



Anthropogenic impacts on aquatic bacteria: a perspective from the tropics

Impactos antropogênicos em bactérias aquáticas: uma perspectiva dos trópicos

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Abstract: Bacterioplankton comprises a highly diverse group of microorganisms, which are dominant in aquatic ecosystems, and play a central role in ecosystem functioning and biogeochemical cycles. Due to their high turnover and dispersal rates, as well as high adaptability and plasticity, microbes are likely to respond quickly to environmental changes and perturbations on their ecosystems. In this opinion paper, we reviewed some studies that addressed bacterial community's responses to anthropogenic impacts in their aquatic environments. Inorganic nutrients and organic matter inputs from the catchment areas are likely to increase due to changes in climate and land use. These changes will impact the microbial community composition and metabolism, as well the amount of energy and carbon flowing through aquatic food webs as mostly demonstrated in studies from temperate and boreal systems. However, due to the low number of studies on microbial communities in tropical ecosystems, our understanding of how they will respond to perturbations in this distinct environmental context is still limited. Research in microbial ecology in southern countries is still in its infancy and deserves more attention in the future, since tropical aquatic ecosystems are hotspots of biodiversity, host most of the world freshwater reserves, and play a key role in global biogeochemical cycles.

Keywords: microbial ecology; bacterial community composition; bacterial metabolism; climate change.

Resumo: O bacterioplâncton compreende um grupo altamente diversificado de microrganismos, que são dominantes nos ecossistemas aquáticos e desempenham um papel central no funcionamento desses ecossistemas e nos ciclos biogeoquímicos. Devido às suas elevadas taxas de dispersão e de mudança na composição, bem como alta adaptabilidade e plasticidade, os microrganismos devem responder rapidamente às mudanças e perturbações ambientais. Neste artigo de opinião, revisamos alguns estudos que abordaram respostas de comunidades bacterianas aos impactos antrópicos em seus ambientes aquáticos. Os nutrientes inorgânicos e a matéria orgânica das áreas de drenagem provavelmente aumentarão devido às mudanças no clima e no uso do solo. Essas mudanças afetarão a composição e o metabolismo das comunidades microbianas, bem como os fluxos de energia e de carbono nos ecossistemas aquáticos, como majoritariamente demonstrado para sistemas temperados e boreais. No entanto, devido ao reduzido número de estudos sobre comunidades microbianas em ecossistemas tropicais, a nossa compreensão de como elas responderão às perturbações neste contexto ambiental distinto ainda é limitada. As pesquisas em ecologia microbiana nos países do hemisfério sul ainda estão em sua infância e merecem mais atenção no futuro, uma vez que os ecossistemas aquáticos tropicais são *hotspots* de biodiversidade, abrigam a maior parte das reservas de água doce do mundo e desempenham um papel fundamental nos ciclos biogeoquímicos globais.

Palavras-chave: ecologia microbiana; composição da comunidade bacteriana; metabolismo bacteriano; mudanças climáticas.



1. Introduction

According to the Intergovernmental Panel on Climate Change (IPCC), in tropical regions, increasing temperatures and extreme precipitation events are likely to become more frequent and intense. These changes will impact the amount of energy and organic matter flowing and transported by freshwater ecosystems, with consequences for the structure and functioning of these systems, that can ultimately have impacts on global biogeochemical cycles. However, the effects of climate changes in planktonic communities of tropical regions are still largely unknown (Sarmiento et al., 2013).

Bacterioplankton comprises a taxonomically, phylogenetically, and metabolically highly diverse group of microorganisms which are dominant in aquatic ecosystems. They are mediators of biogeochemical fluxes, playing pivotal roles in organic matter degradation, nutrients recycling, energy transfer, and CO₂ emissions (Azam et al., 1983; Cotner & Biddanda, 2002). Due to their high turnover and dispersal rates, and high adaptability and plasticity, microbes are very sensitive and respond quickly to environmental changes and perturbations on their ecosystems (Cotner & Biddanda, 2002), being good models to address how ecosystem functioning and services respond to disturbances in a changing world context.

Because of the low number of studies covering bacterioplankton diversity in tropical ecosystems, our understanding of how they will respond to perturbations in this environmental context is still limited. However, this is needed since tropical zones host 80% of the world's biodiversity and 15 of the world's 25 biodiversity hotspots (Harding et al., 2014; Myers et al., 2000), but have received least attention compared to boreal and temperate regions. One of the reasons for that is that tropical regions include the poorest countries in the world, and in those countries, access to sequencing facilities is still a challenge and extremely expensive. At the same time, these countries are those that are more threatened concerning biodiversity loss because of deforestation and changes in land use (Barlow et al., 2016), and also those that host most of the world freshwater reserves (Oki & Kanae, 2006).

The advent of new tools including next generation sequencing and novel modelling approaches have been modifying our view about the diversity of natural microbial communities and their dynamics across a variety of temporal and

spatial scales. These advances have allowed us to unravel the processes and mechanisms underlying microbial diversity and distribution in several aquatic ecosystems (Szekely & Langenheder, 2014; Ruiz-González et al., 2015), and microbial ecology has been progressively integrated to macroecology (Barbéran et al., 2014), e.g. providing some of the most important contributions to recent developments in community ecology (Vellend, 2010; Stegen et al., 2012) described below.

Currently, it is broadly recognized that microbial communities are simultaneously structured by a combination of deterministic and stochastic processes, which vary according to the characteristics of each ecosystem (Stegen et al., 2012). For instance, species sorting concerns to the differential response in deterministic aptitude among species in relation to a complex combination of abiotic environmental variables and biotic interactions (Leibold et al., 2004). In contrast, stochastic processes include random birth-death events. Mass effect consider the movements of immigration and emigration by deterministic or random causes and has recently been suggested to occur often in aquatic environments due to the high dispersion by water flows (Ruiz-González et al., 2015; de Melo et al., 2019). Because speciation happens in an evolutionary time scale, less attention has been focused in the formation of new species in microbial community's assemblage dynamics (Hubbell, 2011; Vellend, 2010).

Given that many aquatic ecosystems are undergoing rapid and deep modifications by climate changes and human mediated activities, there is an increasing interest in understanding how these changes, individually or in combination, are affecting the diversity and composition of aquatic bacterial communities across aquatic systems worldwide. Currently, most of the available studies regarding the microbial response to anthropogenic impacts have focused on growth such as bacterial abundance, biomass, and metabolism in temperate and boreal environments (Sand-Jensen et al., 2007; Hall et al., 2009; Özen et al., 2013). However, few studies have actually tested the effects of anthropogenic impacts on the structure and diversity of freshwater bacterial communities. Here, we provide some examples of how changes in freshwater ecosystems could affect the structure and activity of aquatic bacterial communities, and discuss some possible scenarios for the understudied tropical regions.

2. Impacts on Bacterial Community's Structure

Subarctic and arctic regions are threatened by increasing permafrost thawing due to climate warming (González-Eguino & Neumann, 2016). Similarly, storm-affected areas in tropical zones are likely to experience increases in precipitation and increased risk of flooding. In other words, the on-going climate warming is mobilizing terrestrial carbon pools and increasing the allochthonous carbon inputs from the catchment to surface waters worldwide, ultimately affecting ecological processes and the structure of aquatic microbial communities. These changes could be exemplified by the pure and direct effect of addition of soil bacterial taxa, which are currently considered important sources for bacterial communities located downstream in temperate aquatic habitats (Ruiz-González et al., 2015). Additionally, more complex consequences related with changes in water conditions, i.e. transparency, nutrient concentrations, and quality of organic substrate, are likely to filter the establishment and successful of dispersed bacteria.

It was demonstrated for small and shallow ponds (Roiha et al., 2016) that high concentrations of terrestrial dissolved organic matter (DOM), nutrients, and algal exudates favoured high microbial productivity but selected a less diverse microbial community. In contrast, outlets with a lower degree of exposition to terrestrial DOM and poor in nutrients and humic materials had lower bacterial metabolism, but a more diversified community composition. Overall, these results suggest that terrestrial-DOM inputs are likely to favour heterotrophy relative to autotrophy and decrease microbial diversity.

These findings pointed that also the impact of increased inorganic nutrients inputs (i.e. eutrophication) is another aspect to be considered in synergism with climate warming. Eutrophication might be a result of the interplay of complex socioeconomic factors, which include population and economic growth, dramatic changes in land-use, and the increased consume of artificial fertilizers (de Jonge et al., 2002). Because of that, aquatic systems worldwide, especially in developing countries are experiencing increase in eutrophication trends, and cyanobacterial harmful algal blooms (e.g. O'Neil et al., 2012).

Blooms are known to influence the composition of bacterial communities, especially of some specific taxa (Louati et al., 2015; Berry et al., 2017). During

a late spring-summer bloom in Funil reservoir (Rio de Janeiro, Brazil), two periods could be distinguished (Guedes et al., 2018). The first period was characterized by higher retention time, low transparency and dominance of *Microcystis*, which was positively correlated with Bacteroidetes OTUs (particularly Cytophagales), and negatively correlated with several taxa, including the genera *Planctomyces*, *Limnohabitans*, and *Hyphomicrobium*. The second period was characterized by the dominance of *Synechococcus* and *Cylindrospermopsis raciborskii*, which coincided with lower retention time and less turbidity, and an increase in the relative abundance of Planctomycetes. Specifically, they observed a strong correlation between *Planctomyces* and *Synechococcus*, and positive correlations between *C. raciborskii* and the genera *Gemmatimonas* and *Roseococcus*.

During a monitoring period of six months, cyanobacterial bloom biovolume remained high for a continuous period of four months ($>10 \text{ mm}^3 \text{ l}^{-1}$ of all cyanobacteria) in Yanga Lake, a shallow and ephemeral lake located in Australia (Woodhouse et al., 2016). The lake was mainly dominated by *Dolichospermum*, *Microcystis*, *Aphanocapsa*, *Geitlerinema*, *Oscillatoria*, and *Sphaerospermopsis*, and significant changes in bacterial community composition were observed, a dominance of Actinobacteria and Alphaproteobacteria, when cyanobacterial biovolume were low, and by Actinobacteria, Bacteroidetes and Cyanobacteria when cyanobacterial biovolume were elevated. During periods of high cyanobacterial abundance, Betaproteobacteria, Gammaproteobacteria, Planctomycetes and Verrucomicrobia were also present at substantially greater abundance than at other periods (Woodhouse et al., 2016). Both studies highlight that the structure of bacterial communities in freshwaters are threatened by increased eutrophication on nutrient cycling, especially regarding cyanobacterial blooms. However, to the best of our knowledge, no studies have evaluated consequences of warming and nutrient-enrichment combined for the structure of bacterial communities in tropical waters.

Finally, changes in land use seem to have a great impact on factors structuring microbial communities in aquatic environments. Using the gradient polluted of a subtropical river, the river Chaobai in China, Liao et al. (2018) found differential partitioning in microbial biomass, metabolism, and community composition among three areas with different human activities, less-disturbed mountain areas,

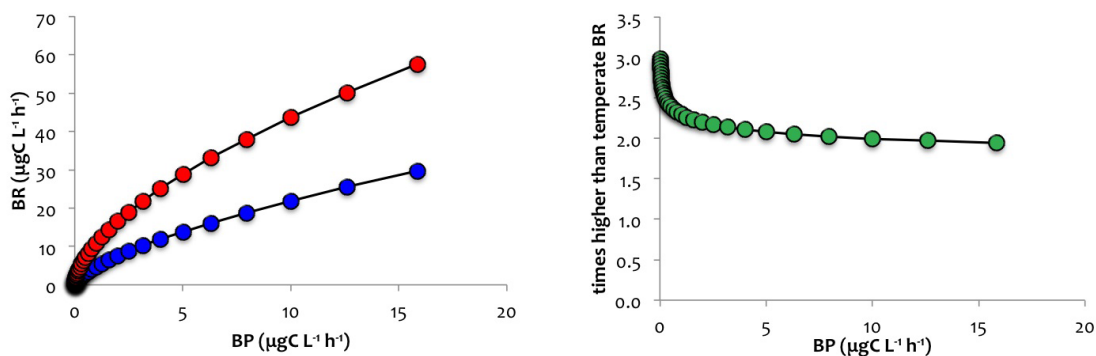


Figure 1. Estimated relationship between bacterial production (BP) and respiration (BR) in temperate (blue) and tropical (red) regions, from a literature review (same database as the one compiled by Amado et al., 2013). The right panel illustrates the tropical:temperate ratio of BR rates (from the left panel): for a given level of BP, BR in tropical regions is expected to be two to three times higher than temperate regions.

urban and agricultural dominated areas. Bacterial communities from mountain areas had significantly higher richness and phylogenetic diversity. In the same study they found that the temperature was the major factor causing variances in sampling seasons, while DOC and chlorophyll-*a* were critical for the variability among areas. Altogether, these results suggest that a combination of factors related to anthropogenic activities and climate change affect the structure of freshwater bacterial communities.

3. Bacterial Metabolism

Besides community composition, microbial metabolism is a subject of big concern regarding anthropogenic impacts on aquatic environments because it directly affects ecosystem services and biogeochemical cycles. Bacterial metabolism (especially bacterial respiration) in warmer regions is expected to be two to three times higher than in temperate regions (Figure 1) (Amado et al., 2013). Therefore, it is likely that increasing water temperatures will have strong impacts on aquatic ecosystems carbon budgets. However, the drivers of bacterial metabolism may act differently according to latitude, as seasonality in the tropics is determined mainly by rainfall rather than temperature (Freitas et al., 2018). Besides, it is likely that temperate systems are more carbon limited, while in tropical systems nutrient limitation is probably more frequent (Amado et al., 2013; Freitas et al., 2018), therefore the effects of anthropogenic impacts might also vary according to geographic region.

One of the few experimental studies that tested the effects of temperature and nutrients input on bacterial metabolism was carried out in tropical humic lagoons, and reported consistent increase

in bacterial respiration, decreasing bacterial production, and decreasing bacterial growth efficiency with increasing temperature. However, the effect of nutrient inputs was more idiosyncratic, but seems somehow related to the availability and quality of the dissolved organic carbon in each lagoon (Scofield et al., 2015).

In fact, climate changes will impact inland water differently depending on the region. E.g., considering the huge Brazilian territory, different scenarios could be expected concerning the result of several environmental driving forces in the structure and functioning of aquatic systems (Roland et al., 2012). Although some regions will experience decreased precipitation (increase in the number of consecutive days with no precipitation), other will experience changes in the frequency of precipitation (increase storms in the summer). Therefore, the amount of energy and matter from terrestrial inputs metabolized by microbial communities will be different (Roland et al., 2012).

There is no doubt that the bacterial metabolism in aquatic ecosystems will be impacted by climate changes and anthropogenic interferences, which will certainly affect biogeochemical cycles, since tropical aquatic ecosystems account for a significant share of global greenhouse gas emissions (Aufdenkampe et al., 2011). In this regard, future studies should predict how changes in environmental drivers in different geographic regions will affect the aquatic biota in different scenarios.

4. Final Remarks and Future Perspectives

The facilitation of access to sequencing facilities and the development of regional networks of researchers in southern countries may be the key to advance microbial ecology in these regions.

A good example of how this could be achieved is the μ SudAqua network (MicroSudAqua, 2019), a group of researchers and students working in microbial aquatic ecology in Latin America, that meet periodically in workshops, seeking to strengthen collaborative research and formation of human resources to promote microbial ecology at the regional level.

In addition to the effects of climate change, anthropogenically-derived water pollution is another major impact within aquatic ecosystems. Until recently the existence of substances as antibiotics, microplastics and chemical pollution in the water environment have received little notice. However, several studies have quantified and described the effect of such pollutants to the structure and functioning of natural microbial communities (see Marti et al., 2014; McCormick et al., 2016; Labbate et al., 2016), which appears to be a hotspot for current and future research in microbial ecology.

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