can subsequently be separated into metagenomic bins each of which provide a strong working hypothesis about the genomes of individual microorganisms. This approach thus allows one to link the identity of microorganisms to their functional capacity which otherwise cannot be obtained just by examining collections of genes. Using this approach, the capacity to degrade lignocellulose in forest soils was found predominantly within the members of the family *Caulobacteraceae,* highlighting their potential importance in contributing to decomposition processes in such ecosystems (Wilhelm et al. 2019).

Although metagenomics is a powerful technique for characterizing the composition and functional capacities of microbiomes, it does not quantify their activity. A direct measure of the functional activity of microbiomes can be obtained by quantifying either RNA transcripts, proteins, or metabolites. In a technique termed metatranscriptomics, the entire set of RNA produced by a microbial community is recovered directly from samples, converted to cDNA, and profiled in a manner similar to metagenomic techniques. As such, the identity and abundance of different transcripts in itself provides rich information on microbiome functioning; however, the utility of such information is enhanced when transcripts are mapped back to genomes thereby linking activity to different groups of microorganisms. For example, this approach revealed the important role of viruses in regulating the carbon cycle within peatland soils. Specifically, viral transcripts recovered using metatranscriptomics were mapped back to viral genomes assembled from metagenomics data, thereby allowing the identification of the active subset as well as genomic features linking them to microbial populations involved in carbon turnover. Moreover, such viruses were also found to both encode and express genes involved in complex carbon degradation suggesting a direct role in cycling carbon within such ecosystems (Emerson et al. 2018).

Despite the tremendous utility of such techniques, applying them to examine more complex facets of soil microbiomes still remains a challenge. For instance, high microbial diversity that typify most soils mean that extensive sequencing data is required for obtaining a meaningful representation of the community. Shallow sequencing data precludes the assembly of genomes of most microorganisms which exist in low proportions within such microbiomes (Howe et al. 2014). Further, the high levels of genetic novelty that exist within soil microbiomes mean that only a minor fraction of metagenomes and metatranscriptomes can be annotated using current databases (Delmont et al. 2012). However, given the potential of such techniques, we expect the development of new approaches which address these

challenges thereby enabling a more holistic examination of the composition and functioning of soil microbiomes.

17.4 Quantifying Functional Activity of Microbiomes Using Metaproteomics and Metabolomics

Regulatory phenomena at the community level are often mediated by sets of different proteins and metabolites. Therefore, their characterization using high-throughput methods termed metaproteomics and metabolomics, respectively, can provide complementary insights into the functioning of entire microbiomes (Fig. 17.2). Proteins and metabolites can be directly retrieved from samples in a manner similar to the recovery of nucleic acids. However, as opposed to the characterization of nucleic acids using next-generation sequencing techniques, proteins and metabolites are profiled using liquid chromatographs coupled with mass spectrometers which together provide readouts on their mass and abundance. Similar to shotgun sequencing techniques, proteins and metabolites are fragmented prior to characterization in order to provide accurate readouts. Fragmentation patterns can reveal the peptide sequence of proteins, while in the case of metabolites they provide information on their chemical composition and structure. Putative identities of proteins are then inferred by matching peptide sequences to proteins in reference databases using homology-based searches, while those of metabolites are inferred by matching fragmentation patterns of mass features to those of metabolites in curated databases. Abundances of proteins and metabolites can be subsequently inferred in a manner similar to metagenomics or metatranscriptomics.

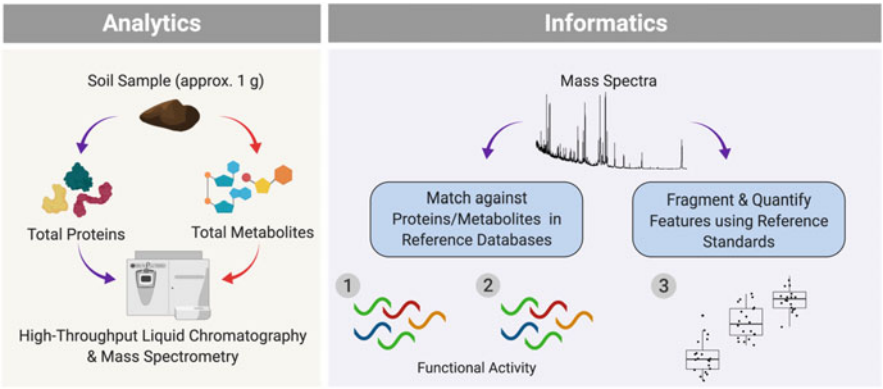

Fig. 17.2 Analytical and informatics workflow for metaproteomics and metabolomics. Total proteins/metabolites are recovered from soil samples, fragmented, and characterized using high-throughput chromatography coupled with mass spectrometry. Putative identities of mass fragments are then inferred by matching them against proteins/metabolites in reference databases (*1, 2*). Absolute quantification of metabolites (*3*) can be pursued by further fragmenting mass features of interest and quantifying such fragments using mass spectrometry (MS/MS)

Using a semi-quantitative metaproteomics approach, the vast majority of extracellular hydrolytic enzymes (such as cellulases and chitinases) involved in forest litter decomposition were shown to be of fungal origin (Schneider et al. 2012), highlighting the importance of fungi in the functioning of forest soil ecosystems. Such an approach can also reveal the physiological adaptation of microbiota to different environmental conditions. For instance, the vast majority of microorganisms in the arctic permafrost were found to express cold shock proteins presumably helping them survive under frozen conditions (Hultman et al. 2015). In addition to its individual utility, combining metaproteomics with complementary approaches such as metagenomics can offer powerful insights into microbiome functioning that cannot be obtained otherwise. For example, using a combination of metagenomics and metaproteomics, methanol-based methylotrophy in the rhizosphere of rice plants was shown to be mainly driven by the activity of bacteria linked to the genus *Methylobacterium*. In addition to helping link proteins involved in this process to specific groups of microorganisms, metagenomics substantially improved the identification of a broad range of other proteins not found in reference databases (Knief et al. 2011), further highlighting the utility of such integrative approaches.

Similarly, complementary insights into the functioning of microbiomes can also be obtained using metabolomics as well as by integrating it with other omics approaches. For example, field observations and experiments with soil isolates showed that the biological diversity of soil biocrusts were maintained in part by the capacity of resident microbial populations to utilize different classes of metabolites released by the dominant primary producer (Baran et al. 2015; Swenson et al. 2018). This was accomplished using an exometabolomics approach which characterizes the set of metabolites secreted by biological entities into their surrounding environment. Using a combination of metabolite profiling and 16S rRNA gene amplicon sequencing, benzoxazinoids, a class of defensive secondary metabolites released by plant roots were shown to significantly alter the composition and functioning of rhizosphere microbiomes which in turn impacted plant performance (Hu et al. 2018).

While the utility of metaproteomics and metabolomics for quantifying the functional activity of microbiomes is clear, their application for characterizing the functioning of soil microbiomes remains a challenge. For example, innate properties of soils (such as high salt concentrations) reduce their compatibility with standard practices in metaproteomics and metabolomics (Beale et al. 2016). They also share several challenges with techniques such as metagenomics and metatranscriptomics; for instance, reference databases currently only capture a minor fraction of the biological novelty often encountered in soils. However, given the tremendous potential of such techniques to improve our understanding of soil microbiome functioning, we expect continuation of efforts to develop new practices that address these challenges as well as the application of these techniques under new contexts.

17.5 Leveraging Molecular Meta-Omics Information for Developing Sustainable Solutions

Molecular meta-omic techniques can provide rich descriptors of microbial communities; however, the utility of such information for developing sustainable solutions depends on our ability to interpret them within a framework which can yield insights into the relationships between microbiomes and the ecosystem. A number of studies have shown that the application of ecological principles offers a powerful framework for obtaining such insights. In the following sections, we highlight how such ecological principles can be used to interpret multidimensional meta-omics data in order to develop sustainable solutions for managing soils in urban landscapes and creating highly productive urban agroecosystems.

17.6 Crafting Sustainable Urban Landscape Management Regimes

Urban landscapes with soils and vegetation as their foundational basis commonly comprise of lawns, parks, gardens (including thematic ones and roof-tops), road-side kerbs, and waterways. Management measures typically focus on maintaining soil health, establishing and sustaining target vegetation at optimal states, managing pests (including weeds and insects), and reducing greenhouse gas emissions. Ecological studies in natural soil systems have convincingly shown that soil microbiome functioning impact processes which determine such outcomes and thus make them attractive targets for planned interventions that aim to maximize desirable benefits.

To maximize desirable microbial functions, a thorough overview of the different microorganisms that exist within soil microbiomes and their functional traits is a prerequisite. This can be accomplished by surveying soils across different landscapes using amplicon sequencing and shotgun metagenomics. The measurement of environmental factors (such as pH, temperature, and landcover) is equally important as this will allow the identification of key drivers that structure such communities and in turn populate the list of modifiable factors that can be subsequently used to steer microbiomes to desirable states. In addition to such surveys, manipulative field experiments can also offer such insights. Data from such studies can be interpreted using the ecological framework on microbial community types which deals with the identification of strongly recurring patterns based on microbiome composition (Gonze et al. 2017). Such patterns have been identified, for instance, across different microbial habitats in the human body including the gut (Arumugam et al. 2011), vagina (Ravel et al. 2011), and the oral cavity (Ding and Schloss 2014). Studies have convincingly shown that communities can switch configurations and by extension functioning in response to changing environmental factors. By extension, soil microbiome datasets either from different urban landscapes or manipulative field experiments should be explored for the existence of such community types and its key drivers. This can be done by first clustering samples based on microbiome composition inferred using amplicon data; second,

exploring the functional trait composition of such community configurations using metagenomics; and finally correlating this information with environmental factors or the treatments being studied. However, it should be noted that the separation of community types based solely on composition does not necessarily imply a difference in their functioning due to functional redundancy. This therefore necessitates quantifying functional activity using metatranscriptomics to reliably identify functionally different community types as well as when testing if modifiable factors (identified using associative techniques) do indeed shift community types to those that fulfil managerial targets. In case distinct community types do not exist, this strategy can be easily extended to steer sub-communities, core microbiomes (subsets of microorganisms shared across a vast majority of samples) as well as functional guilds (groups of microorganisms which perform the same function).

Several examples show that this approach is tractable for steering existing communities to desirable states. For example, pioneering studies identified diet as an important factor associated with gut enterotypes (De Filippo et al. 2010; Wu et al. 2011). Follow-up experimental studies showed that diet indeed was capable of inducing switches in community types and functioning, thus making diet a therapeutic target for regulating gut health (David et al. 2014; Hjorth et al. 2018). Experimental studies have demonstrated that the addition of pyrolyzed plant residues to soil can induce shifts in microbial diversity and biomass which in turn was shown to impact plant performance (Kolton et al. 2017; Mehari et al. 2015). Similarly, plants that grow in soil actively shape the microbiome by modifying soil properties and altering resource availability through root exudation (Hartmann et al. 2009). Thus, plants can also be used to shift soil microbiomes to states that maximize applicable benefits. A classic example of such a strategy is utilizing the capacity of legumes to enrich the soil microbiome for diazotrophs thereby establishing a self-sustaining nitrogen cycle which in turn can support the growth of plants with a high nitrogen requirement in the future (Bradshaw Anthony et al. 1982).

While managerial targets can be achieved using this strategy, it is important that future efforts also focus on understanding generative mechanisms. Only a thorough understanding of the mechanisms underlying such outcomes can help in developing management regimes that are robust in the face of unpredictable environmental change.

17.7 Developing Sustainable Urban Agroecosystems

Urban centers are redefining the ways in which farming is practiced with a view to offset a considerable proportion of the food demand they generate. Agroecosystem configurations range from patches of land earmarked for agriculture, indoor setups to vertical farms, placing soils and crops in new contexts. Obtaining optimal and nutritious outputs will depend on our ability to improve plant–soil feedbacks (PSF) under these new settings. PSFs affect plant growth, nutrition, tolerance to environmental perturbations, and susceptibility to pests and pathogens among others

(van der Putten et al. 2013). Several studies have shown that this feedback is mediated to a large extent by the soil and rhizosphere—soils that lie in close vicinity to the roots—microbiomes (Fitzpatrick et al. 2018; Hu et al. 2018; Semchenko et al. 2018). Therefore, maximizing the beneficial functions of such microbiomes and engineering synthetic consortia that can confer the same are the central focus of several ongoing translative research efforts aiming to maximize agroecosystem productivity in a sustainable manner (Pavagadhi 2019).

In contrast to urban landscapes, shifting existing soil microbiomes to optimal states is not necessarily the prime objective for managing microbiome-mediated PSFs. Rather, one of the ways that this can be achieved is by facilitating the establishment of beneficial microbiomes during the early developmental stages of plants given that such stages are easily accessible to ameliorative efforts. Such efforts should be informed by studies which investigate the composition of soil and rhizosphere microbiomes at different growth stages of plants as well as efforts that seek to understand the dynamics of microbiome establishment. Amplicon sequencing and metagenomics are important tools that can be used to accomplish this as outlined in the previous section. Conceptual frameworks on microbiome assembly in turn can be used to interpret these datasets and to identify key microbial targets which influence assembly as well as timepoints for active intervention. Key microbial targets also termed core microbiomes can be inferred using network theory which delineates such subsets as those that can potentially regulate the dynamics of entire communities through a range of ecological interactions. For example, core microbiomes have been identified across a wide range of plant types (Lundberg et al. 2012; Xu et al. 2018) and how in turn they affect plant performance. Strategies for leveraging core microbiomes to enhance PSFs can range from inoculating seeds with such microbiomes to modifying factors (such as resource inputs in the form of fertilizers) which directly influence their establishment, growth, and functioning within the community. Another approach is to develop core microbiomes with different functional portfolios in vitro using ecological principles which can then be deployed in the field. This can be accomplished by culturing core microorganisms (previously identified using informatics approaches) in a high-throughput manner termed culturomics. Techniques that quantify functional activity such as metatranscriptomics, metaproteomics, and metabolomics can then be used to identify stable configurations of different core microorganisms that can confer plant-beneficial functions. Such an approach can also leverage extensive information on plant-growth promoting microorganisms from existing studies.

Although approaches outlined above remain to be tested, several studies that have examined different components of this approach show that it can be tractable. For example, a highly simplified synthetic microbial consortia could be assembled directly on Maize roots guided by ecological principles thereby enabling highly resolved examinations of community dynamics and function (Niu et al. 2017). In addition to the identification of core rhizosphere microbiomes associated with plants, a number of studies have also shown the importance of such core microbiomes in conferring plant-beneficial functions such as resistance to invasive microorganisms (Cernava et al. 2019). In terms of deploying such microbial portfolios, evidence from

seed inoculation experiments with two or more microbial strains suggest that multiple strains can co-establish in a stable manner and act synergistically to enhance plant performance (Cassán et al. 2009).

Enhancing PSFs and thereby increasing urban agroecosystem productivity remains a grand challenge. Manipulating and managing soil microbiomes that are closely associated with plants under these contexts through approaches outlined above can help in achieving this goal. We expect continuation of efforts that use meta-omics approaches to gain a comprehensive understanding of different facets of such microbiomes as well as to develop solutions which have them as their focal basis.

17.8 Conclusions

Here, we have introduced and outlined the utility of meta-omics approaches for understanding the composition and functioning of urban soil microbiomes, management and manipulation of which offers an attractive way for developing healthy and functional urban landscapes. We have also discussed key challenges which limit the utility of these techniques and expect the development of methods which address these to continue. A comprehensive understanding of urban soil microbiomes can only be obtained by integrating such techniques in a manner which address the questions at hand. Finally, we highlight the importance of interpreting data obtained using such techniques within an ecological framework and discuss ways in which innovative microbiome-based solutions can be developed for managing urban landscapes and developing sustainable urban agroecosystems.

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