Title: Modeling Decomposition: Beyond a Well-Mixed World

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Highlights

- Predicting global carbon (C) cycling requires models capturing critical terrestrial C features.
- Current models overlook two defining features: patchy C inputs (e.g., wood, whose stoichiometry mismatches decomposer demands) and transport networks decomposers evolved to connect them.
- Fungi and termites, global drivers of deadwood decomposition, illustrate the importance of these features: their networks connect spatially separated resources, altering stoichiometric constraints assumed to govern deadwood decomposition and decomposer biomass and necromass turnover rates.
- Network theory advances provide foundations for representing these dynamics. We propose bottom-up and top-down approaches for incorporating their effects into C models.
- Representing resource patchiness and decomposer connectivity is essential to predict when, where, and how terrestrial C is decomposed, redistributed, and retained.

Abstract

Carbon cycle models overlook resource patchiness and networked foraging characterizing terrestrial carbon dynamics. They treat inputs as well mixed and decomposers as acting at local scales, making substrate stoichiometry, rather than spatial access, the primary constraint on decomposition. Using deadwood decomposition by cord-forming fungi and termites as examples, we illustrate how resource patchiness and networked foraging are large carbon cycle components departing from well-mixed expectations.

Deadwood patchiness limits decomposition in organisms incapable of integrating distant substrates. Fungal and termite transport networks alleviate these constraints connecting substrates across space and time, altering deadwood decomposition, decomposer biomass and necromass turnover rates. We outline bottom-up and top-down approaches coupling network foraging and transport models to carbon models, moving the field beyond well-mixed paradigms.

Main Text

Patchiness and network foraging: two defining features of terrestrial carbon dynamics

Terrestrial ecosystems store >4x as much **carbon (C) (see Glossary)** as the atmosphere [1], and rates at which this C returns to the atmosphere remain a major uncertainty in global C-cycle projections [2]. Much of this return is driven by decomposing organisms that mineralize C back to the atmosphere as CO_2, CH_4 and other gases via their metabolism or transform it into complex compounds as part of their own biomass. Several groups are involved in this biotic decomposition, including bacteria, fungi, and invertebrates, such as termites. **Decomposition rates** therefore depend fundamentally on physiology, abundance, and interactions of these decomposers. As such, decomposer-explicit models are increasingly recognized as a more mechanistic—and therefore potentially more predictive—basis for forecasting the C cycle [3–6]. Yet most current frameworks treat C inputs as **well mixed** and decomposers as uniformly distributed, implicitly assuming instantaneous resource encounter and use without foraging or transport costs [7–9] (Fig. 1). In this review, we examine how resource patchiness and **network foraging** adaptations it favors cause terrestrial C cycling to diverge from predictions based on well-mixed assumptions and propose that **network theory** provides a framework for incorporating both features into C models.

The well-mixed abstraction most closely approximates C-dynamics in aquatic environments and of **unitary** broadly-distributed but locally-restricted organisms, with individual bacterial cells as archetypal examples [10] (Fig. 2). A defining feature of terrestrial decomposition, however, is spatial and temporal patchiness of C inputs. Aboveground, dead plant matter enters as discrete, asynchronous inputs, which results in belowground **heterogeneity** that separates C and nutrient pools from one another and from the decomposers that use them [11–13]. The decomposition of deadwood (a C-rich but nutrient-poor pool with slow turnover which represents 8–10% of terrestrial C stocks [14]) is a prime example of how resource patchiness shapes terrestrial C dynamics [14,15]. Irregular branchfall and tree mortality deposit deadwood in patches creating heterogeneous landscapes [16]. Key wood decomposers, such as fungi and termites, are adapted to this patchiness through foraging strategies that produce **transport tubes**, which connect wood patches and redistribute materials among them (Box 1).

Most fungi exhibit foraging behavior connecting resource patches at micro scales through mycelial networks [17–19]. In many specialized wood-decay fungi, microscopic hyphae locate woody resources and then the fungi form macroscopic **cords** or **rhizomorphs**—millimeter- to centimeter-scale transport structures that connect woody substrates redistributing resources across distances of centimeters to meters [20]. Similarly, termites forage outward from nests through extensive **galleries**, i.e., interconnected networks of mud transport tubes [21]. These networks include covered aboveground galleries and **sheetings** [21] and subterranean tunnels with elaborate structures that span scales [22]. Termite network structures are dynamic sets of passages that act both for discovery and transport of termites and materials [23–25]. They are therefore functionally analogous to fungal mycelia, although termite networks are typically collectively constructed and organized around a central nest. In fact, some termite networks persist for >30,000 years [26] and cover 10's of meters [27,28].

We argue that next-generation terrestrial C models should explicitly represent transport capacities of network-forming decomposers. As detailed below, interactions between resource patchiness and networked foraging generate C dynamics that depart from well-mixed predictions. By redistributing resources across space and time [29,30], these networks may accelerate decomposition of patchily distributed substrates (Figs 1 and 2). Their effects may also persist after network activity ceases [21], given that physical structures forming networks may remain as recalcitrant necromass, creating legacies effects on soil C dynamics [31].

Contrasting consequences of networked vs unitary growth in woody patchy environments

In patchy terrestrial environments, network foraging offers decomposers two fundamental advantages over unitary growth: spatiotemporal and **stoichiometric** integration (Fig. 1). Spatiotemporal integration connects resources across space and time, allowing organisms to access them where and when they are needed. Deadwood illustrates this advantage because it enters ecosystems sporadically as large, localized patches. Established networks can mobilize resources toward newly encountered wood, enabling rapid decomposition [32] (Fig. 2). In contrast, unitary decomposers depend on dispersal to reach new patches and must build biomass *in situ* following colonization. The second advantage, stoichiometric integration, addresses challenges of stoichiometric mismatch (Fig. 1) between C-substrates and physiological requirements of decomposers in chemical ratios (e.g., C, nitrogen (N) and phosphorus (P) ratios (C:N:P)) (*sensu* [33]. In C-rich but nutrient-poor wood, networks allow translocation of limiting nutrients from surrounding environments [32] to adjust for chemical unbalances. Network foraging can quickly integrate chemical ratios across broad spatial scales, whereas unitary organisms with limited mobility are restricted to the quality of their immediate substrates (Figs 1-2). Despite the importance and slow turnover of deadwood in terrestrial C dynamics [14,15], global C models largely omit spatiotemporal integration, often representing wood fragmentation as a constant physical transfer into litter pools that is decoupled from decomposer activity [34].

Patchiness and networked organisms as major players in seasonal environments

Spatiotemporal integration through network foraging may be particularly advantageous in seasonal environments, where resource accessibility fluctuates in time. Fungal networks, for example, have been observed to persist for months to years connecting spatially separated woody resources [35,36], while termite transport tubes may sustain decomposition through dry seasons [37]). Thus, we hypothesize that networked decomposers account for a greater share of decomposition where resource availability is strongly seasonal or episodic—for example, in arid regions with pulsed rainfall, temperate and boreal forests with pronounced winters, and seasonally dry tropical forests and savannas (Fig. 2). Resolving these relationships is particularly important because many seasonal regions remain undersampled and their soil C dynamics poorly constrained in models [38]. Studies across seasonal gradients could build on exclusion experiments previously used to partition wood decomposition between termites and microbes [37,39–42].

Next generation C models: decomposer traits as entry points to merge network theory with C modelling

Several traits of decomposers organisms that are already represented in soil C models could serve as entry points for connecting network foraging with terrestrial C modeling. For example, the implications of fungal network foraging to overcome stoichiometric limitations can be directly tied to fungal traits and biomass chemistry relevant in C models. This is the case of **C-use efficiency (CUE),** a key **parameter** in terrestrial microbial C models, which captures variation in fractions of assimilated C retained as microbial biomass rather than lost through respiration. In many microbial-explicit models, CUE is fixed at different values on given substrate quality (often aligned with stoichiometry) and decomposition capabilities of the organisms using the substrates [8]. Impacts of network foraging can be represented implicitly in such models: high quality (low C:N) substrates have higher CUE than low quality substrates (high C:N; [43–45]. However, a few models already implement flexible CUEs that are responsive to substrate stoichiometry [46]. In these models, networked impacts could be represented more explicitly.

Substrate decomposition, microbial **biomass and necromass turnover rates** are other microbial traits often represented in models that can serve as entry points. Decomposition of biomass and necromass is expected to increase as an organism's stoichiometric needs are met, since microbes

must immobilize N to decompose C-rich substrates such as wood [47]. Such turnover rates are frequently included in C models [43–45,48]. As networked organisms are expected to build long-lived structural biomass for network persistence, such biomass should have lower turnover rates [31,49].

Despite these potential entry points for representing network influences on decomposer traits, current microbial models assume all substrates are evenly distributed and immediately accessible to decomposers, ignoring spatial separation of resources and capacity of network-forming organisms to connect them (Figs 1-2; although see [12]. As a result, deadwood decomposition, decomposer biomass and necromass turnover rates and CUE incorporation are strictly constrained by substrate quality, organism broad taxonomy (e.g. fungi or bacteria), and environmental conditions, such as temperature and moisture, with no attention to variable spatial environments and ability of organisms to overcome this variation. It is worth noting that spatial stoichiometric integration through network foraging may not necessarily translate into temporally fixed fungal C:N ratios, because fungi can allocate acquired elements between growth and storage, allowing their elemental composition to vary over time [50]; however, tighter stoichiometry ratios may hold for termites. In sum, a network foraging should lead to higher decomposition rates of deadwood, slower turnover rates of microbial necromass and potentially higher CUE, depending on maintenance respiration required for network upkeep, in networked compared to unitary organisms, all else being equal.

Integration of patchiness and network behavior for a new generation of models

Recognizing that resource patchiness and network behavior shape fungal traits and soil C dynamics raises a practical question: how can these processes be represented in models? The foundations already exist, but models of network foraging and terrestrial C dynamics have largely developed independently. Approaches to modelling mycelial networks range from structural to process-based representations. Structural approaches translate mycelia into graphs, representing branch points, fusions, or resource patches as nodes and the connecting hyphae or cords as edges [17] **Process-based models** instead use explicit rules or equations to predict how local mechanisms (including growth, branching, fusion, extracellular signalling, resource discovery and uptake, and internal translocation) generate network structure and function at larger scales [51]. Related theory examines how networks—including fungal mycelia and termite galleries—balance resource discovery and transport efficiency against costs of construction and maintenance [52]. Yet these models do not translate network behavior into ecosystem level consequences for C uptake, allocation, turnover, or stabilization. Conversely, process-based soil C models seldom represent how decomposers forage across patches and redistribute resources. Integrating these traditions therefore requires coupling spatio-temporal processes captured by network models with C transformations represented by process-based C models. Below, we propose two complementary approaches (top down and bottom up) for integrating resource patchiness and network behavior into C models. We develop these approaches primarily with fungi because process-based C-cycle models, applicable at ecosystem and global scales have some representation of fungi [9,53,54], while still nascent for termites—or soil fauna more generally (but see [55,56].

The first approach is a bottom-up, process-based modeling that connects network and soil C models across spatial scales, from micrometers to thousands of kilometres. At finest scales, we can depict network-forming organisms within spatially explicit individual-based models, either explicitly or implicitly. Individual-based models can represent processes operating at levels of individual decomposers [57,58]. In an explicit implementation, models of fungal growth could simulate how hyphal extension, branching, fusion, and internal resource transport respond to spatial distributions of limiting resources [59]. Network structures and their consequences for C cycling would then emerge from local behaviors of individual hyphae or modules. Although biologically detailed, this approach could require substantial restructuring of existing models and considerable computational resources. A simpler alternative would be to represent network behavior implicitly through

organismal traits. For example, network connectivity (*sensu* [60]) could determine distances over which organisms can access resources within an already spatially heterogeneous environment (Figure 1C), without explicitly simulating underlying network architecture. Greater connectivity could then be associated with tradeoffs in microbial traits, such as growth and turnover rates and CUE, as outlined above. Outputs from these individual-based models could subsequently be aggregated into community-level trait distributions or community-weighted means and used to parameterize ecosystem-scale models [61]. Quantities shared across these scales—including CUE and decomposition and turnover rates—would therefore vary with both resource heterogeneity and network connectivity. Because Earth system models can increasingly incorporate microbially explicit ecosystem models, these effects could ultimately be propagated to global C-cycle predictions [62]. By including network connectivity and resource heterogeneity in smallest scales, we can initiate a series of handoffs between modeling scales that allow us to investigate how changes at individual scales could alter ecosystem and global-scale C cycling.

A second approach is top-down. Rather than scaling fine-scale network processes upward, it uses biogeographical variation in decomposer communities, vegetation, and resource distributions to parameterize their effects on C cycling. In this case, regions with known resource patchiness can be tied to parameter sets associated with patchiness, a link with some mechanistic footing given that mycelial networks are themselves adaptations to spatially heterogeneous substrates [20]. One tractable implementation would be to associate these parameters with existing plant functional types, as currently used in many C models, following the precedent of global maps of mycorrhizal vegetation [63] and microbial-explicit land models [64]. Forested ecosystems, for example, could be assigned decomposer parameters that reflect greater prevalence and activity of networked organisms. This strategy would require establishing whether network connectivity consistently provides unique decomposer traits, e.g., higher deadwood decomposition rates, lower biomass and necromass turnover rates and potentially higher CUE linked to substrate stoichiometry that are tied to parameters currently represented in microbially-explicit ecosystem models used at global scales.

Concluding remarks

Throughout evolutionary history, organisms have solved the patchiness problem that characterizes terrestrial carbon inputs using network foraging strategies. Two major biotic decomposers, fungi and termites, have become particularly well-adapted to decomposing patchily distributed complex C molecules of plants through network based-foraging strategies. Use of networks allows for integration of resources across both space and time, overcoming needs for colonization and population build up, which are required by small unitary organisms. However, network lifestyles are not well represented by parameters currently found in C models. We argue that next generation terrestrial C models should be built around patchy resources and network theory, grounded in biology of termite and fungal networks, as well as legacy effects of the structures they build. In our progress toward more realistically representing terrestrial C cycling, exciting new questions (see Outstanding Questions box) are emerging.

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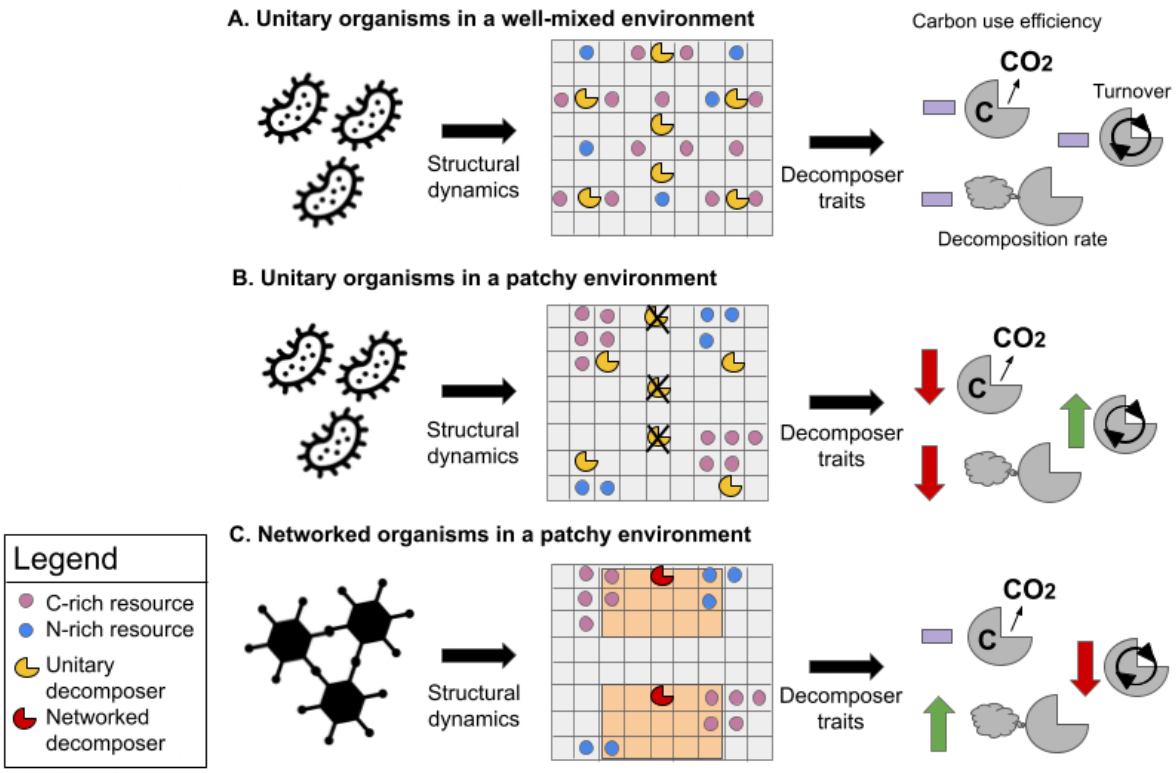


Fig. 1. Implications of organism and environment type on decomposer traits. Depiction of influences of organism (unitary or networked) and environment (well-mixed or patchy) type on decomposer traits that could be integrated into C models. Scenario "A" is status quo with unitary decomposers and a well-mixed environment. As such, light purple dashes represent a status quo response of decomposer traits, whereas green up and red down arrows represent increases and decreases in trait values, respectively. Scenario "B" shows impact of combining unitary organisms with patchy environments, showing the hypothesis that decomposers may be less successful and have reduced carbon use efficiencies (CUE) and decomposition rates with high biomass and necromass turnover rates as a result of stoichiometric mismatch and inefficient C discovery. Scenario "C" shows the impact of combining networked organisms and patchy environments, with orange shading around organisms representing their ability to access resources further from them. In Scenario C, decomposition rates are expected to be high due to stoichiometric balance, while biomass and necromass turnover rates are expected to be low due to structural biomass for network maintenance, and with uncertain impacts on CUE, due to competing influences of greater biomass building and stoichiometric balance.

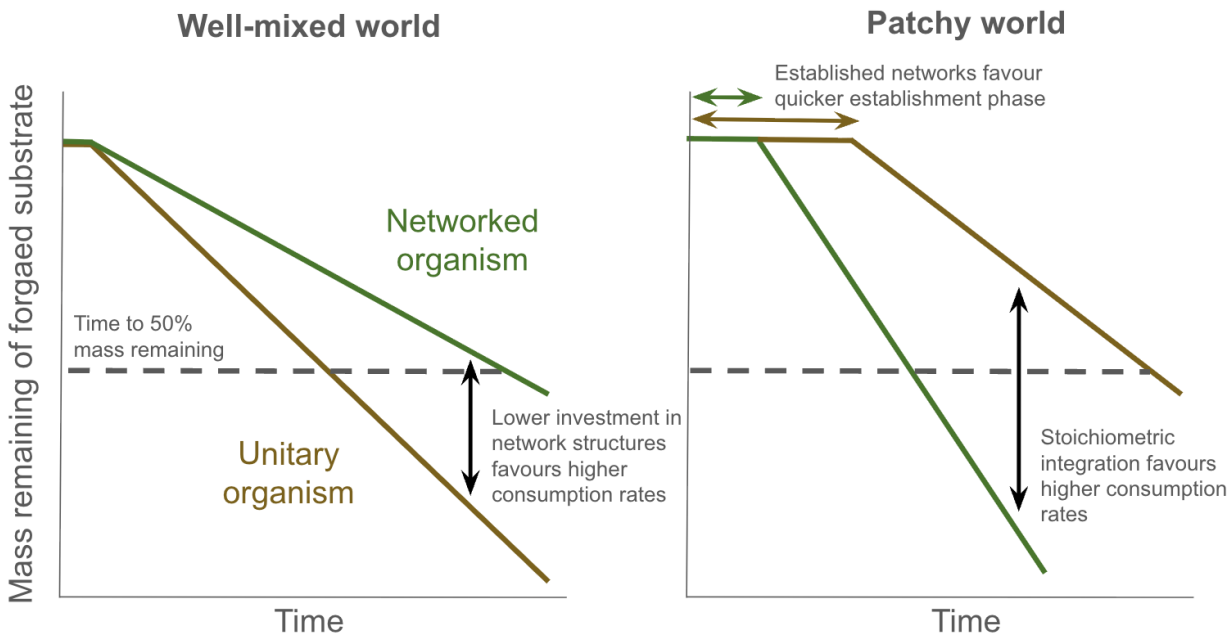
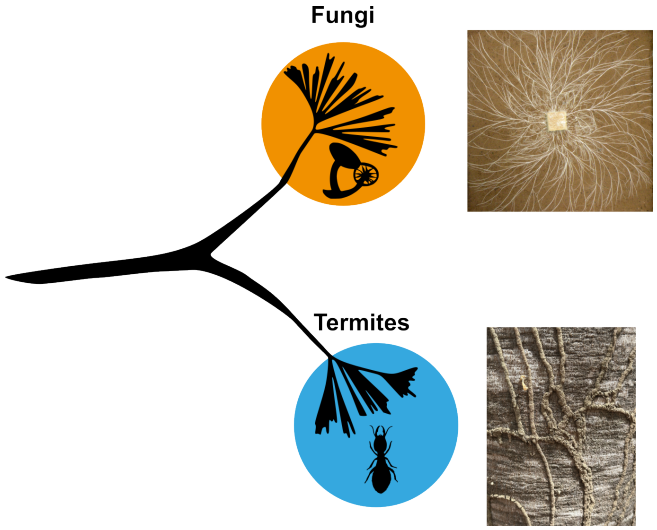


Fig. 2. Conceptual representation of expected differences in decomposition rates driven by networked (green lines) and unitary (brown lines) organisms in well-mixed (left) or patchy (right) worlds. In well-mixed worlds, unitary and networked organisms colonise the resource within similar timeframes, but broad distribution of unitary organisms and lack of investment in network structures may favor higher decomposition rates of their substrates than networked organisms. In patchy worlds, networked organisms have added advantages of colonizing resources earlier than unitary organisms because of their established networks, thereby alleviating spatio-temporal barriers to accessing those resources. Greater stoichiometric integration of resources may favor higher decomposition rates of their substrates than unitary organisms.

Box 1. Convergent evolution of network morphology across fungi and termites



In fungi, filamentous-network bodies evolved as adaptations to patchy distributions of terrestrial environments [65]. Hallmarks of this body type are apical growth, where growth is constrained at the filament tip (i.e., hyphae) [18]. As the tip expands searching for new substrates, new branches emerge forming a foraging mycelial network connecting resources at the microscale [19]. In the case of cord-forming fungi, filaments merge with one another developing macroscopic tubes with specialized structures to transport resources at the centimeter to meter scale [18,20]. As the resulting network remains connected, it creates a transport system where resources, such as C, N and P, can be moved across networks in the soil matrix [29]. Despite apparent simplicity of such growth, resulting networks are not all equal [17]. They range from ephemeral networks that last hours typical of fungi with low capacity to use complex C sources (i.e., sugar fungi) to networks that last days [66] to even years in the case of wood-decaying cord forming fungi [36]. Even within these cord-forming fungi, differences are expected among species in their transport ability across space and time given that observed phenotypes vary in the investment of resources to cords formation, where for some species cords are merely aggregates of hyphae while in others there is a secondary level of organization leading to well defined structures with complex biochemistry [67,68].

A similar level of variation in network organization is observed among termites. Early diverging termites evolved to live within their resources; therefore, they did not need to develop sophisticated foraging networks [69,70]. However, as termites diversified, many species developed abilities to forage outside their nests, necessitating evolution of foraging networks optimizing resource acquisition and transport efficiency. Structure and dynamisms of these networks vary among termite groups. Species that construct aboveground tunnels may build more ephemeral, flexible networks, whereas belowground tunnel systems are generally more stable and persistent [24], with some nests recorded to last >30,000 years. Feeding strategies may also influence the extent to which termites rely on well-developed foraging networks. For example, many rainforest termite species evolved to feed on soil organic matter in a manner similar to earthworms. Because soil resources are generally more **continuous** than patchily distributed vegetation, extensive foraging networks may be less critical for these species. However, studies examining network foraging strategies of soil-feeding termites remain limited.

Outstanding Questions Box

1. **To what degree does alleviating stoichiometric constraints affect CUE and turnover and decomposition rates during network foraging?** Networks integrate stoichiometrically complementary resource patches, but quantitative estimates and modeled representation of patchiness and stoichiometric impacts are lacking.
2. **What are residence times of biomass and necromass C produced by networked decomposers?** Network construction by cord-forming fungi and termites requires complex structural compounds, but data on the residence times of these compounds are lacking.
3. **How much C flows through networked versus unitary decomposition pathways globally?** Both networked and unitary organisms occur across spatial and temporal scales, but relative contributions to C dynamics of each pathway remain unquantified.
4. **Which decomposer traits best link network dynamics to C models?** Integrating network behavior into C models requires accessible measurements of networked decomposer traits but such information is currently scarce.
5. **How do biotic interactions reshape foraging networks and their consequences for C cycling?** Competitors and predators reshape network architecture and transport routes, but their effects on substrate discovery and decomposition and C cycling remain poorly understood.
6. **How do decomposer network scales and lifespans shape C storage?** Short-lived microscopic networks occur in fungi, bacteria, and protists. Their biomass and necromass may be less persistent than that of fungal cords or termite galleries, yet their high surface-area-to-volume ratios could promote mineral association C. Their total contribution remains unexplored.
7. **Does greater resource patchiness favor networked decomposers?** Patchy inputs favor organisms that connect separated resources, whereas mixing and disturbance may reduce this advantage. Effects of mixing and disturbance frequency across ecosystems on community assembly and evolution of networked growth remain unresolved.

Glossary

Biomass and necromass turnover rates: Speed of addition and subtraction of decomposer biomass and necromass. For networked organisms, this will include turnover rates of networked structures, both while they are living and functional (biomass) and after they are dead and non functional (necromass).

Carbon use efficiency (CUE): Carbon organisms use for growth compared to amounts of carbon organisms take up. Organisms with higher CUE use more carbon for biomass addition than gas release (e.g., as CO_2 or CH_4).

Carbon: Carbon, abbreviated C, is a chemical element that is an essential component for life. In plants, it forms complex compounds such as lignin made up of C, hydrogen (H) and oxygen (O). Lignin has many C-C and C-O bonds and is difficult to decompose. It is also a critical component in potent greenhouse gasses, such as carbon dioxide (CO_2) and methane (CH_4) released in respiration.

Cord-forming fungi: Fungi that bundle hyphae into root-like cords with differentiated internal structures, enabling resource transport over distances of centimeters to meters.

Decomposition rates: Speed of breakdown of dead organisms accomplished by cleaving molecules into simpler forms. Biological decomposition often involves release of enzymes to affect this process.

Galleries: System of tubes and chambers termites create in their nests, soil and across substrates such as hollowed wood.

Hyphae: Microscopic tube-like cells that form the vegetative body of most fungi and support their polarized extension by transporting resources toward their apical tips.

Mycelia: Interconnected, web-like networks formed as fungal hyphae grow, branch and fuse with each other.

Network foraging: A strategy in which organisms extend interconnected transport structures to locate, connect, and exploit spatially separated resources.

Network theory: Framework for explaining causes and consequences of connectivity patterns by representing systems as nodes joined by links that enable exchange (e.g., cities connected by roads or wood patches connected by mycelial cords.

Parameters: Coefficients in mathematical equations in process-based models that represent measurable quantities in real systems or fitted values to real-world data.

Patchy/heterogenous: Uneven distribution of resources and/or organisms across landscapes.

Process-based models: Series of equations that describe processes occurring in systems, e.g., process-based carbon models describe biogeochemical processes and provide carbon values as

output.

Rhizomorphs (or cords): Bundles of fungal hyphae forming millimeter to centimeter wide transport tubes.

Stoichiometric ratios: Ratios of different chemical elements in systems, e.g., ratios of C to nutrients such as N or P. Balance of these ratios, e.g., C:N, C:P or C:N:P is often important for processes, such as decomposition to occur.

Transport tubes: Hollow tubes built for transport by different decomposers to move organisms and/or resources across space while protecting them from outside elements. Examples include fungal hyphae, cords and termite mud transport tubes.

Sheetings: Layers of mineral soil, saliva, and dead plant material used by some termites to cover food or other surfaces. They act much like a flattened mud transport tube, protecting termites from the external environment.

Unitary: Individual or solitary organisms with fixed forms and determinant growth.

Well-mixed/continuous: Even distribution of resources and/or organisms across landscapes.