Breaking down microbial hierarchies

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1 Abstract

Microbial communities that degrade natural polysaccharides are thought to have a hierarchical organisation and one-way positive interactions from higher to lower trophic levels. Daniels *et al*. have recently shown that reciprocal interactions between trophic levels can occur and that these interactions change over the duration of a batch culture.

2 Main

Microbial degradation of complex polysaccharides is a major driver of global nutrient cycling and occurs in all natural ecosystems including the animal and human gut, in soils and in oceans [2]. A common feature of this process is that complete polysaccharide degradation is facilitated by a community of microbes rather than by individual species. Despite their different species composition, these microbial communities share a fundamental principle of organization where a cascade of nutrients (electron donors) flows from higher to lower trophic levels [3] (Figure 1A). Within this cascade, species can in theory be mapped into different trophic levels (also referred to as trophic/functional groups/guilds) based on their source of energy. The metabolic by-products of one level are nutrients for the next, lower level. Hence, species belonging to upper trophic levels enable the presence of species in lower levels and shape their identities. For example, chitinases released by different chitin degraders produce distinct sugar oligomers that both selects for specific exploiters and influence the metabolic by-products they release [4].

In a recent publication, Daniels *et al*. provide a nuance to this general notion of a one-way flow of nutrients [5]. In their work, the authors studied the time-course of chitin degradation by the two bacterial species, *Vibrio natriegens* and *Alteromonas macleodii*. *V. natriegens*, a

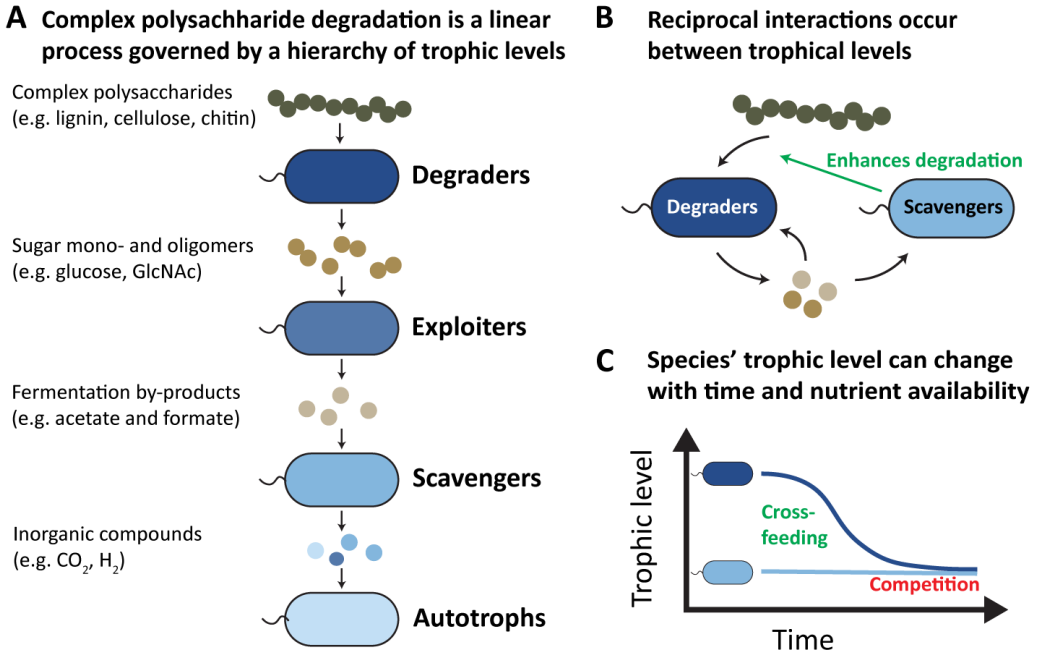

Figure 1: Illustrations of trophic levels and their interactions in complex polysaccharide degradation. The general principle is that degradation is conducted by a hierarchy of trophic levels, where species in higher levels facilitate the growth of species in lower levels (**A**, modified from [1]). However, recent research add nuance to this view, showing that species in lower trophic levels can have a positive impact on species in higher trophic levels (**B**) and that a species' trophic level can change with time and nutrient availability (**C**). Abbreviations: GlcNAc = N-acetylglucosamine

degrader, produces extracellular enzymes that cleave chitin into sugar mono- and oligomers that are small enough to be transported into the cell and catabolized. When feeding on these sugar mono- and oligomers, *V. natriegens* secretes fermentation by-products into the cultivation medium. *A. macleodii*, a scavenger, can neither degrade chitin nor consume the cleaved mono- and oligomers, but instead grows on acetate, a fermentation by-product produced by *V. natriegens*. Thus, during chitin degradation, these two species form a small cross-feeding community that is in line with the general picture of polysaccharide degradation (Figure 1A). However, the authors also find that *V. natriegens* grows better in the presence of *A. macleodii* in the initial phase of cultivation (Figure 1B), due to higher enzymatic activity and chitin degradation. While the mechanism leading to this positive growth effect is not immediately clear, a recent preprint from the same authors shows that scavenger species can upregulate the expression of degraders' chitinase genes to increase chitin degradation [6].

The frequency of reciprocal interactions in polysaccharide degradation and its impact on ecosystem assembly, function and stability is yet to be fully assessed, but the above-mentioned preprint shows that 10/53 pairs of marine *Vibrio* species and 6 different scavengers interact reciprocally between trophic levels [6]. Such interactions, where species in higher

trophic levels benefit from species in lower levels, have also been found between auxotrophic degraders and prototrophic cross-feeders in the human gut [7]. Removal of inhibiting by-products, reactive oxygen species or adjustment of pH are examples of other mechanisms that can lead to reciprocity in microbial communities, allowing species on lower levels to influence species on higher trophic levels. From an evolutionary perspective it makes sense for species on lower trophic levels to support the growth of degrader species that provide their preferred by-products [8]. However, whether this reciprocity is just an accidental effect of the scavenger's metabolism or if there is actually selection for increased cooperation is unclear.

When the chitin is fully degraded and the pool of sugar mono- and oligomers is depleted, *V. natriegens* switches from acetate production to acetate consumption. At this point, *V. natriegens* belongs to the same trophic level as the scavenger *A. macleodii* (Figure 1C), leading to competition between the two species for the remaining nutrients. This transition between different functional levels has also been observed in a model human gut microbiome [1] and demonstrates one of the challenges associated with mapping species onto trophic levels. This result also raises an important question on mapping out species interactions by only considering differences in cumulative or single time-point measures like total yield: Can a single value represent the strength and direction of an interaction between two species and how well does this translate to the natural, changing environment? If not, how does one measure and classify interactions that change over time?

These findings by Daniels et al. were enabled by an elegant experimental set-up where a microfluidics chip (a mother machine) is connected downstream of a batch cultivation [5, 9, 10]. On this chip, each species is cultivated in individual channels and allows for a continuous read-out of each species' growth rate when exposed to the changing batch cultivation medium. It is basically a continuous spent-medium experiment, where one can also measure species' growth heterogeneity. As this approach is scaleable to more complex communities, its full potential should be further explored.

This study bridges two ways of viewing microbial communities, through the lens of interspecies interactions and that of trophic levels. In doing so, it stimulates several open questions in microbial ecology: how do positive and negative interactions change over time? How do interactions shape microbial community composition and function? Are trophic levels well-defined in microbes as in larger organisms? Is it even a relevant concept in microbial ecology? Or is microbial community function better represented by its metagenomic content, or the identities of its member species?

3 References

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