

From competition to cooperation: Paradigm shifts in trait-based ecology change our understanding of the processes that structure microbial communities

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ABSTRACT. Prevailing social, economic and political ideas and paradigms constitute the lens through which scientists observe, assess, and understand the world. This affects how we interpret and understand the mechanisms governing the interaction between organisms and has led, in most cases, to dominant explanations and paradigms that are difficult to overthrow. This is the case of ecological theory, whose perspectives have followed the rationale of societal changes. From the industrial revolution to very recently, species competition for resources was regarded as one of the main drivers of species interactions. Nowadays, a new and rapidly growing way of thinking emerged, fueled by the high sequencing capacities, ultra-resolution microscopy and the slowly growing number of different social and gender perspectives participating in ecological studies: that living beings are not just single organisms interacting with other single organisms, but complex communities of macro- and microorganisms living and evolving together. The information emerging from this field is bringing new light to previously disregarded aspects of the ecological interactions that, in our opinion, will change the main paradigms in ecology. As members of a South American scientific network of Aquatic Microbial Ecology (MicroSudAqua), here we propose to explore alternative explanations for ecological observations, searching for new traits accounting for cooperation between microorganisms as a fundamental evolutionary and ecological strategy.

[Keywords: traits, ecological theory, cooperation, competition, biases]

RESUMEN. De la competencia a la cooperación: los cambios de paradigmas en la ecología basada en rasgos cambian nuestro entendimiento de los procesos que estructuran a las comunidades microbianas. Las ideas y paradigmas sociales, económicos y políticos prevalentes constituyen la lente a través de la cual las científicas y los científicos observamos, evaluamos y comprendemos el mundo. A menudo, esto impregna y afecta la interpretación de los mecanismos que rigen las interacciones entre organismos, y llega a generar paradigmas difíciles de poner en discusión. Un ejemplo es el caso de la teoría ecológica, cuyas perspectivas han seguido la lógica de los cambios sociales. Desde la época de la Revolución Industrial hasta muy recientemente, la competencia interespecífica por los recursos se consideró como una de las formas principales en que las especies interactúan. En la actualidad, presenciamos un cambio en la forma de pensar; su crecimiento es veloz, impulsado por las capacidades de secuenciación masiva, la microscopía de ultra resolución y la cantidad cada vez mayor de diferentes perspectivas sociales y de género con la que se abordan los estudios de ecología. Esta nueva perspectiva implica que los seres vivos no son organismos solitarios que interactúan con otros organismos solitarios, sino comunidades complejas de macro y microorganismos que conviven y evolucionan juntos. La información que emerge de este campo está dando nuevos aportes a aspectos antes ignorados de las interacciones ecológicas; en nuestra opinión, estos aportes cambiarán los principales paradigmas de la ecología. Como integrantes de la Red Científica Sudamericana de Ecología Microbiana Acuática (MicroSudAqua), en este trabajo exploramos explicaciones alternativas de las observaciones ecológicas, buscando nuevos rasgos que den cuenta de la cooperación entre microorganismos como una estrategia evolutiva y ecológica fundamental.

[Palabras clave: rasgos, teoría ecológica, cooperación, competencia, sesgos]

INTRODUCTION

Since the origin of western philosophy and science, more than 2500 years ago, scientists have been struggling to unveil the evolutionary and ecological mechanisms that account for the observed biodiversity patterns. Today, we know more than ever in history about the interactions between organisms and their environment, how they interact and, as a result, shape each other. However, not all the mechanisms involved in life evolution and the ecology have been addressed with the same intensity. This is the case of cooperation and its role in ecology, which has received less attention than competition in terms of the level of formalization and in the quantification of its contribution to community structure and ecosystem functioning (Raerinne 2020). The interactions between species generate a complex evolutionary picture where the fitness of a cell depends on its own phenotype and on the overall community composition. In this framework, the presence of a cooperative trait (e.g., a common good) may change the fitness of other members of the community and these changes can be also beneficial for the fitness of the cell harboring the trait (West et al. 2006). In the case of complex microbial communities, the challenge is to determine which are the relevant cooperative traits, and how to quantify their effects at the community level (when there might be hundreds to thousands of species), in order to unveil how the evolution of cooperation takes place (Pennisi 2009). In this article, we aim to contribute to the debate on how to incorporate cooperation mechanisms to the study of microbial communities using trait-based ecological tools.

Traits-based ecology, its paradigms and biases

The way of looking at the living world and interpreting scientific data is ideologically driven and fueled by the historical development of dominant Western cultures (e.g., Nisbett and Masuda 2003) and mainstream capitalist economics over the past centuries. In the nineteenth century, Darwin developed the natural selection theory through the observation of the variability of organisms in different environmental conditions (Gayon 1998; Shields and Bhatia 2009). Although he did not employ the term trait, recognized how some characteristics of the organisms are fundamental for survival, reproduction and adaptation of organisms to their environment

and determine their distribution. Selective pressures act on these characteristics that are, thus, the target of evolution; natural selection can be therefore measured on these traits. Moreover, in *On the Origin of Species by Means of Natural Selection* (Darwin 1859), Darwin highlighted that, as resources are insufficient for all organisms to survive, there was a continual 'struggle for existence' in nature, that selects organisms whose hereditary adaptations (or traits) made them most fit to a specific environment, and would survive. For Darwin, this happened in an ecological scenario where competition played a major role in driving the struggle and, thus, species evolution. Since the 19th century and through the 20th century, progress has been made in ecological studies, with competitive pressure as one of the most relevant paradigms explaining the interaction between organisms (Law and Watkinson 1989; Bjorbækmo et al. 2020). In fact, research linking functional traits to the competitive ability of co-existing species is vast, and much research on species co-existence is guided by the competitive exclusion principle (Gause 1934). This body of theory relies on the assumptions that resources are scarce, the environment is mostly stable and the main drivers of community dynamics are competitive interactions (Simha et al. 2022). Drawing conclusions based on competition has eventually been reinforced through the years by culture, mainstream economic liberalism, and institutions (Gould 1981; Haraway 1988). The logic behind the use of individual trait approaches in ecology is based on focusing on particular facets of individuals in a given background. Similarly, the R star concept in the resource ratio theory has been influenced by microeconomics thinking in a liberalist context rooted in capitalism (Rapport 1971; Covich 1972; Tilman 1980), while Lotka-Volterra population models have been applied to economic problems under a free-market paradigm (Goodwin 1967). In this context of capitalist thinking, the interpretation of natural phenomena has been developed by the scientific community (Kirk 1997), and that traits-based ecology is established. However, recent investigations have shown that in a Lotka-Volterra model, the interaction coefficients that measure competition are low (<1), indicating that negative interactions between species may not be as relevant (e.g., Fort and Segura 2018; Grilli 2020) and open the question about which interactions are relevant and how to quantify them.

Nowadays, western human society is changing, including historically neglected thinking as is the case for women (Blackwell 1875). As a consequence, there is a growing involvement of women and other minorities in several activities and disciplines. Science and, in particular, evolutionary ecology is not an exception, and new perceptions have brought new ways of analyzing and explaining biological and ecological processes (Schiebinger 1991). One of the paradigmatic examples is the story of Lynn Margulis, a long-time neglected scientist who claimed that the breakthrough in life evolution arose from symbiotic cooperation between two or more organisms (Margulis 1971; Guerrero et al. 2013). In this context, other authors also go beyond the individual perspective to a vision of symbiotic complexes of many species, considering the importance of symbiosis at the ecosystem level (Gilbert et al. 2012).

This debate paper uses available evidence to propose that alternative explanations can help to explain many unresolved facets of ecology. To achieve this, we must be aware that the interpretation of nature and its processes is as diverse as the people who study it. Starting from this premise and using microorganisms as model organisms, we present a brief background on traits-based ecology and its basic assumptions to propose the exploration of new traits that account for the cooperation between organisms as a fundamental evolutionary and ecological strategy. Testable predictions and a new body of theories are needed to make the available data and methods useful.

Soft traits and new traits

In ecology, a trait refers to a physiologic, morphologic or genomic feature that determines the fitness or function of an organism (McGill et al. 2006; Krause 2014). Traits can, therefore, be used to evaluate performance under different environmental conditions and ideally can be scaled up from single organisms to the community level and eventually to ecosystem functioning (Violle et al. 2007; Wallenstein and Hall 2012). One of the appeals of using trait-based approaches is that some traits, which are easy to measure and do not require expensive methods or technology, resume the organism's responses to the environment (e.g., organism dimensions, presence of differentiated structures, etc.). Owing to their characteristics, these are called 'soft' traits (Hodgson 1999). The use

of microbial traits in aquatic ecology studies, especially soft traits, can help to generate knowledge to fulfill different goals, such as evaluating the impact of environmental changes on microbes at different scales, and vice versa, generating and improving tools for environmental management or historical environment reconstruction. This would increase knowledge about the metabolic complexity of ecosystems and help to predict future scenarios, as well as their effect on the human population and vice versa.

Currently, the traits used by microbial ecologists have moved into the molecular realm, fueled by the emergence of molecular biology-based technologies such as single-cell approaches, high throughput sequencing and high-resolution microscopy. Notably, the development of sequencing by synthesis technologies allows the rapid characterization of hundreds of samples at a time, giving a quite detailed perspective on aquatic microbial patterns (i.e., metabarcoding). These resources, combined with functional -omics (meta-transcriptomics, -proteomics), allow inferring the organism's functions provided by their metabolic characteristics, such as the ability to process different carbon sources, or to cycle different nutrients, gas emissions, etc. (Martiny et al. 2015). These post-genomic approaches allow one to determine which genes are expressed where and when, thus providing more sensitive and insightful data on how environmental conditions may influence gene expression (Reid and Bergsveinson 2021). These correlations improve the knowledge about the relationships between the trait (\times metabolic ability) and the environment, making it possible to scale up conclusions from individuals to community processes. These processes can be related to satellite data, which allow, for example, remote sensing of phytoplankton biomass on large spatial and temporal scales (Lobo et al. 2021).

These multifaceted approaches led also to a shift in data interpretation, leaning towards more holistic interpretations. One of the most addressed topics in this matter is the interaction between phytoplankton and heterotrophic bacteria. Evidence is accumulating for a new vision of plankton diversity in which organisms are interconnected through a great number of biotic interactions. Indeed, there is an emerging view that these interactions should be considered within the framework of the holobiont concept (Gordon et al. 2013; Guerrero et al. 2013; Bosch and Miller 2016;

Baedke et al. 2020), which has been increasingly used in association with the hologenome concept (Morris 2018). As evidence about how the close association between macro- and microorganisms influences the ability of the entire entity to cope with adverse environmental conditions becomes clear, also becomes clear that the organisms cannot be analyzed individually anymore. In fact, most microorganisms (prokaryotic and eukaryotic) seem to live in complex aggregates or biofilms, where they found an ideal environment with a gradient of nutrients, genetic exchange and protection from predators and antimicrobial substances (Donlan 2002). Furthermore, analysis of genomes from different organisms revealed that essentially all life forms share ~1/3 of their genes and that many animal genes are direct descendants of microbial genes or are a consequence of horizontal gene transfer. Furthermore, the genome sequences of early metazoans have been shown to contain an important fraction of genes that encode proteins of bacterial origin (Bosch and Miller 2016). Thus, the evidence suggests that gene exchange is an ancient and probably a very relevant process in the co-evolution of the holobiont members.

In sum, while community patterns were considered in the past as the product of competition for resources (e.g., light, nutrients, etc.), the present paradigm tends to shift towards a wider picture that includes cooperation as a frequent mode of interaction. Moreover, based on current evidence indicating that the vast majority of organisms actually constitute a holobiont, or a community of interacting organisms, we could say that the so-called communities of organisms would actually be “communities of communities” that could be envisaged as metacommunities. In addition, as Miller et al. (2018) suggested, the biotic nature of the host requires incorporating feedback between the habitat patch (host) and its local (microbial) community. In this framework, to determine which are the ecological traits accounting for cooperative interactions, recording and quantifying them is necessary in order to mathematically model their relevance in community assembly and species diversity.

Cooperative traits

Cooperation can be tracked by following a certain number of traits that we call here *cooperative traits*. These traits are widespread in the evolutionary history of life as a whole,

but we will focus here on aquatic microbes. We will provide some examples, which have significant impacts at the ecosystem level and beyond.

Photosymbioses, the association between a larger, heterotrophic organism and photosynthetic organisms, are an example. It generally implies a large eukaryotic organism (foraminiferans, radiolarians and corals in the sea, Arcellinid testate amoebae in freshwater, ciliates in both) and small phototrophic eukaryotes living within the heterotrophic organism. In these associations, phototrophs provide photosynthetic by-products (carbohydrates) to the heterotrophic host that, in turn, provide nutrients such as nitrogen and phosphorus, as well as protection against predators and viruses (Matthews et al. 2018). In this case, the trait (the presence of a pigment) appears like a green, yellow or red color on the cytoplasm and would be a soft trait. These associations are particularly widespread and successful in oligotrophic systems where the lack of nutrients limits the growth of both partners. Taking corals as the best-studied example, the sequencing of the genome of *Symbiodinium goreauii* showed traces of positive selection in 2460 gene families used in cooperation (Liu et al. 2018), and this association lasts across broad temporal and geographical scales (Baker 2003). The presence of these genes in an organism could be used as a (hard) cooperative trait. Finally, the presence of more than one organism having a mutualist strategy, such as in photosymbiosis, is also a cooperative trait itself, one that is widespread in many aquatic biomes on Earth, allowing the existence of a high biodiversity even where the reduced amount of nutrients should be a limiting factor.

Mutualist interactions do not always occur intracellularly. Large phytoplankton cells are typically surrounded by an exopolysaccharide-rich zone called the phycosphere, usually populated with bacteria and sometimes with other primary producers (Bell and Mitchell 1972; Seymour et al. 2017), which constitute the microbiome of the phytoplankton (Fu et al. 2020). The interactions occurring in the phycosphere play an important role in carbon and energy flux in the ocean and have implications on the carbon cycle at a global scale (Fu et al. 2020). It has been proposed that physicochemical dynamics and phycosphere size influence the size and stability of the holobiont (Seymour et al. 2017). Thus, the thickness of the exopolysaccharide in a

phytoplankton cell could be used as a soft trait accounting for cooperation between the phytoplankton and its associated microbiome. At the molecular level, interactions between phycosphere microorganisms and between them and phytoplankton can also be detected and/or quantified (e.g., by qPCR, sequencing, in situ hybridization, and other labeling techniques) and used as traits (Thompson et al. 2018; Platt and Whalen 2023).

Including new traits that account for cooperative relationships and symbiosis in the study of phytoplankton dynamics would allow another dimension of functionality to be incorporated into the analysis. Identification of the relative importance of the taxonomic composition versus environmental and temporal stability is an important factor in predicting variability in fitness traits (Jackrel et al. 2020, 2021). Once the host-microbiome interaction and its effects are known, analyzing the thickness of the phycosphere (an easily measurable trait) can provide biological and ecological information (e.g., the stage of the life cycle, exponential growth, senescence, etc.) (Passoni and Callieri 2000).

These are only a couple of examples where cooperative interactions between planktonic microbes have been found to be more relevant than previously thought, being responsible for the evolution, survival and success of all partners involved (Guerrero et al. 2013; Bordenstein and Theis 2015; Bosch and Miller 2016; Cohen and Marron 2020).

Biases and future directions

As occidental scientists, we have several biases when interpreting nature that have cultural, historical, economic and political roots. In addition, there are also gender-related biases that transfer the binary definitions used to distinguish between men and women to

the interpretation of nature. This conceptual framework based on binary questions has permeated our way of examining the relationship between living beings (Morgenrot et al. 2021). The binary definitions give rise to oppositional dualism, where one side is not only described as different from the other but as its opposite, leading to a way of thinking based on competition between two sides (Butler 2002). In this way, we must be careful not to add more confusion by generating a further binary opposition between competition and cooperation. Like many processes in biology, there must be a gradient of states between both types of interactions, the weight and relevance of which have yet to be revealed (Wilson et al. 1997).

The binary thinking that dominated centuries of scientific research is now changing, giving rise to a new way of understanding nature and the great complexity of relationships that weave the fabric of life and support life on Earth. A new perspective on studying the relationships between organisms is emerging and for the little we know about their interactions; it seems that we all live in a kind of partnership essential for health and survival where “we become with each other or not at all” (Haraway 2016). Recognizing the perception of the environment without biases is difficult and challenging, but is an enterprise we must embrace if we want to have a better comprehension of nature.

ACKNOWLEDGEMENTS. We would like to acknowledge all the women and gender diversities that have contributed to ecology, mainly to those who struggle to make their voices heard in times that were far more difficult than now. We also thank MicroSudAqua for bringing together this cooperative network and the reviewers, who contributed with their comments and insight to improve the quality of this manuscript.

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