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Response of microbial communities to environmental stressors and their role in ecosystem resilience

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Abstract

Microbial communities are crucial in the operation of most of the ecosystems, and little is known about their responsiveness to environmental stress. The manner in which such stressors affect the structure and functioning of microbial communities is explained in a three-tiered conceptual framework, which has an impact on the ecosystem resilience, the capacity to absorb disturbances and retain the same relationship among the populations as existed previously. Microbial responses involve community-based aspects like composition, diversity, assembly and metabolic activity, and physiology of an individual. Stressors are diverse in nature, origin, length, and intensity and may be either abiotic factors (e.g., temperature, salinity, pH, nutrients, contaminants) or biotic factors (e.g., competition, predation, parasitism, substrate availability). Some of the key forces include climate change, pollution, land use, and natural disturbances. The lack of understanding of the interaction of the stressor properties with the microbial reactions hinders the predictions of the ecosystem resilience and the creation of the effective strategies of adapting to the changes and implementing the necessary mitigation measures.

Microbial communities have been noted to have quite dramatic responses to environmental disturbances and growing evidence shows that these responses are closely associated with ecosystem resilience. Through studies during the last twenty years, there is increased knowledge of how communities and their environments interact, but there are no solid theoretical, conceptual, and observational frameworks to associate the type, magnitude and frequency of stressors to community processes and, finally, to ecosystem stability. The current changing body of knowledge on the effects of stressors on community structure and ecosystem processes requires a synthesis that reveals the gaps in knowledge and suggests areas of investigation.

Keywords: Microbial communities, environmental stressors, ecosystem resilience, community structure, metabolic activity, ecosystem stability

1. Introduction

The earth has a staggering amount of microbial communities which play a myriad array of roles in the processes of ecosystems [1]. Due to their important functions in the basic ecosystem processes, i.e. nutrient cycling, soil formation and organic matter decomposition, it is necessary to know how microbial community adapts to environmental stressors [2]. They are intricate systems containing many interacting parts that act within gigantic spatiotemporal levels, and the actions of microorganisms at these levels are guided mainly by ecological and evolutionary mechanisms.

Studies on microbial responses to exposure to stressor-inducing factors have flourished in the recent years and there are a number of conceptual frameworks currently available. However, despite the common use of the term resilience in the ecology of microbial communities, there is no formal framework that relates community-level responses and the ecology concept of resilience. The significance of such a systematization is that it does not go far enough to define stressors, record community structure or functioning changes, or even correlate these changes with ecosystem services; instead, theories of ecosystem resilience can be better based on an operational and rigorous comprehension of microbiomes responses to environmental problems. The responses, resilience, resistance, recovery, functional redundancy, resilience, and the indicators of the microbial community are further defined.

Microbial communities also continue to play an important role in the Earth processes and evolution and have their direct impact on ecosystem. The capacity to recover following perturbation, which, in the community, is known as community resilience, is a growing topic of study, especially with regard to climate change, and increasing magnitude and frequency of extreme events. Stressors may cause a taxonomic change to other equilibrium points, but the ability to maintain functions may be retained; surprisingly, the transition phases have been also found in engineered systems that have been subjected to chronic perturbations [3, 4].

2. Principle Framework on Microbial Community Responses.

The interaction between microbial communities and the environment leads to major processes in the ecosystems in diverse habitats like soil and the human body. As a result, one of the critical problems in microbiology studies is the ability to forecast the reaction of community functions and composition to disruptions [1]. Such functions also regulate ecosystem resilience, or the ability of a system to take disturbance without a fundamental state change, however little is known about microbial resilience.

An abstractive model of environmental stressor responses and connection to ecosystem stability among microbial communities by explicit mechanisms and evidence is summarized below. It is focused on key, substantially supported hypotheses and evidence that relate community responses to the overall processes of the ecosystem. The environmental stressors are viewed in a broad spectrum and they include anthropogenic stressors, natural disasters, climatic extremes and invasive species. Since the response to many of these stressors is facilitated by microhabitat [2] large-scale processes continue to be studied to provide an understanding of general principles.

3. Types, Sources and Scales of Environmental Stressors.

Environmental stressors and their effects on microbial communities have far reaching implications on ecosystem functions, resilience and biogeochemical cycling. The classification can be discussed in terms of a number of perspectives: The stressors may be classified in terms of an abiotic or biotic origin, time of occurrence and space scale. The modelling framework includes the environmental disturbance and biodiversity theory over different levels [5]. Stressors can be categorized on the basis of their abiotic or biotic source, acute or chronic length of exposure and local or global scope. The major sources of stressors are climate change, toxic pollution, land use change and natural disturbances such as wild fire and floods. The definition of stressor type and source offers a description of the pattern of microbial community responsiveness and pertinent ecological processes [6]. The density-dependent interactions and cross-ecosystem generality have hypothesis structural changes and counter-scenarios of functional response in acute, acute-after-chronic, and chronic stress.

Microbial adaptation to environmental stressors takes place on a variety of levels, which reflect functional mechanisms, assembly, and genetic alterations. Scales are microhabitat, soil aggregate, bulk soil, sedimentary system, stream, lake and landscape. The major descriptors are community composition, relative abundance, and metabolic activity. The key types of data are multi-omics, geolocation, and

process indicators. Structural measures, including taxonomic composition, α -diversity and β -diversity and metabolic measures, including primary productivity, turnover and pathway activity provide quantifiable connections to ecosystem functions. These indicators have direct relations with ecosystem functions.

Stressors lead to biochemical adaptations, assembly processes within the community level and genomic responses. Some of the physiological and metabolic responses include osmoregulation, compatible solutes accumulation, temporary maintenance of electrochemical gradients, protein repair, protective enzyme expression and downregulation of biosynthetic pathways. Changes in composition, relative abundance, diversity, an assembly-assembly rule change, a niche- partitioning interaction, and functional redundancy are community-level changes. These mechanisms include vertical transmission, evolutionary responses, and horizontal transfer of genes where prokaryotes easily transmit plasmids and mobilizable genomic islands. Accessory and resistance genes that help in adaptation to stress are transferred by plasmids, which means that metabolic shifts in response to biogeochemical cycles occur rapidly. Active soil mobilome and archaeological assemblage are affected differently by soil stressors [7, 8].

4. Stress adaptation mechanisms in Microbes.

Microbial communities are an important part of different ecosystem functions and processes. Their reaction to environmental stressors have great impacts on the functions of ecosystems as they are said to be resilient, which is the ability of an ecosystem to continue its functioning following perturbation. Stressor responses trigger cascades of responses by microbes impacting community structure and functioning because of the stressor type and stressor magnitude, and condition responses in multimultiple stressors. The alterations to the community functioning and the resultant feedbacks to the ecosystem processes are not well understood. Soils are often limited in the provision of essential nutrients and the majority of studies that have tested the response of microbes to addition of nutrients have not incorporated the implications on ecosystem functionality.

Microbial resilience, recovery and resistance to environmental stressors are important determinants of ecosystem resilience. Resistance is used to explain the ability of a group of microorganisms to keep the compositional stability of a population in response to disturbance. Resistance can be increased by the presence of stress-resistant species whose threshold to resources acquisition is set. The existence of several species with similar ecophysiological characteristics and resource-use strategies, which is known as functional redundancy enables alternative avenues of resource acquisition and is also critical in sustaining resistance [1]. The speed of recovery after disturbance is referred to as resilience. A community exhibiting a quick recovery to its initial state before the stressor is very resilient and vice versa, where a community changes to another state with different structure, or functioning, or both, resilience is low [2]. Communities of epiphytic bacteria move up and down a trade-off between resistance and resilience with temperature; at high temperatures resistance is preferential, whereas at lower temperatures resilience is preferential.

The responses of microbial communities to stressors are realized in the form of short-term physiological changes, long-term changes in metabolism, and community reorganization. These reactions have a set of processes that occur concurrently. The changes in community structure when exposed to stressors, the level of adaptation in the activity of the microbes, and the process of returning to pre-stressor community conditions are dependent upon the nature and intensity of stressors, which is indicative of the intricacy of the microbial response. The physiological adaptations of microbes require the environmental manipulations related to the enzymatic activity and other mechanisms.

4.1 Physiologic and Metabolic Changes.

Microbial communities ecologically react to environmental stressors based on a conceptual framework that mediates ecosystem resilience. The human pressures compound and might lead to destabilization of microbial communities. The capacity to absorb disturbances and retain structure (multidimensional stability) and containment of feedbacks that drive change (bifurcation stability) is known as ecosystem resilience. Resilience helps ecosystems to proceed with delivery of important services during stress. The concept of microbial community resilience includes responses at various scales: community composition (identity and abundance of its taxa), and community multifunctionality (number and range of ecosystem functions that it sustains). Individual responses combine to create community responses, which is mainly through the predominating physiological and metabolic processes, though community assembly, gene transfer, and evolution are also factors. Resilience is associated with the central importance of microbes in carbon, nutrient, and detoxification processes, even temporary shifts in community composition or functioning may cause indicators of such processes to go dead suggesting a loss of resilience [1, 2].

Community resilience definition thus needs to be specified in terms of the type of stressor, timing and intensity. Microbial communities exhibit resistance (an amplification in structure of the community) or recovery (the restoration to a reference state following perturbation) and may alternate among alternative, functionally distinct regime even in permanent state. They predict that resilience is determined by the intensity, frequency and duration of stressors and these factors influence the taxonomic and functional organization of polyphyletic communities. The relationships between disturbance and the microbiome properties on similar scales are based on the interactions between the human and biophysical disturbances. Plants and animals moderate the nutrient cycling and hydrochemical processes that forestall desertification by the community. Water-induced perturbations have both positive and negative impacts on the soils, sediments, and rivers and both natural and anthropogenic pulses. Although microorganisms form the basis of ecosystem operation, they are not extensively studied in comparison with plants and herbivores [9, 10].

4.2 Community- Level Dynamics: Diversity, Assembly and Redundancy

The microbial communities play a pivotal role in the operation and stability of ecosystems, and the interactions

between the anthropogenic stressors, the community and ecosystem responses are not well understood. The connection of these two requires more empirical exposure in order to create prediction models and establish management directions, as well as define ecosystem-climate interactions. The synthesis of the existing knowledge entails the effects of stressor type, intensity, duration, and recovery time on community structure and performance, the importance of disturbances in stimulating rebuilding of community structure, and the detail of how functions of microorganisms cascade to ecosystem performance. Such interactions reinforce the need to uphold community diversity, structure and activity to enhance ecosystem functioning and resilience to climate change [11].

Microbial community has taxonomic, structural and functional definitions. Taxonomic approach defines a community in terms of organisms that make up a community. Structural descriptors describe a community based on the total abundance, diversity, dispersal mode, assembly process and the network properties. Lastly, there is functional perspective which defines the metabolic capacity of a community [1]. Integration of models of community processes at both microscopic and macroscopic scales are a key research topic in the systems.

4.3 Horizontal gene Transfer and Evolution under Stress

Horizontal gene transfer (HGT) has emerged as a significant process by which microbes evolve, in which highly mobile genetic regions are transferred horizontally across different communities. These exchanges are the escape of the genome confinement and enable the migration of microbial cells and participate in transfers with populations that are extraordinarily different in relation to the host. This intercommunity HGT is especially effective with genes that are being positively selected and this allows the potential ecologically relevant loci to spread across a community and reach genomes which encode partially overlapping and partially different ecological abilities. In such circumstances of extensive HGT, there is no existence of ecological species in the conventional meaning since genes and not species occupy specific niches appropriately [12]. Microbial cells are widely adapted to various environmental conditions and HGT is one of the processes that are considered essential in adapting to new ecological states. The circumstances may occur in a nursing practice like the development of disturbance of antibiotics and in an unpolluted ecosystem that is prone to alternations in climate or alterations in land-use or other interruptions. HGT studies can explain the evolution of stress-related genes in the community of Shark Bay by permitting close analysis of scenarios of acquisitions of stress [13] and experimental systems can be used to investigate the effects of HGT on acquisition and evolution of stress responses [14].

5. Effects on Ecosystem Functions and Processes

Ecosystem processes can be changed, and the relative abundance of microorganisms in the communities can be altered by climate change, land-use change, pollution, and natural disturbances. Microbial communities address central ecosystem processes like nutrient cycling and decomposing organic matter, and their reactivity to processes that disrupt them defines recovery and resilience of ecosystem activities. The reaction of the microbes to the environmental stressors is related to the type and frequency of stressors, the intensity

of the stressor, and stressor durability. Microbial responses may be quantified at genetic, taxonomic and functional levels, which can offer several and complementary measures of change. However, the processes have been studied much less than biotic responses of more complex organisms. Relative to the plants and animals, microorganisms allow various and controllable investigations of biogeosciences, ecology, and environmental sciences functional processes. The response to environmental stressors of microbial communities has also gained growing interest due to the role of such communities in system resistance, resilience, and functioning as well as the potential of multiple concurring stress factors to induce an impairment of community recovery capacities [1].

In most circumstances, resilience is possible to be supported by processes run by a small number of keystone taxa [6]. Even in the presence of more global changes, the idea of resilience of ecosystem properties related to critical cycles can still be achieved in the presence of acute local stressors. A stress-on-stress framework can be used to evaluate the impact of human induced changes in microbial communities on ecosystem stability and system properties that characterize ecological interactions.

The responses of microbial communities to various stressors, to stress-on-stress interactions, and the ecosystem characteristics that govern these responses are extremely vital in biased projections of risks to ecosystem functions and stability amidst current global change.

5.1 Nutrient Cycling and Pathways of Biogeochemicals.

Microbes have a great influence in the cycle of nutrients which determine the movement of nutrients and their endurance and affect the movement of pollutants in the environment. The flow of the nitrogen, phosphorus, iron, sulfur, and other elements is controlled at various scales by the microbial activities. All these processes regulate the release, retention, transformation and sequestration of nutrients in the soil- water- plant system. Degradation of ecologies leads to the change in the nutrient mobility, where the pollutants are more liberated due to lower frequency control. The nutrient pollutants through streams and rivers often have direct impact on the environmental health. Farming has devastating effects on land, soil, plants and on microorganisms. Severe damages are facilitated by flooding, drought and increased sea levels. Considering the change in the global environment, the ecosystem services including clean water, fertile soil, energy circulation and climate stability are important to the human society. Recognition of key soil and sediment organisms are necessary to the sustainable and stable utilization of the important ecosystem services [1].

5.2 Primary Production and Decomposition.

The main production, the transformation of light energy to chemical one and the integration of carbon into organic substances, has a significant impact on the abiotic parameters of the soil and on the metabolism of microorganisms, their mass and community organization. Microbes also help in one-half to one-third of the total primary production of the earth depending on the ecosystem and the prevailing environmental conditions [1]. The litter decomposition and organic-matter-mineralization process are enhanced during times of excessive soil moisture (heavy

rain or melted snow), and microbes use easily decomposable organic molecules (Sugai *et al.*, 2020). Conversely, most of soil organic carbon includes stable organic matter, which takes a comparatively long time to decompose mostly through fungal species (Sah *et al.*, 2022). Plant debris is the main source of soil organic carbon but microbial biomass may also serve as a significant source of carbon that can be converted to subsequent degradation (Sah *et al.*, 2022).

5.3 Soil, Water, and Sedimentary Ecosystem Situations.

The interplay between environment drivers and anthropogenic stressors influences ecosystem resilience and microbial communities play a central role in these interactions. The abundance, biomass, composition, and the community structure of microbes are considered to be significant indicators of ecosystems reaction to degradative and stressful environmental changes [1]. Interconnected anthropogenic-indoor and environmental stress factors then subdue resilience and exacerbate the maladaptation of eco-services.

The ecosystem conditions that will be taken into consideration include soil, aquatic, and sedimentary. Soil environments are not confined to soil aggregates, but can include the whole watershed that supports a variety of biological communities engaged in the decomposition of organic matter, nutrient cycling and the formation of soil structure. The aquatic environment includes lakes, rivers, oceans and reservoirs, inland and coastal waters and groundwater systems would be more strictly defined as surface and underground aquatic environments. Sedimentary environments These are aquifers, pluvial deposits, extreme environments, lakes, reservoirs and soils, which are closely interacting with aquatic systems.

6. Mediators of Ecosystem Resilience and Stability through Microbes.

Microbial communities are important in the ecological processes and stability. The recovery of microbial community after environmental stress takes place either in the form of recovery of the community composition/function, or in the form of transition to other forms [1]. Resilience is used to refer to the ability of a system to take in the disturbance without losing its functionality. In cases where recovery takes place, resilience can be defined based on disturbance resistance and post-stress recovery rate [15]. Mechanisms that connect disturbance and ecological change are not well understood in spite of some guidance given by conceptual and theoretical frameworks.

The functions of the microbial communities in biogeochemical cycling and other ecosystem processes determine the energy flow and nutrient supply in terrestrial, aquatic, and coastal ecosystems. Understanding response dynamics can guide the prediction of ecosystem processes and biogeochemical cycling during climate change and other anthropogenic stressors of controversy (such as pollution and land-use change). However, regardless of the ecological and societal importance, the changes in methane-cycle sediments in the Arctic shelf are observable but few drivers and reactions in communities are unveiled. The fact that urban- and climate-change effects on permafrost systems are documented testifies to the extent of uncertainty of the underlying microbial processes which should be further explored. [16-18].

6.1 Trajectories of resistance, resilience, and recovery.

Ecosystems may change radically, even disastrously, under human, land-use, and climatic stress. A typical outcome is the augmentation of the rate, length or the intensity of severe stressors, like droughts, floods and chemical pollution. There are various levels of stressors such as plants, animals, but the most ubiquitous and abundant life forms, the microorganisms, have received relatively little consideration regarding ecosystem change, resilience, or state shifts.

Microbial communities can be exceptionally short-termly resilient to a number of environmental stressors. They have an arsenal of physiological and metabolic adaptations that enable them to survive both extremes that are otherwise lethal and to survive even in the harsh selection. Numerous microorganisms live in and are adapted to ephemeral environments, including soil aggregates and sediment particles, where abiotic environments vary greatly on short periods. Consequently, community composition, community functioning, and community resilience studies have numerous findings which can be applied to other community sizes and structures [19, 9, 20].

The microbial ecological theory could make a contribution and even an unification of the ecosystem and microbiome science. Within the framework of the ecosystem theory, plant biogeochemical cycles, fungal biogeochemical cycles, and herbivore biogeochemical cycles provide nutrient retention. The assembly of microbial communities is also similar in how it is involved in the beginning of carbon, nitrogen, and sulphur cycles in soil, sediment, and aquatic environments. Microbial and biotic and abiotic environmental features provide helpful feedbacks that may ensure ecosystem and microbiome stability [1, 2].

6.2 Microbial Keystone Roles and Functional Redundancy

Microbial communities respond to challenges in the environment by varying considerably in structure (i.e. community composition, diversity and biomass) and activity (e.g. nutrient cycling rates). The effects of stressors on community structure and activity may be described in the context of resilience (the capacity of a microbial community to revert to its preperturbation state after perturbation), resistance (the magnitude to which a community is not affected by perturbation), recovery (the time required to restore a community to her preperturbation state), and functional redundancy (the extent to which the functions that a community performs remain the same or close to the same as a community reorganizes after a perturbation). Not only high temperature tends to initiate a resistant towards a resilient response in the algal-bacterial community [11].

Microbial resilience and functional redundancy are the two core concepts in microbial ecology. Highly diverse and functionally redundant consortia tend to be functionally intact during compositional change and to regain their normal state following perturbation quickly [15]. The relevance of the above concepts is supported by theoretical frameworks that consider compositional control and energy-limitation feedbacks: community change during disturbance is lengthened and recovery delayed in ecosystems organized at the community scale without functional redundancy and non-redundant community are better governed by interaction of composition and activity but structurally modified under the same disturbance [1].

6. Coupled Human and Environmental Stressors.

Microbial communities are often subjected to several, interacting human or environmental stressors, but the responses of these interacting stressors on the structure and processes of the microbial community are not well documented, especially when the indicators are required to be measured over extended periods in order to obtain data on the long-term examination and study [6]. On the bigger spatial scales, large-scale climate change (temperature change and UV radiation change or humidity reduction) and more local human-induced changes (change in land-use, nutrient loading, and pollution introduction) substantially influence microbial communities and their ecosystem processes. The nature of disturbance (natural or anthropogenic) such as a perturbation, pollution, or climate change is significant in defining the manner the targeted microbial responses are attained.

How much a microbial community structure and process recovery succeeds upon stress reduction also depends upon the nature of the component human or environmental stressor or disturbance, which differs depending on the type of system in question. Furthermore, it is even more complicated in the larger-scale studies such that the same environmental variable can be concurrently reduced, enhanced, or remain constant at the larger spaces. An example of this is that despite the fact that $\delta^{18}\text{O}$ and δD isotopes in a sedimentary record reflect discontinuous water availability in lakes separated by 300km that experience similar perturbations, the reported differences in community structures in response to the same perturbations demonstrate how landscape-scale predictors can change microbial responses to perturbation [1].

7. Conclusion

The microbial communities are critical in facilitating the rate of ecosystem processes even though they may have relatively low diversity in some ecosystems. These ecosystem-resilient community responses undergo well-characterized biogeochemical processes that require microorganisms, which may act as indicators of a large-scale community recovery. Despite the significant progress in research of these relations, there are still a few gaps in the knowledge that restrict the development of models and predictive ability.

The initial agenda of the future research is to come up with a logical conceptual framework that can be used to define the mechanisms between microbial community composition and ecosystem resilience in a quantitative and accurate manner. Microbial community resistance, resilience, recovery, functional redundancy must be well defined; community reactions, environmental stressors and their types, sources and scales clearly defined and the theory formulated linked to the system with the ecosystem theory. The intensity, duration, and recurrence of stressors have a role in community structure and community functioning at appropriate time and space scales, yet the relationship between stressors and responses on the community- and ecosystem-level has not been well studied. By codifying the explicit processes that relate microbial community dynamics to ecosystem functionality under different regimes of stressors, it would be clearer what model-design criteria should be to include the predicted non-linear feedbacks between microbial communities and the physical domain that are summarized in ecosystem theory.

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