



Ground-nesting ants as engineers of microbial landscapes

Jacob LONGMEYER, Nikesh DAHAL, Nicholas MEDINA & John VANDERMEER

Abstract

As soil-ecosystem engineers, ground-nesting ants modulate their environment in ways that impact microbial communities across scales. Through behaviors such as bioturbation and alteration of abiotic gradients, ants alter habitat complexity, resource availability, and selection regimes for microbes. Interactions such as this are increasingly recognized as important components in shaping the structure and function of ecological communities and reinforce the conception of ants as important ecosystem engineers. In this review, we survey current knowledge on the ecological consequences of ant-driven processes for soil-microbial biodiversity patterns and dynamics at different spatial scales, ranging from individual nests to landscapes, as well as how they are modulated by spatial and temporal context dependency. We discuss the consequences of these ant-driven processes as well as research gaps that inhibit our understanding of ant engineering effects on microbial communities, associated with recent methodological advances for addressing them. Lastly, we provide a table of microbial-ecology methods that are commonly used to capture and quantify microbial communities for myrmecologists interested in exploring new avenues within this emerging field of ant-microbe interactions.

Key words: Formicidae, Hymenoptera, soil, ecosystem engineer, microbes, landscape, ant-microbe interactions, zoogeochemistry, review.

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Introduction

Understanding how species interactions influence population dynamics and community diversity is a central goal of ecology (MAY 1972, CHESSON 2000). In natural ecosystems, interactions occur across biological scales of organization, including animals and microorganisms, shaping species persistence and biodiversity patterns (JANZEN 1977). Recent research has shown that microbial populations can affect animals by influencing the timing of key life-history events (METCALF & al. 2019) and fitness consequences through interaction effects (KNUTIE & al. 2017, GOULD & al. 2018). Similarly, microbial interactions themselves have long been recognized as critical for ecosystem functions, given their central roles in energy flow and matter cycling (LINDEMAN 1942, AZAM & MALFATTI 2007, FALKOWSKI & al. 2008, CORDERO & DATTA 2016). However, the reciprocal aspect of these interactions – how do animals influence microbial-community dynamics and diversity patterns? – remains poorly understood.

Animals play a key role in shaping ecosystem structure and function through both consumptive and non-consumptive effects. Historically, ecological theory emphasized the role of consumptive interactions like predation and herbivory in regulating population and diversity patterns (HAIRSTON & al. 1960, PAINE 1966, OKSANEN & al. 1981). More recent work, however, has expanded on these frameworks to include non-consumptive effects, such as trait-mediated interactions and habitat modification, which can cascade through ecological communities and influence community structure and composition (WERNER & PEACOR 2003, SCHMITZ & al. 2004, PECKARSKY & al. 2008, SCHMITZ 2017). These diffuse, cross-scale interactions are now central to the emerging field of zoogeochemistry, which examines the impacts of animals on microbially-mediated processes like carbon storage and nutrient cycling (VANNI 2002, ESTES & al. 2011, SCHMITZ & al. 2018, LEROUX & SCHMITZ 2025). Within this context, ants emerge as especially important organisms due to

their remarkable abundance and widespread distribution. Recent estimates suggest that there are about 20 quadrillion ant individuals worldwide with a total biomass of 12 megatons dry carbon, which exceeds that of all wild birds and mammals combined (SCHULTHEISS & al. 2022). These patterns, coupled with their status as ecosystem engineers through intimate associations with the biophysical matrix of the soil (JONES & al. 1996, LAVALLE & al. 2006, VILES & al. 2021, WU & al. 2025), position ants as key animals that may exert biotic controls on microbial diversity and processes via higher order interactions.

Yet, the outcomes of such animal-driven processes can vary widely depending on environmental context (SCHMITZ & al. 2015). As such, context-dependency, or the tendency for the strength and direction of interactions to vary based on environmental conditions, is increasingly recognized as a key feature of ecological systems (BERTNESS & CALLAWAY 1994, CATFORD & al. 2022). In microbial ecology, community assembly processes and diversity patterns are often highly contingent on both biotic and abiotic factors (HOEK & al. 2016, BITTLESTON & al. 2020). This variability extends to animal-microbe systems, where local environmental conditions play a crucial role in shaping both the outcomes of species interactions (DAHAL & al. 2023) and their broader ecosystem effects (LI & al. 2021, MEYER & LEROUX 2023, VANDERPLOEG & al. 2023). For example, a global meta-analysis by McCARY & SCHMITZ (2021) found that invertebrate detritivores with bioturbating traits increased decomposition rates by 28% and soil nitrogen availability by 99%. But the effect sizes were found to be substantially variable, highlighting how ecological consequences of even functionally similar organisms can be strongly shaped by contingent factors. These sensitivities are particularly relevant for small-bodied organisms like invertebrates and microbes, whose population dynamics are more prone to non-linear and potentially chaotic dynamics (ROGERS & al. 2022). Such dynamic instability may help explain the pronounced context-dependency observed in these groups.

Among invertebrates, ground-nesting ants represent a particularly compelling yet underexplored model for studying the consequences of animal-driven processes on microbial community assembly, structure, and function. Through localized behaviors, such as bioturbation, nest maintenance, and foraging, ground-nesting ants alter habitat complexity, resource availability, and competitive dynamics, thereby providing a dynamic interface for exploring zoogeochemical processes (HÖLLDOBLER & WILSON 1990, FOLGARAIT 1998, JOUQUET & al. 2006, FROUZ & JILKOVÁ 2008). Similarly, their high abundance and broad global biogeographic distribution affords both observational and experimental studies with natural populations across a range of environmental gradients (SCHULTHEISS & al. 2022). Importantly, ants operate at scales large enough to produce landscape-level effects, yet small enough to allow spatiotemporal tracking, which may not be readily feasible when working with larger animals. Extensive literature on ant natural history and ecology

has also revealed emergent properties – ranging from keystone intransitivities to spatially clustered networks of pest control – that make ants ideal systems for probing the links between cross-scale interactions and biodiversity maintenance in highly heterogeneous and microbially diverse soil environments (WAY & KHOO 1992, VANDERMEER & al. 2008, LAVALLE & al. 2016, VANDERMEER & al. 2019, VANDERMEER & PERFECTO 2023). Finally, ground-nesting ants play important ecological roles by influencing nutrient cycling, soil structure formation, seed dispersal, arthropod and plant community structure, crop yields, and various other ecosystem services (HANDEL & BEATTIE 1990, KRUSHELNYCKY & GILLESPIE 2008, EVANS & al. 2011, DEL TORO & al. 2012, OFFENBERG 2015, VILES & al. 2021, WU & al. 2025).

Research to date shows that ground-dwelling ants generally alter microbial diversity and function within their nest, which spans several genera including *Formica*, *Iridomyrmex*, *Lasius*, *Messor*, *Myrmica*, *Pogonomyrmex*, *Solenopsis*, and *Veromessor* as well as a range of latitudes and ecosystems (FRIESE & ALLEN 1993, GINZBURG & al. 2008, CHURILINA & al. 2017, DELGADO-BAQUERIZO & al. 2019, TRAVANTY & al. 2022, GAMBOA & al. 2025). Specifically, patterns of microbial biodiversity in large and long-lived *Iridomyrmex purpureus* (F. SMITH, 1858) ant nests include enrichment in opportunistic, faster-growing, and copiotrophic microbes as well as those capable of antibiotic production (DELGADO-BAQUERIZO & al. 2019). Additionally, harvester ant (*Veromessor andrei* (MAYR, 1886)) nests have shown enrichment in arbuscular mycorrhizal fungi (FRIESE & ALLEN 1993), which are critical for most plants' acquisition of phosphorus (WEBER & al. 2025). The impacts of ants can be overshadowed by other limiting factors though, such as rainfall and soil moisture in very arid environments (WHITFORD & al. 2012). Another major interaction between ground-nesting ants and soil microbes is that of ant-fungal mutualisms. While important, these interactions have been the subject of several other reviews and thus are not covered at length here (see CURRIE 2001, MUELLER & al. 2001, CALDERA & al. 2009, DEJEAN & al. 2023). Clearly, ant nests can serve as unique reservoirs for microbial biodiversity, which can scale up to affect plant primary production (FARJI-BRENER & WERENKRAUT 2017), such as in agricultural systems (WU & al. 2025). Ultimately, however, research on the underlying mechanisms explaining these ant effects on microbial communities remains scarce and microbial community-assembly processes need to be explicitly tested (NEMERGUT & al. 2013, STEGEN & al. 2013, 2015, TRIPATHI & al. 2018).

The overall impact of ecosystem engineering by ground-nesting ants on soil-microbial communities can be understood as an array of activities that create physical changes in biotic and abiotic resources that consequently may alter their availability to microbes. These activities range over orders of magnitude spatially, from modification of soil aggregate structure to regional soil turnover, all of which have the potential to structure resultant microbial

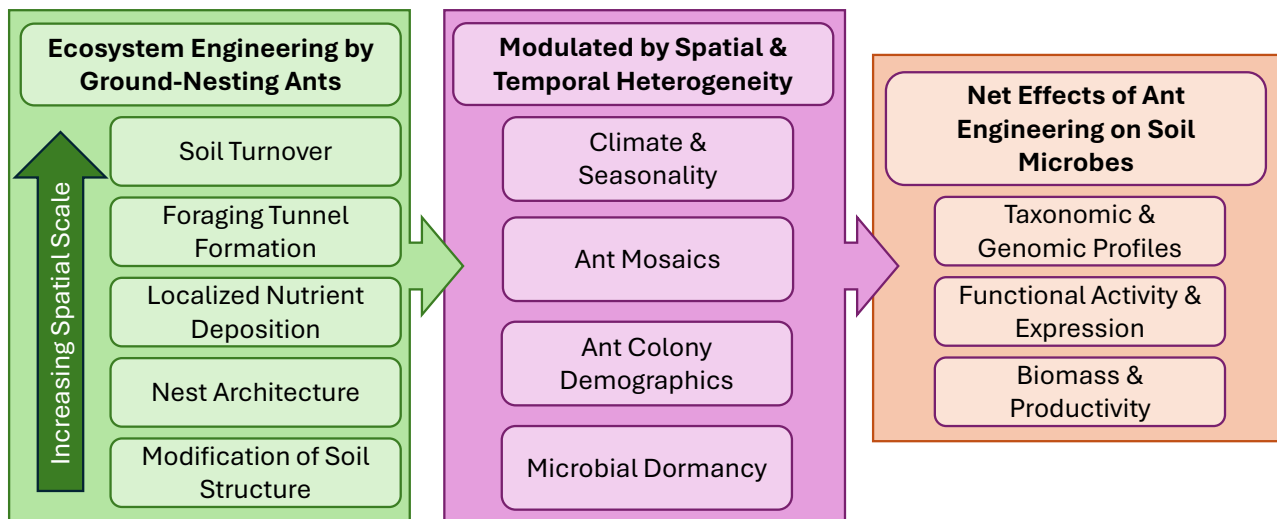


Fig. 1: Ground-nesting ants engage in a wide array of ecosystem engineering activities whose effects are dependent on the spatial and temporal context in which they occur, with varying effects on microbial communities. Note that ecosystem engineering activities performed by ground-nesting ants occur across a wide range of spatial scale, from soil aggregate formation to landscape-level soil turnover. The impacts of these activities depend on various aspects of spatial and temporal heterogeneity, affecting microbial communities along three primary dimensions, including diversity, function, and productivity.

communities. A complicating but critical component is spatial and temporal heterogeneity, not only of the soil matrix in which these interactions occur but also with respect to the internal dynamics of the ant colony itself, which can modulate the direction and magnitude of the engineering impacts that ants impose. These dynamics coalesce into broader spatial patterns of ant mosaics that ultimately affect microbial communities across landscapes.

In this review, we survey current knowledge regarding the ecological consequences of ant-driven processes for soil-microbial biodiversity patterns and dynamics, distinguishing the impacts of ants across spatial scale, as well as important aspects of spatial and temporal context dependency. We also present a guide for quantifying and describing effects on microbial communities, linking common methods to the basic descriptive categories of diversity, function, and productivity. By combining these complex and interdependent parts into a cohesive framework (Figure 1), our hope is to contribute to a more holistic understanding of the role of ground-nesting ants in engineering microbial landscapes. The goal of this review is to identify research gaps as well as to present pathways forward and methods for additional research to improve our understanding of the complex, multi-faceted effects that ants ultimately impart on soil-microbial populations.

Commonly used microbial quantification methods

Although tremendous progress has been made since the invention of the microscope – the event that led to the birth of microbiology as a modern scientific discipline – method selection can be overwhelming due to the sheer number of tools and the varying levels of analytical depth

and biological information they can offer, especially for the myrmecologists seeking to incorporate microbial analysis into their own research. Quantifying microbial diversity is fundamentally challenging, first and foremost due to the ubiquitous yet invisible nature of microbial life forms. Large population sizes, short generational times, high levels of metabolic plasticity, and ability to share genes between distant lineages further complicate this task (POLZ & al. 2013, SOUCY & al. 2015, LENNON & DENEFF 2016). Additionally, in recent years, microbial ecology has been overwhelmed with immense accumulated data generated by high-throughput technologies, lacking conceptual frameworks (PROSSER & al. 2007, PROSSER 2022). As such, rather than providing an exhaustive catalogue, our list is designed to support hypothesis driven method selection – particularly for testing the assumptions and predictions of ecological theories in the context of cross-scale ant-microbe interactions – as well as to facilitate functional studies on how ants may alter microbial processes in soil environments.

Here, we list some methods commonly used today, organized into three categories based on the type of information they can generate: (1) taxonomic and genomic profiles, (2) functional activity and expression, and (3) biomass and productivity (Tab. 1). These categories broadly correspond to microbial community membership, community-level activity at a given time, and the biogeochemical consequences of microbially-mediated ecosystem functions, which constitute the base characteristics necessary for describing a microbial community. Because these methods are broadly applicable across the sections of this review, we encourage the reader to refer to Table 1 as it relates to each section.

Tab. 1: Commonly used methods today to support hypothesis-driven research related to ant-microbe interactions, with example questions based on topics covered in this review. Sections are organized into three categories based on the type of information they can generate: (1) taxonomic and genomic profiles, (2) functional activity and expression, and (3) biomass and productivity.

1) Taxonomic and genomic profiles Who is there? What genes do they carry?			
<ul style="list-style-type: none"> - How do ants exert top-down controls on microbial community (re)assembly through trait-mediated effects? - How do ant nests enrich microbial diversity at the chamber / nest / foraging area scale? - Is soil turnover associated with ant invasions linked to changes in microbial diversity? - What do temporal patterns of turnover look like for different microbial assemblages across the spatial scales of ant engineering? - How do associated microbial assemblages differ according to feeding and nesting strategies of ants? 			
Method	What is measured?	Key applications	Methodological considerations
16S rRNA gene sequencing (bacteria & archaea) and ITS sequencing (fungal)	Abundance of 16S rRNA gene and / or ITS gene marker	<ul style="list-style-type: none"> - Estimating community diversity (structure & composition) based on taxonomy - Constructing phylogenies using a single gene 	<ul style="list-style-type: none"> - Cost effective & lower learning curve (compared with metagenomics) - Low phylogenetic resolution due to reliance on a single, slowly evolving marker gene - More effective than metagenomics for detecting both dominant & rare taxa
Metagenomics	Gene content and abundance at the population & community level	<ul style="list-style-type: none"> - Characterizing functional potential & trait diversity across all domains - Tracking populations through space & time, including evolutionary change - Constructing phylogenies using selected genes 	<ul style="list-style-type: none"> - High resolution data for bacteria, archaea, fungi, & viruses - Higher costs & computational demands (compared with 16S rRNA gene sequencing and ITS sequencing) - Steeper learning curve - Ideal for capturing dominant populations (though higher sequencing depth can capture some rare members)
2) Functional activity and expression What are the microbes doing functionally & metabolically?			
<ul style="list-style-type: none"> - How does the nutrient concentration driven by ant activities (tunnelling, foraging, excretion, etc.) significantly shift patterns of microbial gene expression? - Do microbial communities associated with specific ant species / species assemblages exhibit greater functional diversity or enhanced nutrient cycling? - How do ants alter functional trait distribution in microbial communities within nests and / or throughout foraging areas? 			
Method	What is measured?	Key applications	Methodological considerations
Meta-transcriptomics	Gene expression patterns at the population & community level	<ul style="list-style-type: none"> - Identifying active members based on transcript abundance profiles - Characterizing community-level activities in response to environmental changes 	<ul style="list-style-type: none"> - Highly sensitive to technical errors due to short half-life of RNA - Requires quick sample preservation, high sequencing depth, & complex analysis - Can be paired with other 'omics data for integrated insights about expressed functions / niche differentiation
Metaproteomics	Protein content & abundance at the community level	<ul style="list-style-type: none"> - Identifying proteins responsible for catalyzing ecosystem functions - Inferring contributions of member species to community functions based on expressed gene products 	<ul style="list-style-type: none"> - Complex pipelines - Closer functional proxy given that protein abundance is measured - Can identify post-translational modifications that are key to functional regulation in some cases

Method	What is measured?	Key applications	Methodological considerations
Metabolomics	Metabolite profiles & abundance at the community level	<ul style="list-style-type: none"> - Characterizing metabolic states - Characterizing small molecule sets to infer species interactions 	<ul style="list-style-type: none"> - Sensitive to sample processing & extraction - Broad identification of chemically defined molecule classes - Ideal for physiological profiling at high resolution
Community-level physiological profiling (CLPP) analysis	Utilization patterns of various carbon substrates	<ul style="list-style-type: none"> - Assessing functional diversity across microbial community samples - Profiling carbon-substrate preferences and activities at the community level 	<ul style="list-style-type: none"> - Simple & cost-effective compared with 'omics methods - Aggregated community level measurements that cannot be linked to taxonomic data - Ideal for rapid & high throughput screening of functional shifts
3) Biomass & productivity How do biomass, abundance, and community turnover shift over time and space?			
<ul style="list-style-type: none"> - How do the patterns of resistance & resilience of microbial communities differ inside vs. outside ant nests? - Does waste management in ants improve microbial productivity and decomposition? - What are the net impacts of ant-microbial interactions on ecosystem functioning across landscapes? 			
Method	What is measured?	Key applications	Methodological considerations
Flow cytometry	Cell counts, phenotypic features, & nucleic acid content	<ul style="list-style-type: none"> - Estimating total abundance - Estimating phenotypic diversity - Estimating metabolic population structures (active vs inactive cells) 	<ul style="list-style-type: none"> - Cost effective, easy learning curve, & high-throughput screening - Samples that will be compared need to be run in the same machine - Taxonomic & phenotypic features can be correlated but cannot be linked
Leucine incorporation assay	Rate of incorporation of radiola-beled leucine into newly synthesized proteins	<ul style="list-style-type: none"> - Estimating heterotrophic production rates - Estimating bacterial growth efficiency if combined with respiration assay 	<ul style="list-style-type: none"> - Standard & cost-effective proxy for bacterial production - Does not target autotrophs or fungi
Phospholipid fatty acid (PLFA) analysis	Concentration of phospholipid fatty acids	<ul style="list-style-type: none"> - Estimating microbial biomass - Profiling shifts in redox states & activity to assess soil health 	<ul style="list-style-type: none"> - Cannot resolve taxa beyond broad groups - Ideal for high throughput screening of active microbial biomass and activity
Potential mineralizable carbon (PMC)	Rate of CO ₂ production from respiration of soil organic carbon (SOC)	<ul style="list-style-type: none"> - Estimating decomposition potential of SOC - Inferring carbon cycling rates based on microbial activity 	<ul style="list-style-type: none"> - Highly sensitive to lab incubation conditions - Widely used indicator of soil biological activity and health

Ecosystem engineering by ground-nesting ants

Ground-nesting ants are important soil-ecosystem engineers and consequently have a large impact on the environment in which microbial communities form and persist (JONES & al. 1996, LAVELLE 2002, JOUQUET & al. 2006, LAVELLE & al. 2006, HASTINGS & al. 2007). Through constructing nests and foraging tunnels, ants alter the physical and chemical properties of the soil (CAMMERAAT & RISCH 2008, WILKINSON & al. 2009, FARJI-BRENER & WERENKRAUT 2017, VILES & al. 2021, URBAŃCZYK & SZULC

2023, WU & al. 2025), altering the biotic and abiotic resources available to microbial communities, including soil structure, resource availability, and habitat complexity. This occurs across several orders of spatial scale, from soil aggregate formation to foraging tunnels throughout the myrmecosphere to landscape-level soil turnover, partially illustrated using a representative ant species, *Solenopsis invicta* BUREN, 1972 in Figure 2. Here, we review each of these aspects, highlighting potential avenues for further research into the various mechanisms through which ants mediate microbial communities.

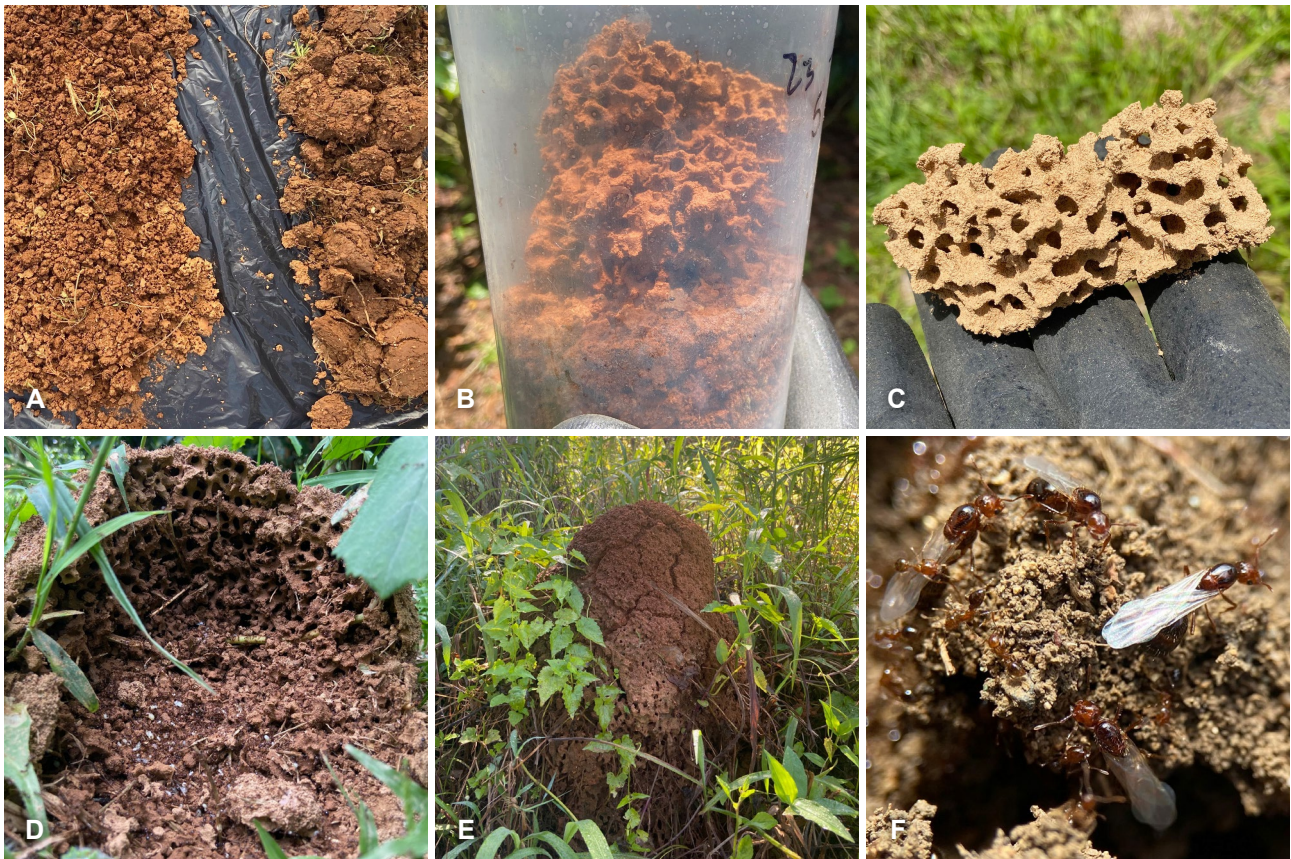


Fig. 2: Examples of bioturbation and soil-ecosystem engineering of a representative species, *Solenopsis invicta*. (A) Soil from the nest mound (left) and adjacent soil (right), where nest mound soil is much looser and easily broken apart, whose aggregate structure has been reworked by the ants. (B) and (C) Detailed photos of the internal structure of the nest mound and its pores, increasing aeration of the nest mound. (D) The internal structure of the nest mound exposed, revealing a highly porous network of tunnels and chambers with different functions. (E) A nest mound, which can be long-lived and tens of centimeters tall. (F) Alates and workers preparing for a nuptial flight on top of the nest mound, spreading to new localities to turn over new soils. Photo credits for (A) - (F): J. Longmeyer.

Modification of soil structure

Ant nests are physically built and organized to maintain a homeostatic environment, including factors such as soil temperature, moisture, nutrients, and concentrations of gases (COX & BLANCHARD 2000, JONES & OLDROYD 2006, BIERBASS & al. 2015). To do this, they must excavate relatively large quantities of soil, resulting in ants being an important source of bioturbation globally. VILES & al. (2021) found that ants move a median of 1.5 tons of soil per ha annually and up to over 60 tons of soil per ha annually for species like *Aphaenogaster longiceps* (F. SMITH, 1858) in Australia and *Pogonomyrmex badius* (LATREILLE, 1802) in Florida, USA. There has been relatively little attention to how ants modify soil structure (CAMMERAAT & RISCH 2008), despite the increasing recognition of soil structure as important for shaping soil-microbial communities (KRAVCHENKO & al. 2014, BAVEYE & al. 2018, KRAVCHENKO & al. 2019) as well as nutrient cycling (KRAVCHENKO & GUBER 2017, VOGEL & al. 2022, MEDINA & VANDERMEER 2023).

As part of their nest (and niche) construction process (VANDERMEER 2008, LALAND & al. 2016), ants are fun-

damentally integral parts of the soil fragmentation and formation process shaping overall soil geomorphology (WHITFORD & ELDRIDGE 2013). Intuitively, ant body size is expected to correspond with mandible size (TSCHINKEL & al. 2003), which then corresponds with soil fragment size excavated and particles used for nest construction (AVILA-NÚÑEZ 2023), leading to changes in soil texture and bulk density (CAMMERAAT & RISCH 2008). This species-specific effect on soil fragment size may then lead to microbial community compositional differences between ant species and possibly even colony developmental stage as worker size distributions shift (TSCHINKEL 1988, WETTERER 1999, HOLBROOK & al. 2011). This interspecific variation in excavation processes likely lead to differences in soil porosity, average pore size for workers to travel through, and pore network connectivity, all of which have significant impacts on soil-microbial activity (KRAVCHENKO & GUBER 2017, KRAVCHENKO & al. 2019). Ant-nest construction can also shape soil aggregation, which is also increasingly recognized as important for long-term soil fertility and organic matter storage (AHMADI & al. 2011, BLAUD & al. 2014, CHAPLOT & COOPER

2015, RILLIG & al. 2017, CHEN & al. 2022). During the nest-construction process, in addition to preferring to use slightly harder soils, for example, mineral or compacted soils, ants use their saliva to help cement soil particles together (BRIAN 1983). As a result, ant nests likely affect soil aggregate characteristics, such as stability and / or average diameter (ECHEZONA & IGWE 2012), but direct research on this aspect of soil development remains limited. Soil aggregation can shape microbial community diversity and composition (BACH & al. 2018), such as through biofilm formation (BÜKS & KAUPENJOHANN 2016, LEHMANN & al. 2017, WU & al. 2019), but additional distinguishing underlying mechanisms that are specifically mediated by soil aggregates (BAILEY & al. 2013) remains an area for future study.

The effect that ground-nesting ants have on soil fragmentation and formation processes thus likely maintains a role in shaping microbial community dynamics. For example, how do variations in ant body size across different ant species correlate with differences in soil macroaggregate formation processes? How does this alter soil aggregate distributions and biofilm formation? Does this aggregated soil, bound with ant-based compounds, house unique microbial assemblages (Tab. 1)? These questions can be tackled in several ways. For example, soil aggregate stability can now be easily and inexpensively assessed through SLAKES, a smart-phone software that analyzes soil slaking in water, which has been shown to perform on par with traditional methods (FLYNN & al. 2020, RIEKE & al. 2022), and soil aggregate size distributions can be estimated from images using pattern spectra, which is much less labor intensive than traditional methods (BOSILJ & al. 2020). Scanning electron microscopy (SEM) has also recently been used to investigate the spatial organization of microbes and biofilms in the fungiculture systems of attine ants, allowing unprecedented ability to visualize the structure and organization of ant-nest biofilms in situ (BARCOTO & al. 2024). Methods like this allow for the investigation of new questions such as how microbiota are organized spatially within biofilms and how they physically interact with one another, which may help to elucidate how unique microbial assemblages are generated and maintained within the ant nest. Basic characteristics of biomass and productivity like total abundance, phenotypic diversity, and proportional activity levels can be quickly and inexpensively assessed using flow cytometry, which has recently been applied to soil microbial communities (BRESSAN & al. 2015, KHALILI & al. 2019).

Nest architecture

Fine-scale variation in bioturbation processes during ant-nest construction then scales up to shape whole nest sizes and geometry. Various studies characterizing nest architecture exist for common ant genera including but not limited to *Formica* (MIKHEYEV & TSCHINKEL 2004), *Campotonotus* (TSCHINKEL 2005), *Odontomachus* (CERQUERA & TSCHINKEL 2010), *Atta* (MOREIRA & al. 2004, SOARES & al. 2025), *Acromyrmex* (VERZA & al. 2007), *Linepithema*

(HALLEY & al. 2005), *Aphaenogaster* (TSCHINKEL 2011a), *Solenopsis* (CASSILL & al. 2002), and *Pogonomyrmex* harvester ants (TSCHINKEL 2004). However, the relationship between nest architecture and microbial communities remains poorly understood, in part because ant nests and soil-microbial communities are often studied separately (BOTTINELLI & al. 2015). Factors such as air flow and nest depth likely have significant effects on microbial community assembly. For example, soil depth profoundly affects microbial community composition, with dramatic shifts in diversity, abundance, and taxonomic structure occurring across soil profiles, likely due to shifts in gas exchange and nutrient availability (EILERS & al. 2012, FENG & al. 2019, HAO & al. 2021, MUNDRA & al. 2021, XIN & al. 2023). In contrast to this, soil samples across the vertical depth of nests of *Veromessor andrei* failed to show any relationship between soil depth and bacterial diversity, which suggests that ant activity can sustain higher microbial diversity deeper in the ground (GAMBOA & al. 2025). Ground-nesting ants affect gradients of both gases and nutrients as they respire, aerate soils, and translocate nutrients during nest construction and maintenance, and future studies should analyze not only how these gradients are altered but how they correlate with changes in the microbial community compared with adjacent soils (Tab. 1), which are likely tied to biogeochemical cycles and ultimately contributions to ecosystem function (SWANSON & al. 2019). Experimental alteration of gas gradients within ant nests like that done by TSCHINKEL (2013) with CO₂ would be a useful tool in isolating the impacts of these gas gradients on microbial diversity, function, biomass, and productivity (Tab. 1). Understanding the effects of the architecture itself, that is, overall depth, tunnel and chamber size, number, and density, on microbial communities would also be of interest and could be addressed by comparing different developmental stages of an excavated ant nest within the same species or also by comparing different architecture styles between species. BOOTS & al. (2012) compared three ant species, *Lasius flavus* (FABRICIUS, 1782), *Formica lemni* BONDROIT, 1917, and *Myrmica sabuleti* MEINERT, 1861, based on feeding and nesting strategies, and they found that all three species maintained unique microbial communities within their nests. These findings suggest that feeding and nesting strategies may play a role in determining microbial assemblages, but further research is needed to generalize.

Localized nutrient deposition

One important mechanism for creating environmental gradients by ants is localization of nutrients, whether in the form of ant food or ant waste. While caches of seeds or invertebrate prey are managed and may occasionally fall victim to spoilage, this is not necessarily the case for waste products from the nest, which are often rich in organic carbon and other digestible substrates with higher levels of microbial activity and decomposition (CLAY & al. 2013). Management of said waste can provide an important mechanism of concentration and translocation of nutrients

for microbial populations. Waste-management behavior among ant species varies widely and is influenced mainly by the pathogenicity of the waste and vulnerability of individuals to infection (PEREIRA & al. 2020). For example, *Atta cephalotes* (LINNAEUS, 1758) has highly developed waste-management practices, where underground waste dumps have dedicated dump workers that quarantine themselves from the rest of the nest (BOT & al. 2001). Management of these dumps includes aeration via tunneling and selective sorting of waste into different areas of the dump, which may result in species sorting that prevents the growth of pathogenic microbial species, where species are filtered based on environmental preferences and tolerances. On the other side of the spectrum, some ant species create waste piles outside their nest on the ground surface with no additional management (BOT & al. 2001, FERNANDEZ & al. 2014). In these situations, the relevance of mass effects or neutral processes are likely higher, compared with deterministic ones like species sorting, in shaping microbial community assembly across space. Mass effects refer to the influence of high immigration of microbes, often overwhelming local environmental conditions and neutral processes refer to stochastic demographic processes. There also exist many other cases along the spectrum, such as *Lasius niger* (LINNAEUS, 1758) that constructs “toilets”, which are designated waste piles inside the nest for defecation (CZACZKES & al. 2015). Taken together, it is clear that waste management among ants has a large impact on the nest microbiome since waste serves as both hotspots for microbial metabolism as well as source for propagules that can inoculate neighboring sites. As such, species sorting effects from ant sanitation and hygiene behavior may work in opposition to mass effects of microbial inoculation from feces and other waste piles to together form a dialectic whole influencing soil-microbial community assembly within and around ant nests.

It is also important to consider that microbial assembly processes are shaped by interactions with the pre-existing microbial environment as well as the inocula originating from elsewhere, such as ant waste. Indeed, ground-nesting ants tend to have a protein-rich diet consisting of insects (FRIZZI & al. 2020) as shown in their waste (HUDSON & al. 2009), unlike leaf-dwelling ants that more likely focus on tending carbohydrate reservoirs from tended hemipterans and / or extrafloral nectaries (VANDERMEER & al. 2010, 2019). Furthermore, trophically similar herbivorous ant gut-bacterial communities were found to be similar amongst one another, even across phylogenetically distinct lineages, suggesting strong effects of diet on convergent evolution as core community members (i.e., Rhizobiales bacteria) are likely key in aiding ant nitrogen metabolism (ANDERSON & al. 2012). The impact of varying ant life histories on nest microbiomes remains under explored, despite its potential to drive microbial community diversity patterns and dynamics (DAUBER & WOLTERS 2000, BOOTS & al. 2012).

Ant nests are also dynamic spaces that can maintain specialized microbial communities dependent on chamber

function. Among most ant species, there exists some sort of spatial organization within the nest. This includes restriction of workers to specific locations as well as designation of different chambers to different functions (HÖLLEDOBLER & WILSON 1990, SENDOVA-FRANKS & FRANKS 1995, TSCHINKEL 2004), which is maintained through unique chemical signatures (HEYMAN & al. 2017). For example, ant nests and chambers of the arboreal ant *Azteca alfari* EMERY, 1893 harbor unique microbiomes, where nest microbiomes are different from exterior microbiomes, and different chambers within the nest maintain different microbiomes based on function (LUCAS & al. 2019). Despite these findings, similar patterns were not found in the ground-nesting ant *Veromessor andrei* (see GAMBOA & al. 2025), but further research should be conducted on other ground-nesting ants to clarify general patterns (Tab. 1). Differentiation of microbiomes based on chamber function is likely a product of many contributing factors, including limited movement of workers, surrounding soil microbiomes, microbiomes of chamber contents, a combination of hygienic behaviors, and nest architecture promoting certain environmental qualities. These are to some extent experimentally tractable, especially in laboratory colonies, where movement of individuals, background microbiomes, and nest architecture can all be manipulated to tease apart individual contributions. Further, over longer evolutionary time scales, this variation in microbiome composition within ant nests may affect trait distributions and evolution within microbial communities, resulting in complex eco-evolutionary feedback.

Tunnel formation

Most studies looking at effects of ants on soil properties and microbial communities are focused on the nest, but ants also impact microbial communities beyond the footprint of the nest mound, exerting influence across their foraging territory. For soil-dwelling ants like those in the genera *Solenopsis*, *Atta*, *Acromyrmex*, *Pogonomyrmex*, and *Dorylus*, tunneling activity represents an important behavioral feature that modifies soil bacterial communities within foraging areas. For example, *Solenopsis invicta*, the red imported fire ant, is a globally distributed invasive ant species that engages extensively in tunneling, which can be as deep as 11 cm (MARKIN & al. 1975) and extend as far as 15 m away from a nest (TSCHINKEL 2011b). During tunnel construction, MARKIN & al. (1975) found that *S. invicta* first forms an aboveground ant trail but soon excavates vertical shafts every 10 to 24 cm along that trail, which then branch into several more horizontal tunnels. These branching tunnels eventually meet tunnels from other vertical shafts, forming a contiguous underground tunnel to the food source. This process occurred over as little as 48 hours. Constant and rapid bioturbation throughout the colony’s foraging area like this may enhance microbial activity, where mixing and aeration of soils by ants brings otherwise dormant microbes into contact with new digestible substrates, enhancing rates of chemical transformations (LAVELLE & al. 1995, 2006).

Tunnel excavation also oxygenates soils, providing one mechanism for altering microbial community composition and function (FENCHEL & FINLAY 2008), and increases soil porosity and hydraulic conductivity, which can lead to increased microbial activity (TORBERT & WOOD 1992, WU & al. 2025). These, however, have not yet been explicitly tested in ant foraging tunnels, specifically how tunneling activity may affect microbial diversity, function, biomass, or productivity (Tab. 1). TRAVANTY & al. (2022) found that soils colonized by *S. invicta* had significantly different bacterial communities compared with unaffected soil, which they hypothesized to be due to changes in physicochemical attributes of the soil. Nest soils had elevated abundances of several taxa including Actinobacteria and species within *Acinetobacter* (Moraxelleraeae), which produce antifungal compounds and may help to prevent fungal growth within the nest. However, this study was performed on nest soils which possess a relatively small footprint. Future studies should extend to the broader areas foraged by ants to test if these ant-driven microbial diversity patterns are ecologically relevant and consistent across spatial scales (Tab. 1). There are few studies that investigate foraging-tunnel formation behavior under natural conditions (MARKIN & al. 1975, BERGHOFF & al. 2002), leaving traits like tunnel turnover, extent, and density largely unknown for most ant species, all of which could have influence on microbial persistence and activity throughout the locality covered by ant foraging.

Characterizing tunnel traits non-destructively is experimentally difficult. BERGHOFF & al. (2002) were able to approximate foraging tunnel paths of *Dorylus laevigatus* (F. SMITH, 1857) through non-invasive subterranean baiting, but the baiting itself likely influences tunnel formation dynamics. Another possibility is the use of three-dimensional X-ray computed tomographic imaging (XRCT), which has been used to analyze tunnel construction dynamics by *Pogonomyrmex occidentalis* (CRESSON, 1865) (BUARQUE DE MACEDO & al. 2021) and *Lasius flavus* (see MINTER & al. 2011), but this methodology is not able to be performed in field settings, limiting these experiments to laboratory setups. One interesting recent development is the concept of ecoacoustics, or the use of piezoelectric sensors in situ to detect unique mechanical vibrations from soil biota (ROBINSON & al. 2024). This has found some success in tracking earthworm tunnels and plant roots (LACOSTE & al. 2018), and it may be possible to track unique sounds emitted by ants (BARBERO & al. 2009). Destructive sampling, while only providing “snapshots”, could still be useful for characterizing tunnel extent and density, which often involves casting tunnels with wax, plaster, or metals with low melting points (MARKIN & al. 1975, TSCHINKEL 2010). By characterizing tunneling habits of ants, it will be possible to better understand the larger impact that ground-nesting ants may have on soil microbes within their foraging areas. For example, sections of foraging tunnels could be analyzed according to Table 1 on the basis of tunnel age, metrics of worker usage, distance from the nest, or also generally compared with adjacent, undisturbed soils.

Soil turnover

During excavation processes, ants not only deposit soil aggregates onto the surface but also mix aggregates between depths underneath the surface and in the process, they alter soil textures, horizons, and nutrient profiles (LOBRY DE BRUYN & CONACHER 1990, 1994, RICHARDS 2009, WILKINSON & al. 2009). Applying this to broader scales in time and space, ground-nesting ants eventually perturb the entire surface area of the areas they inhabit. Through this broad modification of the physical environment, they may then impact the competitive dynamics for soil microbes, shaping broader-scale biodiversity patterns through shifts in the distribution of functional traits. For example, ant-nest entrances of the ant community in semi-arid Australian landscapes were estimated to occupy 100% of the soil surface over the course of 100 years (LOBRY DE BRUYN & CONACHER 1994), and PERFECTO & VANDERMEER (1993) estimate a complete forest soil turnover rate of 200 - 300 years for *Atta cephalotes* in Costa Rica. While these broad, region-level effects of ecosystem engineering may be difficult to test for native species, effects may be most impactful for microbial communities and also experimentally feasible during species invasions, introducing new regimes of bioturbation to the soil in combination with ant-driven processes that occur at smaller spatial scales. One notable example of this is the invasion of *Solenopsis invicta*, which is known to alter soil bacterial communities and increase levels of ammonium in the soil, which is often a limiting nutrient for plant growth (LAFLEUR & al. 2005, TRAVANTY & al. 2022). Although MORRISON (2002) found that the effects of *S. invicta* on native ants and other arthropods mostly dissipated 12 years post-invasion, whether its continued presence or legacy effects result in longer-term consequences for microbial communities and rates of soil turnover remain unknown. *Solenopsis invicta* is also now spreading throughout Australia and Asia (WYLIE & al. 2020), which could provide an opportunity to investigate how microbial communities and bioturbation processes are altered pre- and post-invasion (Tab. 1). As species introductions represent one of the key drivers of global biodiversity change in the Anthropocene, understanding how invasive ants mediate microbial dispersal and reassembly at regional scales is important in predicting critical processes like disease spread, nutrient cycling, and the resilience of microbial communities.

Terrestrial ant mosaics: incorporating spatial and temporal heterogeneity

As dynamic entities, understanding ant-microbe interactions necessitates consideration of both spatial and temporal heterogeneity. While most studies on ant-microbial interactions focus within the bounds of the nest, ants also impact microbial communities beyond the footprint of the nest mound, exerting influence across their foraging territory and interacting with other surrounding ant colonies. Functional domains in soils, a concept coined by ANDERSON (1995) and elaborated on by LAVELLE (2002) to describe “spheres of influence” of ecosystem engineers.

Functional domains are particularly useful in conceptualizing both the spatiotemporal aspects of regulation of microbial activity and soil processes but also the hierarchical position soil engineers assume when compared with the many other factors at play. Ants and other macrofaunal soil-ecosystem engineers sit at a critical nexus across spatial scales, wherein they exert controls on the architecture of soils through the creation of aggregates and pores across plot scales, which then form the habitat and substrate access to microbial food webs (LAVELLE & al. 2006, 2016). While functional domains of some soil-ecosystem engineers like plant roots and earthworms have established terms like the rhizosphere and drilosphere, the myrmecosphere, or functional domains under the influence of ants, is less well established but provides a useful distinction for research in this area (LAVELLE 2002, KING & al. 2013, KING 2016). The functional domain of ground-nesting ants can be understood as the sum of structures produced by an ant colony – such as soil aggregates, mounds, pores, and tunnels – that create environments supporting specific communities of associated organisms (LAVELLE 2002). Ant species vary greatly in the behaviors they employ to maintain their nests, and studies have reported species-specific effects on microbial community composition and activity (DAUBER & WOLTERS 2000, BOOTS & al. 2012, FERNANDES & al. 2024). Thus, when considering communities of ants beyond a single nest, one can begin to visualize a mosaic of ant colonies, each assemblage uniquely affecting microbial diversity in particular ways.

The concept of ant mosaics has already been well-characterized within the sphere of arboreal ants and is defined by mutually exclusive territories of dominant ants that also house several co-occurring non-dominant or submissive ant species, thus creating unique assemblages of ant species (ROOM 1971, BLÜTHGEN & STORK 2007). Ant mosaics have been shown to structure arthropod communities and related ecosystem impacts, with resident ants shifting the biotic contexts of ecological interactions (LESTON 1973, DEJEAN & al. 1997, STÜBER & al. 2021). While traditionally applied to arboreal ants, much less work has been applied to spatial segregation in foraging territories of ground-nesting ants. We believe that this framework of ant mosaics can be useful for understanding not only the distributions of ground-nesting ants and other arthropod communities but also the soil microbiome and its subsequent impacts on ecosystem processes, particularly in environmental contexts where top-down controls are ecologically relevant.

Ant mosaics are spatiotemporally heterogeneous. With the passage of time, mosaics can either shift or remain static, and PERFECTO & VANDERMEER (2013) suggested that competitive intransitivity drives shifting mosaics whereas competitive hierarchy drives static ones. Additionally, the presence of parasitoids can introduce non-linear higher-order effects that complicate the spatial dynamics generated by intransitive competition, which has been shown both empirically and theoretically (VANDERMEER & PERFECTO 2020, 2024). Contrary to traditional notions of

ant mosaics, dominant ants can also drive the disassembly of co-occurrence patterns that would otherwise occur among subordinate ants (SANDERS & al. 2007). While ground ant nests may seem stationary, they are more mobile than conventionally thought, and nest relocation likely plays a role in mosaic re-formation as well, although nest movement is poorly characterized for most ant species and can be influenced by many non-mutually exclusive factors (MCGLYNN 2012).

All of this can affect the so-called “pattern mobility” of ant mosaics through time, which will have important implications for temporal aspects of ant-microbe interactions. Landscape-scale ant mosaics result in a heterogeneous soil matrix with differing selective regimes on microbial communities, and variation in pattern-mobility rates influences how synchronized or divergent environmental conditions are between patches, which in turn likely shapes the structure and composition of microbial communities. For example, we hypothesize that a mosaic with high pattern mobility may reduce heterogeneity across patches in the landscape and thus homogenize microbial community structure and composition through strong mass effects. Landscapes with short-lived colonies or colonies that relocate frequently may therefore be hypothesized to have more homogenous microbial communities across space compared with those with longer-lived, more stationary species.

Another important aspect of studying temporal dimensions of ant-microbe interactions is widespread dormancy behavior, which allows microbes to persist under adverse conditions until they become favorable once again for growth (MCDONALD & al. 2024). Dormancy can alter traditional metacommunity paradigms depending on how much dormancy covaries with dispersal, and it likely strengthens colonization legacies and priority effects, while also causing time lags for mass effects (JONES & LENNON 2010, WISNOSKI & al. 2019). This is relevant within the ant-mosaic context as pattern mobility may interact with microbial dormancy, influencing the relative strength of priority effects during community-assembly processes. Although the majority of previous work has focused on the impacts of ants within their nests, the total area influenced by ants throughout their functional domains extends beyond the nest. Yet, the consequences of these beyond-nest effects for soil-microbial community composition and function remain poorly understood. The dynamic nature of ant mosaics – constantly appearing, disappearing, advancing, and retreating – presents important questions about the legacy or memory effects of past ant activities and their role in microbial-biodiversity maintenance (CANARINI & al. 2021, MEDINA & VANDERMEER 2023). Future research should examine how variation in nest-pattern mobility shapes microbial-community reassembly processes at the locality scale. It is not known, however, how the changes in environmental cues associated with ant activities may mediate dormancy patterns within microbial communities and its impact on microbial biodiversity. Additionally, it is important to retain a functional perspective in mind

as impacts on microbial community structure do not necessarily translate into shifts in community function as functional redundancy is common in microbial communities (TALBOT & al. 2014).

Effects of ecosystem engineering can also depend on the demographics of the ant colony. DAUBER & WOLTERS (2000) found that for *Lasius flavus*, young mounds lacked typical features that characterized the microbial communities of mature mounds, suggesting that nest residence time is an important factor shaping microbial communities. Once a colony is established, how long does it take for a distinct microbial community to be established? Presumably this would differ between newly founded colonies and mature, relocated colonies. Once a nest mound is abandoned, how long does it take for the microbial community to once again resemble that of adjacent soil? How long do altered soil characteristics like nutrient concentrations, temperature, moisture, and bulk density persist after a nest mound is abandoned, and is their decay correlated with microbial community structure? Some work has been done on characterizing the temporal stability of fungal and bacterial communities during a colony's residence. Mounds of the ant *Formica exsecta* NYLANDER, 1846 were found to have bacterial communities that were not only different from adjacent soil but also temporally stable across years, whereas the fungal community showed greater variation (LINDSTRÖM & al. 2019, 2021). Actinobacteria and Protobacteria were the main taxa that were enriched and consistent through time, and the authors hypothesized that this was due to reduced temporal fluctuation in litter inputs and temperatures in the subarctic climate. In contrast, BRINKER & al. (2019) found that the ground-nesting ant *Lasius fuliginosus* (LATREILLE, 1798) actively manages a fungal associate that stabilizes their carton-nest structure, and that fungal communities were both stable and distinct from adjacent soil over time whereas bacterial communities were not, which makes sense given the importance of the fungal associate to the well-being of the colony. To better understand the link between nest residence time and microbial diversity, more research that is aimed at characterizing the variation in species-specific nest-movement patterns and their association with mound microbiome is needed. This will require tracking of cohorts of ant nests from establishment to abandonment and ideally differentiating nest founding from nest movement. Throughout these surveys, microbial communities can be characterized according to methods in Table 1 along with soil characteristics of interest, of which there is a wide array of possibilities. Studies like this will allow for better characterization of the effects that ant colonies have on microbial communities across their life cycle and ultimately across landscapes.

Ant-microbial interactions should also be expected to depend on interrelated factors like climate, latitude, and seasonality. Ants may be most impactful to shaping microbial communities when they are able to stabilize fluctuations of stressful environmental conditions, namely those areas with strong seasonality or harsh climates. In

moisture-limited ecosystems, ant nests and refuse dumps provide concentrated spots of nutrients and have higher water retention capacity, alleviating the primary limitations to microbial activity (FARJI-BRENER & GHERMANDI 2004, WAGNER & al. 2004, FERNANDEZ & al. 2014). Nests of *Atta cephalotes* also increased the resilience of soil-microbial communities to drought conditions in tropical forest soils (SHULMAN & al. 2024). In a subarctic climate, LINDSTRÖM & al. (2021) found that ant nests of *Formica exsecta* showed stable populations of bacterial taxa due to reduced temporal fluctuations in litter inputs and temperature. It is already known that ground-nesting ants actively stabilize environmental conditions within their nests, but it is unclear if this is relatively more important for microbial communities when the surrounding environmental conditions are harsher. DELGADO-BAQUERIZO & al. (2019) found higher soil-microbial diversity in ant mounds spanning over a thousand kilometers from mesic, humid forests to semi-arid plains in Eastern Australia, but mounds were not analyzed individually so variation across ecosystem types could not be assessed. This question could be addressed utilizing natural variation across space, as was done by DELGADO-BAQUERIZO & al. (2019) and KING & al. (2013), but could also be investigated through experimental manipulation of environmental variables in laboratory colonies (Tab. 1). Also of note is the differentiation between per-nest impact versus net impact. For example, per-nest impact may be greater in ecosystems with low primary productivity and higher latitudes where climates are generally colder, but net impacts are likely greater where ants are more abundant, which is generally in ecosystems with higher primary productivity and where temperatures are warmer (KING & al. 2013, KING 2016).

Future directions and conclusions

Within the emerging field of zoogeochimistry, ant-microbe interactions represent an exciting nexus to probe questions about the role of top-down animal effects on microbial diversity, dynamics, and ecosystem function. Although the implications of such animal-driven effects on microbial diversity remain largely unexplored, recent empirical findings and methodological advancements in microbial ecology offer promising avenues to link ant-driven processes to microbial spatial dynamics and broader developments in ecological theory. This synthesis is particularly relevant today as the field of microbial ecology is increasingly data-rich yet lacking in cohesive theoretical foundations (NEMERGUT & al. 2013, ANTWIS & al. 2017, PROSSER & MARTINY 2020, HUG 2024). Since many aspects of ant-microbe interactions are spatially explicit, we also encourage dedicating analytical and sampling resources to investigating spatial effects. Such efforts are particularly urgent today as species introductions and loss in the Anthropocene continue to drive the assembly and disassembly of existing ecological communities.

Of course, ecosystem engineering is not the only way in which ground-nesting ants interact with soil microbes. Ground-nesting ants make extensive use of various anti-

biotic substances from a plethora of glands and microbial symbionts to directly control and shape microbial assemblages within their nests (MORGAN 2008, YEK & MUELLER 2011, VANDER MEER 2012, FLYNN & RAMALHO 2025, MAURICE-LIRA & al. 2025). Ants also engage in direct translocation of microbes across space, mostly through social hygienic behaviors such as necrophoresis, grooming, and social isolation (see OI & PEREIRA 1993, SUN & ZHOU 2013, ZHUKOVSKAYA & al. 2013), although they can also actively disperse microbes across larger distances through nuptial flights (PAGNOCCA & al. 2008). Lastly, ants maintain ecological relationships with many organisms apart from microbes, and these can manifest into higher-order interactions that indirectly impact microbial communities. While all of these are beyond the scope of this review, we encourage research and consideration of all of these disparate areas to support a holistic understanding of ant-microbial interactions.

Ground-nesting ants act as ecosystem engineers, shaping soil-microbial communities through their diverse activities. By examining their impacts across multiple spatial scales and emphasizing the importance of spatial and temporal heterogeneity, this review provides a framework for understanding the broader ecological consequences of ant-driven processes. It also offers practical guidance for quantifying microbial diversity, function, and productivity, highlighting research gaps and proposing methods to direct future work and deepen our understanding of the complex and multi-faceted influences ants impart on microbial landscapes.

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Declaration on use of generative artificial intelligence tools

The authors declare that they did not utilize generative artificial intelligence tools in any part of the composition of this manuscript.

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