Beyond microbes: are fauna the next frontier in soil biogeochemical models?

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Abstract

The explicit representation of microbial communities in soil biogeochemical models is improving their projections, promoting new interdisciplinary research, and stimulating novel theoretical developments. However, microbes are the foundation of complicated soil food webs, with highly intricate and non-linear interactions among trophic groups regulating soil biogeochemical cycles. This food web includes fauna, which influence litter decomposition and the structure and activity of the microbial community. Given the early success of microbial-explicit models, should we also consider explicitly representing faunal activity and physiology in soil biogeochemistry models? Here we explore this question, arguing that the direct effects of fauna on litter decomposition are stronger than on soil organic matter dynamics, and that fauna can have strong indirect effects on soil biogeochemical cycles by influencing microbial population dynamics, but the direction and magnitude of these effects remains too unpredictable for models used to predict global biogeochemical patterns. Given glaring gaps in our understanding of fauna-microbe interactions and how these might play out along climatic and land use gradients, we believe it remains early to explicitly represent fauna in these global-scale models. However, their incorporation into models used for conceptual exploration of food-web interactions or into ecosystem-scale models using site-specific data could provide rich theoretical breakthroughs and provide a starting point for improving model projections across scales.

I. The case for explicit representation of decomposers in models

Soil organic matter (SOM) formation concepts emphasize that plant inputs do not become stable SOM until they first pass through microbial biomass (e.g. Grandy and Neff, 2008; Schmidt et al. 2011; Cotrufo et al. 2013). SOM pools derived directly from partially decomposed plant litter (e.g. light fraction or particulate organic matter) typically make up only 5-15% of total SOM (Gregorich et al. 2006; Grandy and Robertson, 2007); the rest is derived from highly processed, unrecognizable plant-derived inputs and dead microbial biomass (i.e. necromass). Reflecting this new understanding, microbial physiological characteristics including carbon use efficiency (CUE) and microbial growth rate (MGR), both potential drivers of necromass production over time, are emphasized in recent conceptual models (Cotrufo et al. 2013), and have now been experimentally shown in the field (Bradford et al. 2013; Kallenbach et al. 2015) and lab (Kallenbach et al. in review) as drivers of SOM formation.

New soil biogeochemistry models are capturing the importance of microbes by explicitly representing microbial communities and their direct contributions to SOM formation (Sulman et al. 2014; Wieder et al. 2014; 2015). These models minimize the direct flow of plant inputs to SOM (Fig. 1). Instead, plant inputs shape the size and activity of the microbial biomass, which is the proximal input to SOM. For example, in the MIcrobial MIneral Carbon Stabilization model (MIMICS), the chemistry of litter inputs influences the kinetics, size, CUE and MGR of the microbial decomposer community (Wieder et al. 2104; 2015), and ultimately how much microbial derived C is transferred to SOM pools. These new microbial-explicit models appear to more accurately simulate global SOM stocks and their response to perturbations, and, by more accurately representing SOM formation, provide a basis for the linked development of prediction and theory.

Thus, the representation in models of the microorganisms responsible for SOM transformations is showing promise; yet, the decomposer food web is complex and includes soil fauna, which represent an array of functions that can directly and indirectly influence soil biogeochemical processes. These functions include shredding and redistributing litter, altering soil physical properties including aggregation and pore space structure, microbivory, and accelerating nutrient cycling in soil and litter (Verhoef and Brussaard 1990; Brussaard et al. 2007; Coleman 2008). Given the promise of microbial-explicit models, and the range of potential effects of fauna on soil processes and SOM, here we consider the advantages and drawbacks of adding fauna to already complex soil biogeochemistry models (Fig. 1).

II. Fauna – A potential driver of microbial necromass production and SOM dynamics

Soil fauna have multiple effects on litter decomposition, which is the first step in the formation of SOM (Table 1). For example, the litter comminutors, which reduce litter particle size, can increase the surface area of litter while translocating and inoculating plant material with microbial decomposers (Chamberlain et al. 2006, Soong et al. 2016). Gut passage of plant litter by saprotrophic fauna can also modify litter chemistry and has been shown to enhance microbial activity during early stages of decay, likely due to the enrichment of litter with microbes and creation of decomposition “hotspots” (Hanlon and Anderson 1980; Wickings and Grandy 2011). Meanwhile, bioturbators can alter the distribution of organic matter in soil aggregates and alter the dynamics of decomposition (Tonneijck and Jongmans 2008; Yavitt et al. 2015). Previous studies have also shown that litter decomposition and N mineralization are sensitive to changes in the overall structure, diversity, density, and activity of faunal communities (Hattenschwiler et al. 2005; David 2014; Wickings et al. 2012; Soong et al. 2016).

However, while litter decomposition is a critical first step in SOM formation, the two processes are distinct with unique controls. Both are broadly controlled by climate and decomposer community activity, but the biochemical recalcitrance of plant litter (i.e., lignin and N concentrations) is a critical factor in litter decomposition but not in SOM dynamics (Rinkes et al. 2013; Kleber et al. 2015). Similarly, although shredding of plant litter by soil meso- and macro-invertebrates is an important control on decomposition rate, its direct downstream effects on SOM dynamics may be relatively diffuse.

In contrast to the overriding effect of recalcitrance on plant litter decomposition, the formation of SOM and its persistence in soils largely depends upon the association of microbial-derived compounds with aggregates and mineral surfaces, which protect SOM from further microbial attack (Grandy and Neff, 2008; Dungait et al. 2012; Heckman et al. 2013). By transforming and redistributing plant litter in soil and by promoting soil aggregation (Bossuyt et al. 2005; Chamberlain et al. 2006; Frouz et al. 2009), litter comminutors and bioturbators may have important effects on the factors that control SOM persistence. However, recent evidence suggests that these fauna-driven processes may have less direct impact on soil microbial communities than previously assumed (Coulis et al. 2013; David 2014). Alternatively, microbivores may have the most direct effects on SOM because of their impact on microbial community activity, growth, and turnover. Microbivory, via direct grazing on microbial biomass or consumption of microbially-colonized substrates, is a key feeding strategy exhibited across a wide range of taxonomic groups and size classes of soil organisms including protozoans, nematodes, annelids and arthropods. By feeding on microbial biomass, fauna exploit the soil microbe’s ability to degrade recalcitrant organic matter, and thus bypass the typical low nutritional quality of plant residue. Previous studies have found that microbivory can modify the structure, diversity, and activity of soil microbial communities. For instance, in a recent meta-analysis, Trap et al. (2016) illustrate that bacterivory by protozoa and nematodes generally reduces soil microbial biomass, but tends to accelerate microbial activity, thus increasing microbial metabolic quotients. In contrast, Crowther et al. (2012) found that microbial grazing, specifically fungivory, led to enhanced microbial biomass. Other studies have also observed that microbial grazing by soil meso- and macrofauna including oribatid mites and isopods can modify microbial activity (Wickings and Grandy 2011; A'Bear et al. 2014). While the magnitude and direction of effects are not consistent, microbivory by a variety of different organisms can alter microbial activity and biomass, which are the proximal controls over SOM dynamics.

III. How and when – a primer to represent food webs in models

As a starting point to incorporating fauna into predictive models, explicit representation of food webs must modify the rate of biogeochemical turnover, or the fate of carbon (C) and nitrogen (N) in soils (Schimel and Schaffer 2012) to justify their complexity. This is likely to occur when biotic interactions modify ecosystem responses to environmental perturbations in unexpected directions (Bradford and Fierer 2012). Fauna-microbe interactions exhibit this potential for unexpected, non-linear response to environmental change. For example, the response of fauna to a changing climate might alter microbial communities in opposite directions to the direct effects of climate on microbial communities. We know that abiotic constraints from energy limitation and substrate availability may broadly limit microbial activity and biogeochemical fluxes across soil environments (Mikola and Setälä, 1998). Accordingly, current biogeochemical models project changes in microbial activity with relaxation of these abiotic constraints, resulting in accelerated soil C turnover with environmental warming. If, however, changes in temperature, moisture, or nutrient availability relax these bottom-up constraints on microbial decomposers, one outcome could be that biotic, or top-down controls from food webs dampen the magnitude of ecosystem response, providing a stabilizing effect on ecosystem biogeochemical dynamics (Crowther et al. 2015). These dynamics may not be projected from simpler model structures that ignore food webs.

The most straightforward way to begin representing top-down effects in biogeochemical models would be to implicitly represent faunal effects on microbial communities and their activity by modifying static parameters with functions that consider how abiotic factors affect biotic processes and rates of biogeochemical transformations. For example, if warming releases bottom-up limitations on microbial communities, but grazers dampen the observed biogeochemical effects, we could assume a lower temperature sensitivity of soil organic matter turnover (e.g., Q_{10} value) than would be expected from laboratory incubations or cross-site observations. Current microbial-explicit models, including MIMICS, represent microbial biomass pools with defined turnover and biomass-dependent substrate uptake rates. Fauna could be represented in such models by increasing biomass turnover rates under conditions where microbivores are expected to be especially active, including those with ideal combinations of temperature, moisture and substrate quality. Increasing turnover rates would subsequently decrease standing microbial biomass and substrate uptake rates and potentially alleviate stoichiometric constraints (e.g. N limitation) in the model. In another scenario, microarthropod alteration of the chemical quality of plant residues that microbes ultimately transform to mineral-associated SOM (Wickings and Grandy, 2011; Wickings et al. 2012) could be represented by changing the C:N ratio of inputs to soil biogeochemical models (Soong, et al. 2016). Lab and field faunal exclusion experiments across a wide range of ecosystems would further help to parameterize the effects of fauna on microbial activity.

Fauna could also be incorporated more explicitly in models by following a food web approach. We could represent fauna as a pool of C and N that feeds upon microbial biomass, similar to how microbes in microbial-explicit models currently feed on litter and SOM pools. Previous studies have observed close associations between microbial biomass and the densities of microbivorous nematodes and protozoans (Ingham et al. 1985; Bardgett et al. 1999; and see Review by Trap et al.(2016)). However, the response of soil microbial communities and processes to microbivory is not always consistent, and can vary with microbivory intensity (Crowther et al. 2012a), microbivore community composition (Ronn et al. 2002) and under different soil conditions (Cheng et al. 2016). Thus, additional field experiments would be necessary to test for generalities in the magnitude and direction of the response of microbial biomass and activity to microbivory, and to quantify the importance of microbivore density/activity relative to other constraints on microbial biomass across space and time.

Models serve multiple purposes and can operate at different scales. One essential purpose of models is to develop new theory and concepts, some of which may be used to guide experimental work. Theoretical and conceptual models are often a critical first step to developing the insights into specific biogeochemical pools, processes and drivers in soils necessary to develop predictive models. Indeed, the current development of microbial-explicit soil biogeochemical models is based on a rich foundation of conceptual and theoretical models incorporating microbes into SOM dynamics (e.g. Schimel and Weintraub 2003; Allison et al. 2010). These models inspired new research leading to improvements in our understanding of microbes in SOM dynamics and ultimately the incorporation of microbes into models capable of predicting biogeochemical patterns across large spatial and temporal scales (Wieder et al. 2013).

To date, there have been a number of insightful models examining nutrient and energy flows through communities and food-webs, and these have put forward critical predictions and concepts describing the specific role of fauna in biogeochemical transformations (Hendrix et al. 1986; Hunt et al. 1987; Verhoef and Brussaad 1990; De Ruiter et al. 1995; Adl and Gupta 2006; Osler and Sommerkorn 2007; Carrillo et al. 2016). However, to begin representing food web interactions in microbial-explicit models that predict ecosystem- or global-scale processes, we must be able to better predict how belowground fauna-microbe interactions change across ecosystems. Despite an extensive and ever-growing understanding of how soil faunal communities vary among systems (e.g. Global Soil Biodiversity Initiative), we believe that we do not currently have this capacity, as key aspects of fauna-microbe interactions that are likely to influence biogeochemical processes remain poorly characterized. For example, while most soil fauna clearly depend on microbes to meet their nutritional demands, the exact mode by which microbes are exploited (endosymbiosis, consumption of microbially-degraded plant tissue, or direct microbivory) can vary significantly among faunal taxa. This variation is likely to have important consequences for downstream SOM dynamics, yet our understanding of the exact modes by which fauna exploit microbes is far from complete (but see Lussenhop 1981; Bonkowski et al. 2000; Maraun et al. 2003; Smrz and Norton 2004; Berg et al. 2004; Crowther et al. 2011). Further yet, the importance of different modes of microbial exploitation under different climatic conditions and disturbance levels is virtually unknown. This currently limits our ability to predict the direction and magnitude of microbial and thus biogeochemical responses to faunal activity under variable scenarios of climate and land-use (Figure 2). Thus, there remain many potential mechanisms and corresponding mathematical representations of faunal effects and arguably not enough evidence to prioritize supporting one or two mechanisms above all the others in models.

Efforts to include fauna-microbe interactions in soil biogeochemistry models would also benefit from a more thorough understanding of belowground predator-prey population dynamics. Density-dependence, for example, is likely to be a critical feature in faunal regulation of microbial biomass and activity. Previous studies have quantified density-dependent relationships between soil fauna and microbial processes (Aira et al. 2008; Kaneda and Kaneko 2008; Crowther and A'Bear 2012; A'Bear et al. 2014) and in their recent review Crowther et al. (2012) contrasted the impacts of high versus low intensity fungivory on soil fungal processes. Yet, compared to our understanding of density dependence in governing aboveground trophic interactions, and the delivery of ecosystem services such as pollination, biological control, and primary productivity, our knowledge of how soil microbial processes respond, both in magnitude and direction, to changes in faunal density across time and space is still incomplete. Thus, many questions remain about the fundamental relationships between microbes and fauna and how they may relate to SOM formation and persistence: Does microbivore population size consistently track that of soil microbial biomass? Which fauna-microbe interaction type (stimulation or suppression) leads to greater accumulation of microbial products in soil? What is the relationship between microbivory rate and substrate use efficiency of saprotrophic microbes? Until such questions are more thoroughly addressed across spatial and temporal scales, incorporating fauna into Earth system models will not improve confidence in model projections. Further, caution should always be used when increasing the structural complexity of models operating at large spatial scales in order to avoid problems with computational constraints and the potential of developing a model that can replicate existing data but inaccurately represents the real world and thus future scenarios (i.e. ‘equifinality’; Beven and Freer 2001; Luo et al. 2009). However, incorporating an explicit biomass pool for fauna would allow for theoretical exploration of the effects of microbivory and top-down effects of fauna upon soil organic matter dynamics. Incorporating fauna into theoretical models and into ecosystem soil models will enhance dialogue between modelers, ecologists and soil scientists, and provide a basis for extending these efforts to larger scales (Tang and Zhuang 2008).

Figure legends

Figure 1. Three simple conceptual representations of different ways microbes and fauna could be represented in models. *Microbial Implicit*. Microbial kinetics and growth efficiencies are typically static parameters embedded in the model (e.g. decay constants or transfer efficiencies between SOM pools) or less frequently scale with environmental parameters, but are not explicitly a function of microbial community characteristics. These models emphasize the importance of enzymatically degraded plant litter in SOM formation. *Microbial-explicit, bottom-up*. Microbial processes and/or communities are explicitly represented in the model. Growth efficiencies, growth rates, and decomposition kinetics may vary among communities. These models emphasize the importance of microbial necromass contributions to soil organic matter (SOM formation). *Microbial-explicit, top-down with fauna.* Similar to microbial-explicit, bottom-up models, but microbivory by microarthropods (represented here) and fungal- and bacterial-feeding nematodes provides a constraint on microbial community size and physiology and thus SOM formation. Although fauna can have a range of effects on litter decomposition and SOM formation, here we focus on microbivory because of its potential influence over the size, turnover, and efficiency of the microbial biomass, the proximal input to SOM.

Figure 2. Potential fauna effects on microbial activity in response to temperature. Microbial activity increases with temperature up to their temperature maximum (here using 35°C only as an example). Fauna may have a narrower temperature range of activity than microbes (here generalized as 10-30°C), and over this range of activity fauna may either decrease or increase

microbial activity (represented by hashed lines and shading, highlighting the potential variation in microbial activity due to fauna).

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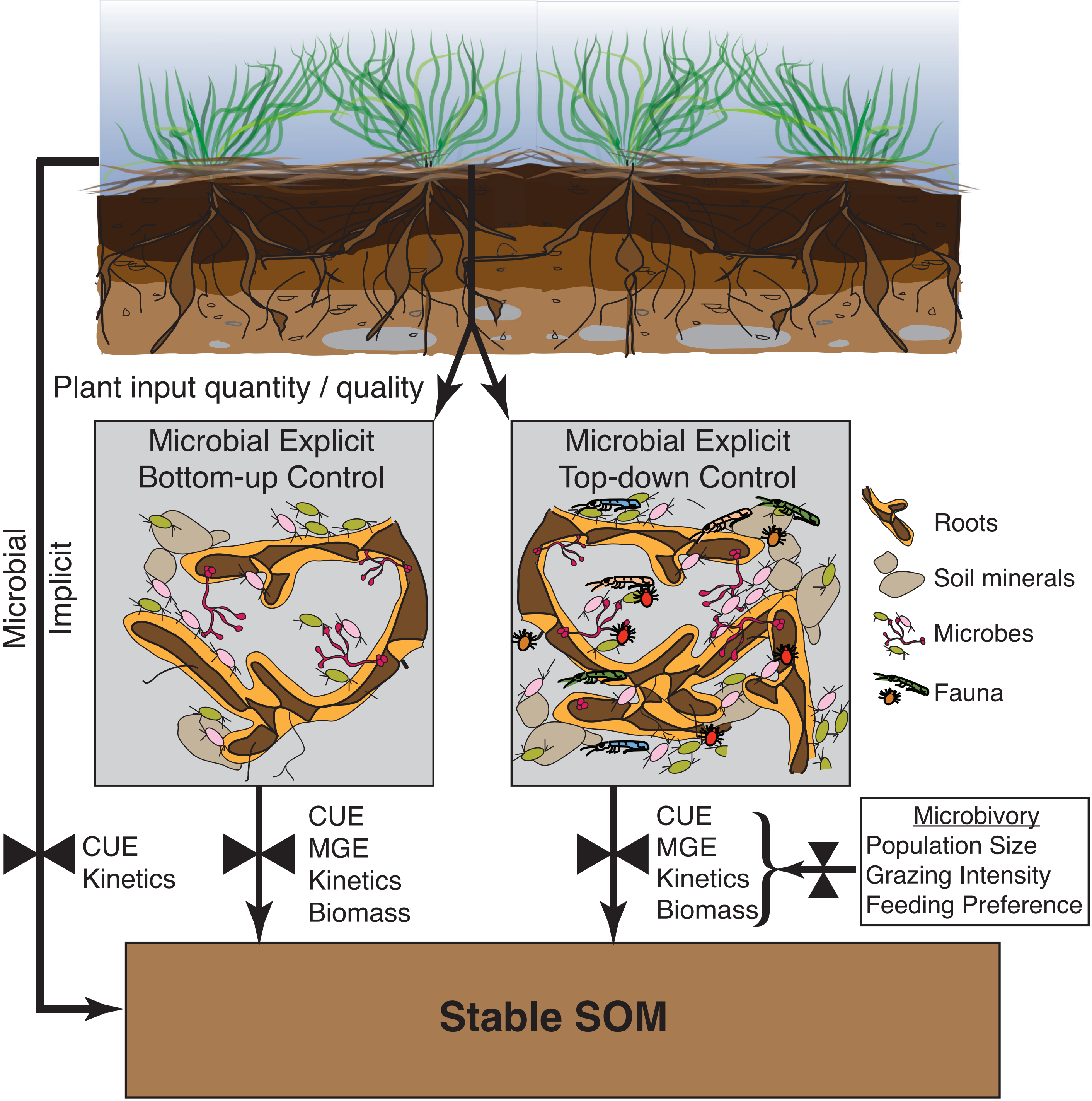
Plant input quantity / quality
Microbial
Implicit
Microbial Explicit
Bottom-up Control
Microbial Explicit
Top-down Control
Roots
Soil minerals
Microbes
Fauna
CUE
Kinetics
CUE
MGE
Kinetics
Biomass
CUE
MGE
Kinetics
Biomass
Microbivory
Population Size
Grazing Intensity
Feeding Preference
Stable SOM

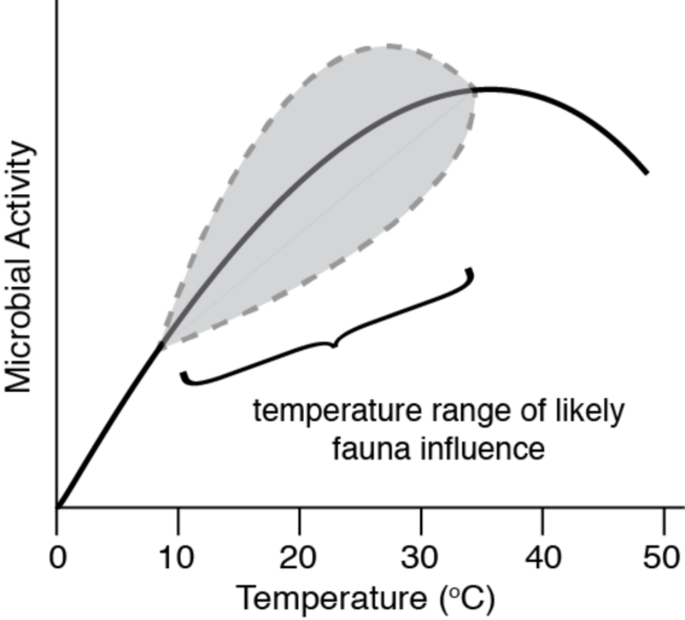
Microbial Activity
temperature range of likely
fauna influence
0
10
20
30
40
50
Temperature (°C)

Table 1. Fauna functional groups and their effects on litter decomposition and soil organic matter formation

Faunal Functional Group	Effects on Litter Decomposition	Potential Effects on SOM formation/recycling
Comminution	Increased surface area Translocation, redistribution Inoculation Increasing moisture	Altered microbial substrate availability and spatial
Microbivory	Suppression of decomposition through overgrazing Stimulating growth, turnover, activity Stoichiometry, chemical changes Microbial community structure (density-dependent effect?)	**Influence on microbial products and enzymes**
Bioturbation	Soil O_2, moisture mixing Translocation/redistribution Resource heterogeneity Chemical controls on microbial community	Aggregation Soil Physical Properties Resource Heterogeneity pH, other chemical properties