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SYMPOSIA PAPER

Different Meaning in Different Sizes: Ecology in Size Scales

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Abstract

Any given ecosystem includes macro- and micro-organismal ecology. I examine the concept of stability and its meaning in these two size scales. Historically, the stability concept follows species population dynamics and equilibrium. In micro-ecology, however, classification is rare and, in the majority of cases, not possible. Therefore, the microbial taxonomic composition is regarded in a nonspecific way, as opposed to animals and plant communities. Such different consideration leads to the emphasis on functional stability in micro-ecology versus the structural in macro-ecology. I discuss the implication of these differences in meanings and the possibilities of integrating them.

1. Introduction

In any given ecosystem, we have two different size scales: the macro-organismal ecology of animals and plants (i.e., macro-ecology) and the micro-organismal ecology of microorganisms (i.e., micro-ecology). The size scale has implications on the time scale of shorter life cycles and higher evolvability rates. These scale differences have methodological and conceptual implications such as the classification challenges in microbiology. Thus, when looking at ecological systems with both micro and macro scales, it is important to ask whether one theoretical framework fits both. The concept of stability in ecology follows criteria of the structure and function of a community or ecosystem. Both structure and function and their relations are important in understanding ecological systems, their stability, and persistence (decay or succession). However, there are differences in the emphasis on structure and function between micro- and macro-ecology. These differences are largely due to the challenge of microbial classification and their biochemical nature.

In my analysis of stability, I discuss function in its ecological meaning as descriptive of processes of interactions causing constant gradual state changes within a system contributing/influencing the system's stability and persistence as a whole (Jax 2005). Thus, my discussion of function is mainly descriptive about the systems' interactions and their effect on the cycle of matter and energy flow, e.g., trophic interactions such as metabolic interactions, predation, and decomposition. Function in ecology has both the meaning of addressing matter and energy flow in a system such as an ecosystem function, and in the local meaning of a specific causal role such as predator-prey, decomposer, or consumer. The latter addresses different populations and the role of their interaction in the network/system, and the former looks at the biogeochemical cycle in terms of the flow of energy and flux of matter.

Historically, stability and its related concepts of persistence, resilience, and resistance follow species population composition and dynamic distribution. Therefore, classification in macro-ecology is an important starting point allowing the examination of biodiversity and population equilibrium. Ecological structure describes the system's biodiversity and species composition and is measured by species-population richness (the number of species) and distribution, i.e., how evenly the individuals are distributed among populations (Justus 2008). Thus, for such measurements, ecologists need to be able to classify and identify species, distinguish between populations, and follow their distribution. Classification also enables accumulating knowledge about the species' physiological traits, life cycle, habitat, co-occurrence, and interactions with other species.

Thus, in macro-ecology, the structure is central in the prediction of stability with the diversity-stability hypothesis correlating redundancy and complexity with stability (Odum 1953; MacArthur 1955; Elton 1958). This issue is central in ecology with long-lasting debates over the positive biodiversity-stability correlation used as a proxy for the understanding of functional stability (deLaplante and Picasso 2011). The stability of the structure is examined through the levels of populations' resilience, resistance, and persistence. Resilience examines the population's ability (and timing) to return to equilibrium after perturbation. Resistance follows the degrees of changes after returning to equilibrium, and persistence is measured by the duration before the system goes through a tipping point (Justus 2008; Mikkelson 2009; Odenbaugh 2001; Cuddington 2001).

In micro-ecology, classification is rare and in the majority of cases not possible. Microbial communities in ecology are characterized by their metagenomics sequencing and biochemical function. The former is the taxonomic composition measured separately in each sample clustered in operational taxonomic units (OTUs)[1] and the latter examined through the analysis of RNA transcriptions and metabolic capacities. OTUs are not species, thus, the taxonomic composition is regarded in a nonspecific way. Also, because microbial interactions with their close environment directly change the biochemical composition, the microbial function can be studied using molecular analysis such as metabolomics detecting microbial metabolites byproducts, together with transcriptomics analyzing RNA transcriptions. Thus, following microbial metabolic activity and functioning at the community level is available independently of classification.

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[1] OTUs follows the phylogenetic species concept clustering individual organisms with similar patterns of ancestry and descent using sequencing of OTUs. OTU is a classification method independent of cultivation relying on genomic sequencing, which faces the biggest challenge posed by the microbial world of rapid and constant changes. Thus, for example, the OTU is not universal and can only be applied separately to each sample. Also, the threshold of similarities by which microbes are clustered is arbitrary, somewhere between 95 and 97 percent of the DNA sequence (He et al. 2015; Hugenholtz et al. 2016).

In the following table, I present a general take on what macro- and micro-ecologists mean by structure, and how this relates to their practices and understanding of the function and the functioning system. This clarifies also the different attention to structure: macro-ecology uses the structure (i.e., classification, population analysis, and co-occurrences) as indicative of the functioning system (i.e., trophic and cross-feeding interactions), while micro-ecology can approach the matter and energy flow directly without species specificity using meta-analysis at the community level.

	Macro	Micro
Structure	- Classification of species-populations, richness, distribution, and co-occurrence - Species properties and life cycle	- Very few species identified: Microbial taxonomic composition with general phyla and OTU's per sample
Practice	- Study populations' trophic interactions directly or indirectly through the environment: food network, and cross-feeding	- Correlations between composition and biochemical changes. - Comparisons among samples
Function	- Function in terms of species interactions and their role in contributing to stability - Investigating trophic interactions and the stability of the functioning system based on classification and structure	- Function in terms of metabolic and chemical interactions and their contribution to the biochemical processes/cycles - Functional properties measured directly from a sample using molecular biology (transcriptomics and metabolomics)

In this paper, I examine the differences in understanding stability between the macro and the micro. I discuss the problem of classification in microbiology elaborating on the challenges presented by the microbial properties of horizontal gene transfer (HGT) and mobile genetic elements (MGE) leading to view structure and function separately with the understanding of functions at the community level. Then, I discuss the idea of eco-evolution and present three case studies demonstrating this notion. I show the micro-ecological understanding of stability is in terms of functional stability independent of the stability of the structure. This aspect of stability follows processes of interactions and the relations of interdependence between systems. Lastly, I discuss these differences arguing that they are not mutually exclusive, suggesting ways the microbial perspective on stability can be applied in macro-ecology, which can also help incorporate the microbial ecological systems.

2. Stability of structure vs. function: the challenge of classification in microbiology

In macro-ecology classification is needed to follow the network of interactions and their functional properties such as decomposers, predators, or producers. For example, when an ecologist looks at the various insects living on and interacting with certain plant species, they identify the specific plant population, life cycle, distribution, and interactions with its environment. Then, they identify the species living on and interacting with the plant, such as beetles, ants, or aphids, classifies them, learns their life cycle, distribution patterns, and follows their interactions. They will also need to make distinctions among populations while making field observations choosing the useful or appropriate model available.[2]

In microbiology, observations are always through the microscopic lenses where identification and classification are based on molecular biology. Adding to this already challenging reality, many of the microbial traits are constantly and rapidly changing due to their high mutation rate and molecular interactions. Thus, for example, early microbiology established the practice of cultivation in isolation and controlled conditions stabilizing this rapid volatility (O'Malley 2014, 69). However, the practice of cultivating bacteria in the lab is limited because a vast diversity of microbes cannot exist in isolation. Taxonomic profiling of microbial communities through direct sequencing of phylogenetic markers (e.g., 16S rRNA) improved the ability to identify uncultured microbial lineages. Independent-culture classification techniques use either reference to already identified species phyla, or in the vast majority of cases using the proxy of OTUs (Hugenholtz et al. 2016). These cultivating-independent methods address the question of who is out there in terms of microbial diversity and composition. This taxonomic information, however, does not answer the question of what they do, leading to the question of function.

Another reason why functional genes are not studied in connection with their organisms is the phenomena of HGT and MGE, which not only change the taxonomic composition in a given community, but also appear to be not random and somehow coordinated among the individuals and groups within the community (Rainey and Quistad 2020). Therefore, to understand the microbial traits and characteristics, micro-ecologists use a wide variety of methods (e.g., metabolomics and genetic engineering) to discover functional genes such as nitrogen fixating or antibiotic-resistant genes, which are not necessarily connected to their owner/user as a species but rather as a group clustered by OTUs (Green et al. 2008; Gibbons 2017; Mony et al. 2020). Thus, in micro-ecology, the dynamic distribution of traits centers on functional genes and clusters, not species (Hugenholtz et al. 2016; O'Malley 2014; He et al. 2015).

The concept of population is also challenging to the extent that we might think of it as incompatible with the concept of population in plant and animal biology (Mony et al. 2020, 2; Westcott and Schloss 2015). Macro-ecologists who study species-population dynamics have access through classification methods to information about their properties and traits. However, the OTUs clustering does not provide information about the groups' properties and characteristics at the same level of generalization as species. Thus, the notion of stability in microbial ecology is defined by different criteria such as the stability of microbial landscape or niche as a whole (Mony et al. 2020; Baquero et al. 2021).

Microbes function through metabolism and molecular signaling in the form of minuscule biochemical processes, which change their molecular environment. These microscopic changes accumulate to a significant geographical effect composed of small interacting systems performing the biochemical cycles. Good examples of

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[2] It is important to note that the concept of species in the macro world is already complicated and has multiple approaches such as the interbreeding, ecological, and phylogenetic species-concepts (Ereshefsky 1992).

such accumulating impact are the nitrogen and carbon biogeochemical cycles. The small to large impact, however, goes through chains of events of mutual interactions between microbial groups in the community, and between communities. That is why the context of microbial communities is an important factor, including the understanding of interdependence and mutual effect between communities. Thus, the consideration of the microscopic ecological systems as interacting open systems is an important part of micro-ecologists' practice (Mony et al. 2020; Rainey and Quistad 2020).

When looking at the stability of function in the microbial system two important phenomena play a role. One is the microbial functional redundancy where microbiologists observe taxonomic fluctuations within a functionally stable system (Green et al. 2008; Konopka 2009). This possible redundancy is speculated to be in large part the result of HGT and MGE interactions (Konopka 2009; Mony et al. 2020; Quistad et al. 2020; Slipko et al. 2021). The second phenomenon is functional dependency through interactions of cross-feeding, where one group consumes metabolites released from another group in a community (Lawrence et al. 2012). These cross-feeding interactions occur also between communities as demonstrated in the Winogradsky Column,[3] which is the basic process of interactions behind the larger geological biogeochemical cycles all life on this planet depends on.

Both functional redundancy and functional dependency change the way of thinking about the relations between structure and function. The structure or microbial composition dynamic is an important aspect of the ecological system facilitating function, but the function of a system also depends on its molecular environmental context, which includes other systems. Thus, the observation of relations between function and structure that is within a system not including other systems is partial (Rainey and Quistad 2020). These micro-macro differences are a matter of degrees regarding individuals' and systems' interdependence. However, some levels of interdependence might be less approachable at the macro scale due to time and size scope. Thus, further study with a new way of inquiry and practice is needed. The aspect of functional redundancy is perhaps a unique characteristic of the micro scale due to the microbial interactions of HGT and MGE.

In the next section, I discuss three examples demonstrating these types of relations and the idea of eco-evolution and function at the community level. The concept of eco-evolution refers to the interplay between ecological dynamics and evolutionary processes at multiple levels. Eco-evolutionary feedback refers to the bidirectional interactions between ecological changes affecting evolutionary processes and the effects of evolutionary changes on ecological processes (Pelletier et al. 2009). Addressing this eco-evolutionary feedback in micro-ecology also involves the

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[3] A device invented in 1880 by the Russian microbiologist Sergei Winogradsky demonstrated functional dependency between microbial communities with different metabolic processes. The column consists of mud and water mixed with different nutrients such as cellulose, eggshells (containing calcium carbonate), and a sulfur source. After a while, the mud and nutrients in the cylinder device start to sink, creating different patches with different levels of nutrients and oxygen. The microbial communities growing in the different patches have different metabolic functions, from anaerobic cellulose-degrading bacteria at the bottom up to aerobic photosynthetic cyanobacteria at the top, demonstrating a biochemical cycle.

understanding of microbial interactions, metabolic activity, and function at the community level (Rainey and Quistad 2020).

3. Eco-evolution and function at the community level

Accumulating data from micro-ecology studies reveals differences in behavior and characteristics between closed and open microbial ecological systems. Microbes interact differently when in isolation (monoculture), in isolated close community (polyculture), or in an open ecosystem environment (mesocosm or samples). They interact with the environment, reacting to changes but also generating small chemical modifications through their metabolism creating biochemical cycles, and thus depend on each other for their persistence. Therefore, in the case of microbial communities the relation between structure and unctionn is both randomly affected by environmental changes and microbial composition such as wind, water fluxes, infections, migration, or priority effect, and also, directed and coordinated by the microbial molecular interactions and quorum sensing (Quistad et al. 2020).

The studies I present in this section show the possible link between the activity of HGT and MGE within microbial communities and their functional stability or trajectory of stability through compositional fluctuation and environmental modification. These studies hypothesize that microbes can coordinate and direct their genetic distribution, diversification, and abundance depending on the environmental changes of metabolites and nutritional sources while performing small-scale environmental modifications through their metabolic activity (Rainey and Quistad 2020; Quistad et al. 2020). I start with the study by Lawrence et al. (2012) comparing adaptation, evolvability, and productivity between monoculture and polyculture plates of the same species. They measure adaptation of five species cultured in isolation compared with polyculture plates of all five species together. Their findings suggest the same species developed different metabolic pathways in polyculture than isolation. Also, the new pathways were aimed at consuming the waste of each other's metabolites when cultured together, developing cross-feeding interactions (Lawrence et al. 2012).

The second study by Quistad et al. (2020) looked at ecological communities as a whole using mesocosms growing in garden compost and paper as a cellulose source of carbon. Using a bi-weekly transfer of MGE for twenty-four months, the mesocosms were divided into two groups of horizontal communities (HC) and vertical communities (VC) by their treatment of MGE from one generation of mesocosm to the next (Quistad et al. 2020, 2–3). Using genomic sequencing they observed amplification and dissemination of specific MGE in the HCs that are predicted to contribute to community function (Quistad et al. 2020). The HCs also show an increase in the production of ammonia, which also correlates with the detected movement of ecologically significant MGE.

The researchers hypothesize that the raising activity of MGE is connected with ammonification and directed by the nitrogen-limited environment. Thus, the increase of MGE with ecological significance correlates with the community function, pointing to the functional role of such activity. They also observed microbial diversity changes in both VC and HC in a nitrogen-limited environment. They hypothesized the diversification was the result of the growth of certain genera that were below the level of detection at the beginning of the experiment. Thus, the increase in the OTUs frequency is because of their functional or metabolic properties helping in maintaining the communal functional stability (Quistad et al. 2020, 8).

The third study by Slipko et al. (2021) tested the hypothesis of positive selective pressure imposed by concentrations of ciprofloxacin antibiotics in Waste Water Treatment Plant systems (WWTP). They compared the compositional changes of Antibiotic-Resistant Bacteria (ARB) and Antibiotic-Resistant Genes (ARG) in correlation with the microbial composition and functional stability in two WWTP sludge systems of WWTP: one as control and the other spiked with antibiotics. The results show no differences between tested and control systems of both compositional fluctuation and functional stability (Slipko et al. 2021, 7). These findings suggest the internal fluctuation of ARB and ARG may be a better explanation of their variability and abundance than selective pressure driven by antibiotics flux (Slipko et al. 2021).

If selective pressure was the determinant of the spread of antibiotic-resistant elements, then a significant difference between tested and control systems would have been observed. However, over twenty weeks of the experiment, the data show similar fluctuations with functional stability in both systems, suggesting another determinant for variability placed in the communities' embedded complexity and dynamics. Interestingly enough, after week twenty, the control tube suffered the spread of filamentous consuming chunks of microbial communities, leading to the breakdown of interactions and function. Slipko et al. hypothesize this happened due to the protection by the flux of antibiotics in the test tube. This hypothesis suggests that antibiotics and antibiotic-resistance have a role in maintaining functional stability (Slipko et al. 2021, 8).

All three examples discussed here demonstrate the following: 1) small biochemical cycles of cross-feeding consuming and producing metabolites facilitates microbial function at the community level and between communities; 2) HGT and MGE are essential in microbial interactions helping in functional stability; and 3) functional stability is not necessarily correlated with structure and compositional stability. Thus, because of the intimate interactions and feedback between environmental chemical composition, microbial composition, and metabolic pathways, there is no clear dichotomy between biotic and abiotic interactions (Mony et al. 2020).

These studies show the significant role of mutual interactions and interdependence relations within the community in evolution. Micro-ecologists' understanding of microbial function is of the biochemical processes within the ecosystem that depend on resources, microbial composition, interactions, and genetic transfer. Thus, in some cases maintaining functionality includes the constant fluctuation in microbial composition (Slipko et al. 2021, 9).

4. Stability as the persistence of function or structure: nonmutually exclusive difference

There are three basic differences between macro- and micro-communities. The first two that relate to size and time scales are the methodological challenges of classification on the one hand, and the molecular approach to function tracking matter and energy flow on the other. Thus, separating the questions of who is out there and what do they do, as well as the understanding of the interdependence between small ecosystems, lead to the third conceptual difference regarding the meaning of stability. Function at the community level becomes the subject of inquiry in microbial ecology, and the meaning of stability is in terms of functional persistence. This perspective changes the role of classification in micro-ecology, raising the possibility of thinking about classification in a nonspecific way. For example, the range of properties such as virulence, proliferation, adaptability, and pathogenicity hold at the level of the community and not the specific properties of organisms or populations.

Furthermore, stability is understood within the perspective of cycles of gradual change within an open system mutually affected by environmental conditions and other communities interacting in proximity. Functional stability as a process within context follows the trajectories of the constant changes, and interdependency between individuals and systems. Therefore, when the breakdown of stability occurs, it is not a matter of gradual or cyclical changes but rather the nongradual loss of interactions that binds the organisms together in a functioning system (Baquero et al. 2021; Slipko 2021; Rainey and Quistad 2020). Stability is the persistence of the functioning system in constant adjustments by compositional fluctuations, molecular interactions (e.g., antibiotics and antibiotic resistance), and environmental changes. This approach to stability is different from what I have described as the meaning of stability in macro-ecology, which follows species-populations dynamic and their perturbation returning to equilibrium.

The stability in macro-ecology also involves fluctuation and structural changes but does so differently. Changes in population density and richness are looked at as accumulation leading to a tipping point where the system no longer persists. This way of understanding stability is slowly shifting in micro-ecology, with the understanding that compositional fluctuation plays a role in maintaining functional stability (Slipko et al. 2021). Thus, composition or structural change are viewed within the context of a larger process of biochemical cycles or, in other words, metabolism interdependence. Functional stability also includes environmental perturbations such as rapid gut environmental fluctuations or the changes in vaginal conditions and chemical composition during the menstrual cycle. In the majority of healthy physiological conditions such changes do not lead to the breakdown of functions.

The meaning of stability in micro- and macro-ecology reflected in methodological and conceptual differences are not mutually exclusive nor exclusively conjugated with micro or macro. The distinction I make here is drawn from differences in practice also leading to differences in perspectives. This micro and macro distinction also clarifies another aspect in the way of understanding stability in ecology in general. Thus, both meanings exist in both micro- and macro-ecology. For example, the breakdown of functional stability in the control sludge system in the Slipko et al. experiment was due to outside invasion affecting the structure and composition. Here, it is clear that the structure and its maintenance are crucial. Another example from the other direction is when the functional stability (i.e., trophic cycles/network) in macro-ecology is maintained through compositional changes (Ulanowicz 2018). Some possible ramifications of such new understanding, in my view, is the possibility of incorporating the notion of eco-evolution and structure-functioning mutuality in macro-ecology aspects such as the invasive versus. non-native species debate.

However, this is still up for scientific inquiry due to methodological challenges of measuring exchanges in the flow of energy in macro-ecology and the ethical significance of biodiversity conservation (deLaplante and Picasso 2011).

Furthermore, these differences in the meaning of stability can also be connected to ethical and epistemic values attached to these two different perspectives of micro- and macro-ecology. In micro-ecology animals and plant biodiversity have social, cultural, and political values while the value of microbial diversity depends on their functional contribution to the ecosystems' function or host-organism physiology. Thus, as a result of both the methodological challenges and the different conceptual and epistemological perspectives, micro-ecologists are more concerned about functional stability than the stability of key populations in a system. More specifically, micro-ecologists look at the system's functional stability of matter and energy flow in correlation with the microbial composition, while macro-ecologists look at biodiversity and structure as indicative of the functioning system.

5. Summary and perspectives on the micro and macro integration

I argue that the micro-ecological perspective gives another meaning for stability in ecology: 1) the emphasis on stability of processes and functions, not composition and biodiversity; 2) functional stability includes constant fluctuation both environmental (i.e., biochemical cycles), and compositional; 3) the emphasis on function as a complex system of processes involves interactions with the environment in an open system and the notion of interdependence between individual cells, groups, and communities. A good example of such interdependence is the relation of cross-feeding, and also the coordination of growth and metabolic pathways facilitated by quorum sensing, HGT, and MGE.

Looking at the ecological system from the perspective of an open (not closed) system can also help in understanding the connections and mutual influences between micro- and macro-ecological systems. Thus, when connecting small and large systems we can further ask in what ways the different meaning of stability can change research questions from centering on the structure to better understanding functional processes. A good example of such inquiry is in soil microbiology (Mony et al. 2020). Another example is the dynamics of a pandemic (i.e., the spread/migration of a pathogen) that considers functional stability and its role in restraining the pathogen. Also, the possible shift in the antibiotic-resistance crisis, from the arms race metaphor to thinking about antibiotics' functional role (Slipko et al. 2021, 8).

Lastly, two important aspects to study when looking at small and large ecological systems and their mutual influences: the process of mutuality of interactions and the importance of context and interdependence relations as a factor shaping the interactions. Thinking of these aspects of stability may be of importance not only for the understanding of microbial transmission/distribution/dispersal such as infections and pandemics, but also to give another perspective on the stability-biodiversity connection in macro-ecology.

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