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Multitrophic microbial interactions for eco- and agro-biotechnological processes: theory and practice

Muhammad Saleem and Luke A. Moe

Department of Plant and Soil Sciences, 311 Plant Science Building, University of Kentucky, Lexington, KY 40546-0312, USA

Multitrophic level microbial loop interactions mediated by protist predators, bacteria, and viruses drive eco- and agro-biotechnological processes such as bioremediation, wastewater treatment, plant growth promotion, and ecosystem functioning. To what extent these microbial interactions are context-dependent in performing biotechnological and ecosystem processes remains largely unstudied. Theory-driven research may advance the understanding of eco-evolutionary processes underlying the patterns and functioning of microbial interactions for successful development of microbe-based biotechnologies for real world applications. This could also be a great avenue to test the validity or limitations of ecology theory for managing diverse microbial resources in an era of altering microbial niches, multitrophic interactions, and microbial diversity loss caused by climate and land use changes.

Using microbial trophic interactions in ecosystem biotechnology and agroecology

Loss of biodiversity from natural [1] and artificial ecosystems [2] may impair ecosystem services (Glossary). Although functional redundancy or keystone species may compensate for the loss of biodiversity in the short term, a continuous human-mediated external selection pressure may cause tremendous reduction in ecosystem services in the future [3]. This principle has led researchers to explore microbe-based biotechnologies aimed at the restoration and conservation of the natural ecosystems. Although the use of microorganisms (i.e., bacteria) in bioremediation of contaminated sites, wastewater treatment, and plant growth promotion is an emerging approach [4–6], introduced bacteria can be challenged by micropredators such as protists and viruses in natural ecosystems [6–12] (Glossary).

However, over the past few decades, as the interactions between protists, bacteria, and viruses have become more clear, the role of multitrophic level microbial loop interac-

Corresponding author: Saleem, M. (m.saleem@uky.edu).

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Glossary

Amenalism: Type of interaction in which one species is inhibited whereas other is not affected.
Biodegradation: Breakdown of chemicals into by-products.
Biogeographic patterns: Diversity patterns are regulated by spatial scales.
Bioremediation: Microbial conversion of chemicals into non-toxic compounds.
Commensalism: Type of interaction in which one species is benefited without inhibiting other species.
Composition-environment relationships: Relationship between microbial community composition and environmental factors.
Consumptive effects: Predators like protists recycle nutrients that are used by prey (bacteria).
Copiotrophic bacteria: Fast growing bacteria utilize more labile nutrient resources.
Dispersal: Movement and establishment of microbial cells from one place to another.
Distance–decay relationship: Community similarity decreases across distance.
Diversity–disturbance relationship: Describes the effect of disturbance (i.e., anthropogenic or natural) on species diversity.
Diversity–functioning relationship: Relationship of species number (richness) and relative abundance (evenness) with biotechnological and ecosystem processes.
Drift: Species diversity and functioning depend on stochastic processes (i.e., birth, death, colonization, etc.).
Ecosystem services: All ways by which humans benefit from ecosystem biodiversity.
Functional equivalence or neutrality: Equivalence in species functioning and diversity.
Immobilized nutrients: Nutrients sequestered in dead organic matter.
Intra-guild predation: Predation among members of the same taxa, such as protist–protist or bacteria–bacteria predation.
Latitudinal diversity gradient: Microbial diversity across a latitudinal gradient.
Local/deterministic processes: Local habitat factors that determine the niche breadth of a species.
Microbial loop interactions: Interactions among microorganisms that mediate nutrient and energy transfer to higher trophic levels.
Microbial niches: Range of conditions favoring microbial survival and fitness.
Multitrophic interactions: Multidirectional interactions that could be direct or indirect, beneficial or harmful among species across food chain.
Mutualistic interactions: Interactions that benefit both interacting species by exchange of public goods.
Non-consumptive effects: Predators like protists improve habitat conditions better for prey (bacterial) foraging.
Oligotrophic bacteria: Slow growing bacteria capable to utilize recalcitrant organic pool.
Parasitism: One species exploits another species in a non-mutual symbiotic relationship as a parasite.
Relative abundance distribution: Relationship between the number of species reported in the ecosystem as a function of their detected abundance.
Selection: Habitat conditions favour some species or their particular traits, which determines species diversity and functioning.
Speciation/mutation: Evolutionary changes determine speciation, species diversity and functioning.
Symbiosis: Persistent and long-term beneficial interactions between species.
Trade-offs: If one species trait is favored, other will be conversely affected.
Traits: Ecological, molecular, morphological, biochemical, etc., distinct properties of species that determine their survival and fitness.
Trophic cascades: Reduction of prey abundance by predator that reduces prey performance.

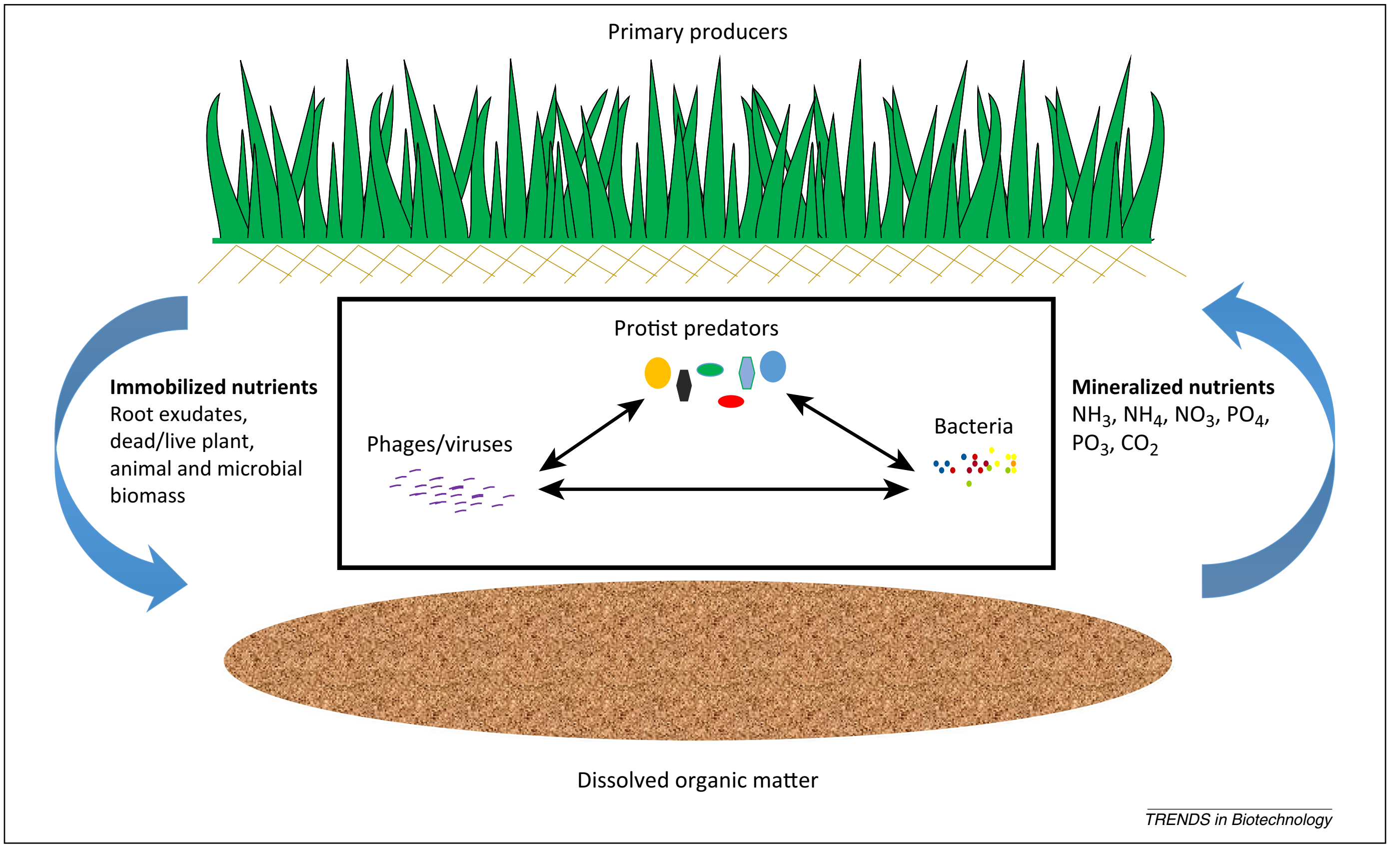

Figure 1. A conceptual view of microbial loop. The concept of the microbial loop was first put forward by Azam *et al.* [82]. The microbial loop is composed of organic matter, phages, bacteria, protists, primary producers, and other higher trophic level organisms (herbivores and predators). The trophic interactions between viruses, bacteria, and protists mineralize the immobilized nutrients, and make them available to microbes, plants and other animals. Through this process, nutrients are transferred into higher trophic level organisms.

tions in accelerating contaminant biodegradation [13–15], improving wastewater quality [16,17], and enhancing plant growth [18,19] has been broadly acknowledged. Despite the vital role of these interactions in different biotechnological and ecosystem processes (Figure 1), little information is available about their applied functional ecology within the context of ecological theories, principles and concepts (e.g., Table S1). This dearth of knowledge greatly hinders their application in biotechnology and ecosystem productivity. This review article represents an effort to encourage ecology theory research in multitrophic level microbial loop interactions, and to enhance their application in different eco- and agro-biotechnological processes in an era of climate and land use changes.

Microbial loop interactions in eco-and agro-biotechnological processes

The trophic interactions among viruses, bacteria, and protists are known as microbial loop interactions. These interactions largely determine the transfer of energy and nutrients to higher trophic level organisms such as primary producers (plants) and consumers (herbivores and predators) in the food web [20]. By mobilizing the captured nutrients in the abundant organic resources (e.g., dead organic matter, root exudates, microbial biomass, etc.), microbial loop interactions link below- and above-ground multitrophic interactions in the food web (Figure 1), thereby determining the multi-functionality and services of ecosystem across different trophic levels. Although the following sections review the role of these interactions mainly in some selected eco- and agro-biotechnological processes, the same framework could also be applied to other microbe-based biotechnologies.

Biodegradation and bioremediation

Protist–bacteria trophic interactions

Increasing nutrient bioavailability to contaminant degraders: Theory suggests that predators can impact prey abundance and activity via consumptive or non-consumptive effects [21]. Consumptive effects imply that predators recycle the immobilized nutrients that increase prey activity and functioning. Non-consumptive effects mean that predators modify the habitat conditions that increase the access of prey to nutrient resources [21]. Protist predators enhance bacterial metabolic activity through these effects, which in turn accelerates the biodegradation of contaminants under nutrient limited conditions [22]. For example, toluene removal by *Pseudomonas* sp. strain PS+ (max. 0.37 fmol cell^{-1} h^{-1}) was increased up to 7.5 times in the presence of the flagellate *Heteromita globosa* (max. 1.38 fmol cell^{-1} h^{-1}) [23]. Likewise, biodegradation of benzene in the same system increased up to three times (0.73 ±± 0.13 fmol cell^{-1} h^{-1}) as compared to a control (absence of *H. globosa*) (0.26 ± 0.03 fmol cell^{-1} h^{-1}). In both cases, accelerated biodegradation was attributed to enhanced bacterial metabolic activity caused by protist-released nutrients in the system [23,24]. In a similar study, protist predation tended to enhance bacterial removal of organic