



OVERVIEW

Progress and perspectives in aquatic microbial ecology: highlights of the SAME 14, Uppsala, Sweden, 2015

Eva S. Lindström¹, Paul A. del Giorgio^{2,*}

¹Department of Ecology and Genetics/Limnology, Uppsala University, 75236 Uppsala, Sweden

²Département des sciences biologiques, Université du Québec à Montréal (UQÀM), Montréal, QC H3C 3P8, Canada

ABSTRACT: The presentations and discussion during the Symposium of Aquatic Microbial Ecology (SAME) in Uppsala, Sweden, in August 2015 highlighted new directions and challenges in the study of aquatic microbial communities. In this virtual Special Issue, plenary speakers and meeting awardees explore these challenges. The contributions cover a wide range of topics from the use of molecular analyses of microbial communities to cultivation and stoichiometric analyses. The virtual Special also includes theoretical developments on the concept of rarity to community assembly. A common theme for the Special is, however, the importance of a combination of different approaches in order to deepen our understanding of the ecology of microbial communities.

KEY WORDS: SAME 14 · Molecular tools · Cultivation · Stoichiometry · Assembly · Rarity · Community assembly · Ecological interactions

Many microbial meetings nowadays are dominated by presentations demonstrating the application and development of 'omics', i.e. tools for molecular analysis of diversity and functional capabilities of microbial communities. Not surprisingly, this was also the case at the 14th Symposium of Aquatic Microbial Ecology (SAME 14), which was held in Uppsala, Sweden, in August 2015. The presentations and discussions during the SAME, however, also strongly highlighted new directions and challenges in our efforts to understand the regulation and ecological functioning of aquatic microbial communities. In this virtual Special, plenary speakers and meeting awardees of the SAME 14 explore these various challenges and opportunities.

Over the past decade, high-throughput approaches have resulted in major advancements in our understanding of the large-scale biogeographical patterns of microorganisms (e.g. Comte et al. 2016, Walsh et

al. 2016, Damashek et al. 2017). Finer scale temporal and spatial distributions of microbes (e.g. Székely & Langenheder 2014, Dann et al. 2016, Kirchman et al. 2017), as well as some of the main drivers of these distributions (e.g. Hanson et al. 2012, Péquin et al. 2016, Stahl & Ullrich 2016, Burrel et al. 2017, Reich et al. 2017), have also been identified. These approaches have not only yielded new insight on how communities differ across ecosystems and time, but the increasing sequencing depth currently available has revealed an unprecedented level of resolution of the internal structure of these communities and in particular of the rare microbial biosphere. In their contribution to this virtual Special, Newton & Shade (2016) review the extant information on the structure of the rare biosphere, explore the various lifestyles of rarity, and point to a diversity of patterns in the relationship between abundance and life style, i.e. oligotrophy and copiotrophy. These authors con-

*Corresponding author: del_giorgio.paul@uqam.ca

clude that a change in paradigm is in order, one that moves away from dichotomies, i.e. rare versus abundant, and explicitly embraces the reality that there is a continuum in life styles and eco-physiological strategies and that there are dynamic links between the 2 extremes.

The mounting evidence of a complex and extremely dynamic structuring of microbial communities has led to increasing efforts to unravel the rules of assembly of these communities and the factors underlying these rules, in particular the balance between local selection and dispersal. In this regard, 2 different contributions to this virtual Special focus on this fundamental ecological question. On the one hand, Petro et al. (2017) have carried out an exhaustive meta-analysis of extant data to explore the patterns of community assembly in marine sediments and identify large-scale patterns across ecosystems, as well as with depth at a given site. Their results highlight systematic shifts in bacterial dominance and composition that suggest both widespread dispersion across sites and strong site-specific selection. Vass & Langenheder (2017), on the other hand, take a meta-community perspective to the assembly of freshwater bacterial communities. They highlight the need to consider historical events (such as past environmental shifts and episodes of dispersion) as well as priority effects as major drivers of community assembly. These authors point to gaps in our current understanding and suggest ways to help unravel these drivers, including emphasis on time series and integrated spatial studies.

In their contribution, Krabberød et al. (2017) explore the application of meta-genomic and meta-transcriptomic approaches to determine not just the extant taxonomic and functional composition of these complex microbial communities, but also the ecological interactions between microbes. They propose some interesting new technical and conceptual approaches that should help the development of this area. A concrete example of the above is offered by another contribution to this virtual Special: Farnelid et al. (2016) offer an excellent case study of a molecular-based study on the ecology and distribution of a unicellular symbiotic nitrogen-fixing cyanobacterium (UCYN-A). This unusual cyanobacterium has a reduced genome, lacking genes for oxygenic photosynthesis and therefore relying on the symbiosis with a haptophyte. Genomic approaches have yielded unprecedented insight into this unique ecological interaction.

It is interesting that in spite of the fundamental insight gained from a molecular perspective, Far-

nelid et al. (2016) nevertheless conclude that it would be highly desirable to cultivate these organisms, since there are many dimensions of this complex symbiotic interaction that are difficult—if not impossible—to address only with molecular techniques. This view was in fact echoed throughout the SAME meeting, with multiple voices converging to highlight the need to combine genomic approaches with culturing to explore the physiological and evolutionary underpinnings of the patterns that have been observed. In this regard, Hagström et al. (2017) in their contribution to this virtual Special offer a historical perspective on the issue and remind us that only a few decades ago, the prevalent idea was that bacteria could simply not grow in ambient seawater and that the subsequent cultivation of marine strains has been determinant in the change of paradigm concerning growth of bacteria in extremely dilute environments. The patterns of growth and response to environmental conditions observed in culture set the basis of our current understanding of the eco-physiological strategies underlying bacterial growth and survival in natural environments, and Hagström et al. (2017) urge the community to pursue these efforts by using new and improved cultivation strategies.

Following up on this same theme, Salcher & Šimek (2016) also emphasize the importance of obtaining pure cultures for studies of the autecology of taxa and for whole-genome sequencing, serving as references for studies of functional genes, for example. The authors review several methodological approaches and, more importantly, outline some of the possible reasons why cultivation attempts have so often been unsuccessful. They also emphasize that future cultivation attempts should benefit from information from molecular studies, i.e. a 'full cycle isolation approach'. To take this point further, Garcia (2016) develops the idea of working with mixed cultures of 2 or more bacterial strains, rather than the traditional approach based on single isolates. Garcia develops the hypothesis that most microbes may not be able to grow axenically, since they rely on metabolites provided by other members of the communities or because metabolites are removed by another member of the community. The mixed culture approach may potentially overcome some of the difficulties traditionally encountered in efforts to isolate and study environmental bacteria *in vitro*. The use of mixed cultures that are drawn from the same communities and that include taxa that actually interact in nature may also serve as simplified model communities for experiments, enhancing our understanding of the performance of these taxa under more realistic scenarios.

Further, these cultures may open the possibility of improving the recovery of pure isolates.

It is clear that there is much to be learnt concerning mechanisms behind community assembly, but the ecosystem consequences of microbial community structures because of functional traits are even less explored and may need other approaches than either culturing or molecular exploring. In their contribution to the virtual Special, Moorthi et al. (2017) focus on protists' cellular stoichiometry and explore how the relative contribution of mixotrophs versus photoautotrophs may fundamentally alter seston stoichiometry and the stability of foodwebs at the whole ecosystem level. Their conclusions are based on an extensive literature survey including field studies as well as experimental studies, where N:P ratios of individual species growing under different conditions are explored, demonstrating the power of a combined approach. Thus, molecular studies will no doubt continue to yield increasing insight into the phylogenetic, taxonomic, and functional composition of the complex microbial communities that inhabit all aquatic ecosystems of the biosphere. The SAME 14 contributions, however, all suggest that the next inflexion point in our understanding of the ecology of microbial communities will come from combining and integrating approaches: those that focus on the genetic make-up of these communities, on the adaptations and strategies of their individual players, and on the complex interactions within and among trophic levels, and those that explore the resulting activities and stocks of these communities.

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