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Viral interactions in ecosystems and their role in regulating microbial communities

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Abstract

The vital contribution that viruses make in the regulation of the ecosystems especially their responses with the microbes is underestimated as compared to their recognized roles in the well being of humans and in agriculture. Viruses are ubiquitous elements of complex and dynamic microbial communities, which are essential elements in biogeochemical cycles, nutrient turnover as well as material exchange in terrestrial and aquatic ecosystems. Micro-organisms maintain a high selective pressure on each other: virulent predators or the mobility of functional capabilities are subject to evolutionary and functional capacity. A review of literature that relates to the format and operation of virus-microbe interactions is thus relevant, particularly due to the emerging evidence that climate disturbance is shifting micro-bial richness and food web structure all over the planet.

Viruses are the most diverse, the most abundant, and widespread biological objects on the planet. They have enormous morpho-logical and genomic diversity and infect all cellular forms of life, such as archaea, bacteria, as well as eukaryotes. At present, 155 distinct classifications are known (with subfamilies, families, genera and subgenera being included), and metagenomics studies have shown that 99.7 percent of the viral diversity remains unidentified. The formation and consequences of the interaction between viruses and microbes are governed by several fundamental points, such as the chemical nature of the media, the biophysical and biochemical characteristics of the surfaces, and outer membranes of the microorganisms, and the native bacterial and eukaryotic communities. Research into the viral interactions with prokaryotic hosts can be used to identify more novel methods of controlling antimicrobial resistance and biofouling.

Keywords: Virus–microbe interactions, microbial ecology, biogeochemical cycles, viral diversity, climate change, metagenomics

1. Introduction

Microorganisms Microorganisms are found in almost all environments on Earth in the form of bacteria, archaea, protozoa, microalgae, fungi, and viruses. Microbes become very abundant in the soil and oceans with prokaryotes and viruses constituting the majority. Bacteria: Bacteria to bacteria, bacteria to fungi, bacteria to viruses, bacteria to their hosts: The interactions between microbes are critical in the formation and stability of microbes. Symbiotic, mutualistic, or parasitic relationships may arise as species become symbiotic, mutualistic or parasitic. Mutualism is beneficial to both partners, where when the nitrogen-fixing bacteria live on the roots of plants or gut bacteria synthesize vitamin, K, these interactions are regulated through the expression of genes ^[1]. Commensalism is beneficial to one partner only, whereas parasitism is harmful to the host, such as pathogenic bacteria, including *Bacillus anthracis* or *Borrelia* spp ^[1].

Viruses have a significant impact on microbial communities by causing virus-induced deaths, which allows reshuffling of the community, as well as altering host cell metabolism and fitness. Prophages may modify the properties of the host through gene interference, superinfection exclusion and horizontal gene transfer of toxin genes which enhance bacterial virulence. Bacteriophages can also defend against secondary infections and this can have an impact on the community structure. Lytic viruses introduce genes that restructure host metabolism, e.g. photosystem genes in cyanophages and those that regulate nutrient cycles. The knowledge of viral mechanisms is confined to model systems that are mostly well-

known. The future of viral ecogenomics will be to hasten the identification of new methods of manipulation of microbes depending on selected environmental parameters [2].

2. Diversity and Ecology of Viral Communities

Viruses, the most common biological species in the biosphere, are major elements of ecosystems, which determine the circulation of biogeochemicals and food webs, as well as affecting biodiversity and community structure. They invade a wide species of hosts including eukaryotes and control hugely the population of microorganisms. Viruses have a significant impact on soil microbial processes and community characteristics in freshwater, soil, and extreme environments. However, the present knowledge of viral diversity and ecological role in most of the ecosystems is primitive.

An increasingly broad toolset of techniques, such as metagenomics, microscopy, spectrometry, flow cytometry and modeling, is used in the emerging field of virology to characterize viruses across domains, investigate their role in regulation of microbial assemblages, and obtain insights about biogeochemical implications [2]. Viruses can alter prokaryotic communities, mediate nanoscale community architecture, sustain ecosystem stability and cause organic carbon flux in aquatic systems [3]. When examining saline and terrestrial environments, it has been demonstrated through work that viruses change the structure of the community by inactivating individual taxa, regulate the turnover of free prokaryotic genomes through horizontal transfer, and are associated with the process of soil-plant exchange. Research into extreme and engineered systems has found that the biome of viruses is as diverse as freshwater ecosystems and plays a critical role in system resilience and biotechnological opportunities.

Effective strategies in life include all life forms that are that even the primordial virus that may have co-adapted with the hosts and exists in a dormant form indefinitely and the next generation of life is the emergence of microbes and its ability to have a strategy of replication to divide into daughter cells every so often. The abundance of viruses complicated the virosphere of nature and coevolved with the life of microbes. Viruses remain the most numerous biological types on Earth, and they are 100 times smaller than the microbial cells, which amounts to an enormous diversity of biological forms and have such great evolutionary abilities that there are no analogues.

Important functions of viruses in biogeochemistry can be examined as the regulation of host population, alteration of bacterial community structure, regulation of horizontal gene transfer, and regulation of bio-geochemically active genes. Biogeochemical cycles and ecosystem services also include organic carbon, nitrogen and Phosphorus cycles, CH₄ and N₂O emissions to the atmosphere, degradation of anthropogenic pollutants, and growth promotion of plants by viruses.

3. Viral Control of Bacterial Populations

The interactions of microbes and eukaryotes may have a strong impact on the composition of microbial communities. Some studies propose that phages are major controllers of the community of microorganisms in a diversity of environments [1]. It is believed that these influences take place mainly by lysing bacterial and archaeal hosts with the

involvement of viruses. It is becoming increasingly apparent that effects of the viruses on the microbial populations also occur via the lysogenic way of life and that changes in the abundance of viruses in a position to trigger lysogenic infection may also have significant effects [2]. Viruses are often numerically abundant in many systems and the lytic and lysogenic processes of viruses can often be important in terms of controlling the makeup of microbial community.

3.1 The lytic and lysogenic cycles in the environment

Viral life strategies that prevail in the ecosystems are not fully defined. Whereas environmental bacteriophages are largely temperate (less than 50% of marine bacteria are lysogenic) all of the previously lysogenic populations is induced to give rise to lytic phages upon the provision of nutrients [3]. The addition of the resource also results in accelerated growth of higher lytic rates in certain aquatic systems without lysogenic induction. The transition can be caused by depression of the lysogenic state by temperature, salinity, nutrient or toxic shock, signal in infected cells, or phage phage interaction. In the case of bacteriophages, the lytic cycle leads to total destruction of the cell that is infected and an explosion of nutrients whereas lysogeny may take days to months under different conditions which means that it has a differentiated effect on the time and supply of nutrients [2].

3.2 Horizontal gene transfer through viruses

Horizontal gene transfer promoted by viruses is the second way of how viruses control the environmental microbial populations. Despite HGT being considered as a major evolutionary process in microorganisms, the mechanisms through which genes are exchanged in them are not well known. Viruses lack the plasmids and other related mobile elements that can confer property inheritance of a donor cell to an aspiring one and, therefore, their ability to induce HGT has been doubted. However, an increasing mass of evidence suggests that HGT can be performed as a component of infective circles of bacteriophages and eukaryotic viruses in prokaryotic and eukaryotic systems [4]. HGT through viruses would seem to take part in the evolution of species, ecological adjustment, as well as acquisition of new functional attributes that will most probably help to preserve the diversity within the community and ecosystem functioning. Sharing of functions of genes through these pathways is versatile and includes confirmatory, mainly metabolic, immune response, and regulatory pathways.

3.3 Nutrient cycling and Viral shunt

Viral lysis of the prokaryotes promotes the reuse of the organic matter and nutrients, and its application to the operation of the biogeochemical cycles and ecosystem services. This has been described as the viral shunt by analogy to the phrase of microbial loop of the movement of organic carbon and energy using heterotrophic bacteria [5]. Viral infection returns inorganic nutrients on the prokaryotic biomass to dissolved organic matter (DOM) and then to dissolved inorganic nutrients. In the viral lysis, larger cells are transformed to smaller particulate organic matter (POM) and closely packed genomic material decreases the proportion of carbon-to-nitrogen (C:N) ratio of emitted matter. The efficiencies of high prokaryotic growth are sensitive to the release of the dissolved organic carbon (DOC) in the carbon cycle and DOC forms the biggest

carbon pool in the upper ocean ^[6]. It is also indicated that viruses can also amplify degradation of organic matter and nutrient mineralization and other geochemical reactions increasing the proportion of stored carbon and primary producer growth in soil and groundwater ^[2].

4. Impacts of Viral Interactions on Microbial Community Structure

Viruses have important functions in the control of microbial communities in both direct and indirect relations. Direct mediation is carried out by viral infection of microbial hosts, whereas indirect mediation takes place by the discharge of materials of lysed host cells that modify the accessibility of nutrients and organic carbon. These two forms of interaction happen at the same time. Interactions vary in relation to environmental conditions, e.g. season, time of the day, and magnitude between microsystems to complete landscapes ^[3]. The top-down and bottom-up control of microbial communities is mediated by a virus-host interaction. When the resources of the host are scarce, community structure is bound by the availability of the resources. With high supply of resources, the top trophic predators like viruses set up a top-down control of the community structure. The impact of such predation pressure is on the nutrient levels, biodiversity, the make-up of species, and community stability ^[2]. In response to the lack of nutrient availability to allow the growth of a diverse range of microbial species, diversity is low following disturbance. The availability of more resources is beneficial to the recovery of the community structure and development of alternative community states. Deaths caused by the virus impact the capacity of a community to rebound after disruption. The ability of the viral predation to cause modulations of the recovery time and the number of co-existing species exemplifies how the viral infections alter the pathway in which a community takes on its way to the recovery state. The low nutrient availability exposes the non-targeted communities to a prolonged duration of restoring order in the community since it limits the growth of more members within the communities ^[7]. The viruses can regulate the population of the microbes at the top-down level by killing, and at the bottom-up level by modifying the resources. Top-down control involves direct killing of bacteriophage, bottom-up process involved in control relates to the capacity of microbial communities to adapt and develop in the presence of quantity of energy and nutrient. In the case of energy or nutrient resource constraint (e.g. in oligotrophic systems), models suggest that viruses can increase diversity through a co-existence and resource partitioning mechanism ^[8]. On the other hand, in case of abundance of resources, multiple species have enough energy to be maintained ^[2]. Consequently, it is possible to theorize a trade-off between top-down predation force that decreases diversity and bottom-up nutrient constraint that favors coexistence. Given that the effects of viruses in these two regimes are antagonistic, the relative significance of top-down control by viruses can be assessed by the current nutrient concentration as compared to the nutrient concentrations necessary to maintain a community of the of the observed composition. Viral predation impacts the dynamic of recovery of a community once disturbed and the ability of the community to resist disturbance and degree of functional redundancy in the community ^[8]. Greater levels of viral concentrations have the potential to cause greater resistance

to disturbance in phytoplankton communities; the mechanism behind this may be by linking faster population turnover of resident taxa or simply a cumulative impact of latent viruses without marked shifts in the taxonomic composition. Modeling has indicated that community interchange influences community recovery dynamics as well as that viral top-down control may either strengthen or weaken the degree of recovery, with the balance between community fixation and interchange rates. Viral-microbial interaction dynamics may vary in space and time across ecosystems. Even in the case of observation scales spanning weeks to months, there are possible seasonal effects in the relative abundance or activity of viruses. In temperate marine systems both along coastal and in the oligotrophic lakes, different viral populations seem to fluctuate periodically in synchrony with particular phytoplankton or bacteria hosts ^[9]. In one day, diurnal viral prokaryotic predation preys cycles are captured in bacterial community resilience ^[8]. On-land, soil viral communities are dependent upon land use type, location of sampling and seasonality; soil type is also an alteration of soil bacterial virome ^[2].

5. Techniques of the analysis of Viral-Microbial Interactions

Viruses are the most populated living beings on earth and they contribute a lot to the mortality of the microbes. To comprehend how viral predation affects microbial communities and processes at the ecosystem level an experimental and analytical framework based on these properties is needed to maximize sampling and data collection. Different methodologies are created to investigate viral-microbial interactions in an environmental system, such as genome-based methodology, imaging, and experimental. These methods have produced an abundance of information about viromes and virus-host interactions in a variety of ecosystems. Further studies are required to ascertain the exact mechanisms by which viral predation controls the microbial communities and ecosystem processes ^[10, 2, 1].

5.1 Metagenomics and viromics

There is little literature on a viral metagenomic method to study the circulating viral pool within an aquatic environment and the description of the trends in the viral community structure using bioinformatics analyses. The art of the state is depicted with the research of the coastal area of the nine greatest urban centres that are positioned all along the Greek coastline ^[11]. The hierarchical approach is used in this area, and environmental samples presented by groups of urban centres are ranked by their ecological quality to apply viral metagenomics. There is a concomitant growth of abundance of viruses with auxiliary metabolic genes that respond to energy pathways in samples that are highly disturbed by humans. The diversity of energy-specific auxiliary metabolic genes recorded is also a much wider one in contrast to more pristine coastal ecosystems. The surveillance of this type of functional genes in the virome therewith is a very sensitive measure of ecological quality that has happened in a coastal area subjected to different levels of disturbance. It is also possible to detect the presence of genes, which are related to energy pathways followed by some biogeochemical cycle, even in greatly disturbed environments, which speaks of the bioremediative

possibilities and once again underlines the significance of the virome within the coastal ecosystem.

Changes in host metabolism caused by viruses and their effects on ecosystem operation as well as methodological annotation and interpretation of the virome are poorly understood but form some of the most important challenges to the broader aspect of viromics [2]. Extensive study of environmental viromic data is also essential because most of the viruses cause metabolic rewiring in the host that is infected. The presence of viruses in the surface and subsurface aquatic ecosystems across nearly all microbial taxa that make up the bottom of aquatic food webs makes aquatic ecosystems an ideal site with which to conduct large-scale viromic studies. The availability of sequencing technologies that have a read length that is suitable to metagenomics, and a fast-expanding repository of environmental viromes makes it possible to consider the viral community preliminarily, the expected variety of members and the chosen hypotheses of how the members could shape the biogeochemical cycling of carbon nitrogen phosphorous and silica in marine ecosystems [12].

5.2 Flow cytometry, microscopy and imaging techniques

Flow cytometry allows quantifying and sorting viruses and microbial cells at a single-cell resolution. Enumeration involves the use of stained samples, whereby the virus particles are labelled directly with a nucleic acid fluorescent dye or chastened virus-targeting antibodies, which can also be used to detect viruses infecting particular hosts in situ by a flow cytometry-activated cell sorting (FACS) [242,243]. Besides counting and sorting, flow cytometry can also be used to determine the size and fluorescent profile of the stained entities, informative properties of viromics, genome size distribution, or the abundance and community structure of the microbes.

The optical visualization of viruses and their interactions with hosts is typically done under the maximum resolution through Scanning and Transmission Electron Microscopy. Also Scanning Transmission X-ray Microscopy (STXM) has been used to differentiate algal viruses on an environmental marine particle due to its nutrient voracity and the potential to mineralize dissolved organic matter (DOM), although is an experimental technique not readily applicable. To provide an even more ideal picture of depletion and enrichments of organismal abundance due to the presence of a virus, Fluorescence In Situ Hybridization (FISH)-Network Imaging Scanning Cytometry (NISC) has proven useful in dissecting the aspects of virus-infected community composition and dynamics, relative to host depletion over time, space, and biogeochemical gradient. [13, 14, 15].

5.3 Experimental designs of ecosystem-scale investigations

Microbial ecosystems can be used as an effective model to examine interactions of viruses and microbes and determine general ecological rules. One of the popular methods is complex systems that simulate natural environments, i.e. laboratory mesocosms with high-throughput sequencing to track community-wide dynamics. Since the structural changes alone are not enough to describe the ecosystems, the measurements should also be involved in the experiments to monitor the associated ecosystem functions as well as to obtain a holistic picture [10].

Mesocosms may be natural or may be gathered by the environment and supplemented with nutrients to spur growth. Experimental strategy using in situ manipulation of both biotic and abiotic factors may supplement such vessels to characterize and quantify a particular ecological process and variable in the field [2]. Synthetic systems permit the substitution of complete complexity by building simplified model minimal consortia at the other extreme. Specific microbial member selection develops two or more genetically non-identical species that are aggregated in vivo, and one bacterial member is expected to be a putative viral host to define the interactions between the virus and the microbe in the community in a straightforward way.

6. Case Studies in Ecosystems of Various types

Viral lysis is a cause of 3-64 percent of prokaryotic death and 5-50 percent of dissolved organic matter (DOM) generation in the waters [3]. Approximately, 1.42 10^{24} viruses are infectious at any time within the oceans infecting 10-26 percent of prokaryotes each day and yielding 290-830 Tg of carbon each year [2]. Viral shunt of cancer bacteria can explain more than 90 percent of overall DOM. The prokaryotic viruses (phages) have a significant effect on population dynamics, community structuring and biogeochemical cycling. Viruses in the sediment are also highly diverse and contribute to the regulation of microorganisms in the soil and sediment habitats as well as influence international biogeochemical cycling of carbon, nitrogen, and phosphorous. The phage-mediated top-down control of microbial communities has the potential to affect the cycling of functional root-resident plant bacteria. The transfer of genetic material through bacteriophage infective or as free viruses facilitates genetic diversity, and helps in structuring communities and functional abilities amongst ecologies.

6.1 Aquatic systems: oceans and freshwater bodies

6.2 Soil and land atmospheres

Microbial and viral communities impact soil and terrestrial environments and have a role in carbon processing and climate-change feedbacks. In the permafrost, there is deep soil carbon that is susceptible to microbial degradation in case of warming. Viruses are an unidentified volume in this undiscovered land, yet their interactions with organisms are essential to the biogeochemical cycles. The recent developments in metagenomics have revealed a lot of genetic diversity among microbes and viruses and the possible functions of associated genes in soil and permafrost [16].

Numerous ecosystems are seriously understudied and cannot be fully comprehended in terms of stability and dynamics of viral-community across space and time. The effect of environmental factors on the viral count and community structure of soils is incompletely understood. Time-series data is required to estimate temporal variability and viral community responses to changing conditions. It has been difficult to establish low-cost, reproducible ways of measuring viral abundances and community compositions in soils. Different protocols of extraction that depend on soil types are needed to capture viral particles but they should be tested in each habitat. Community survey is complicated by the absence of common viral marker gene, as polymerase and structural proteins genes are specific to the specific viruses. Entire viral-community surveys generally require

less specific methods, including primers that produce banding patterns that can be examined using gel electrophoresis, which is tedious and subjective. Variation of results during duplicate runs are usual. It can also be used to monitor changes in the abundance of a viral community and its structure over time across various land uses and environmental gradients to identify patterns and other factors that may affect viral ecology in the terrestrial setting [17, 18].

6.3 Extravagant and artificially created environments

Microbes are complex systems of community that are highly spatially and temporally varied in terms of type, distribution and capacity. The changes in microflora structure have been provoked by global climate change and anthropogenic disturbance, which threatens the life of the ecosystem and humans. Microbes such as bacteria play an important role in nutrient recycling and carbon fixation. Although revealing the microbial dynamics of diverse aquatic and terrestrial ecosystems is important, engineered ecosystems that are designed to serve biotechnological applications have recently attracted more attention. Since bioleaching has been tested at acid mine drainage location to waste treatment reactors, engineered systems have proven useful in exploring microflora control and nutrient cycling in austere environments both as a means to learn about environmental restoration and resource recovery [11].

7. Consequences to Microbial Community Process and Ecosystem Services

7.1 Biosphere Biogeochemistry and greenhouse gases

Viruses are the most prolific biological objects in the biosphere that have a significant influence on the abundance and metabolic activity of their microbial hosts. These interactions affect the mortality of the microbes, the provision of organic and inorganic nutrients to the microorganisms, and the persistence and resilience of the microorganisms. As a result, the interactions through viruses control key microbial activities, such as carbon and macro-nutrient cycling worldwide, greenhouse gas emissions, soils and snack water activity. It has been found that viruses are predators that decrease the populations of hosts, alter the diversity and structure of microbial communities by top-down regulation, horizontal gene transfer, and the structuring of microbes into cooperative networks. Viruses have also been shown to enhance the activity of the remaining microbial community in soil and aquatic environments and promote mineralizing and recycling of carbon than controls, which did not have viruses. Studies of viral infection and viral communities in particular ecosystems (e.g. the ocean) have provided insights into the ecosystem-wide consequences of viral activity on microbial communities and services. The knowledge of these dynamics can improve biotechnological applications like bioremediation, bio-refining, pathogen control, and bioengineering as well as the broader quest of sustainability in human endeavors and development [19].

7.2 Health of the ecosystem and management of diseases

Several theories have reported the regulation of pathogenic taxa by community members [2]. This kind of antagonistic interactions is the main feature of the microbiome in disease regulation and the health of an ecosystem [7]. All these observations lead to the consideration that viruses may be

used as regulators of pathogenicity and vectors of biocontrol agents and are a lesson to designing biocontrol strategies.

7.3 Effects on microorganism diversity and stability of the ecosystem

Viral infections and related gene transfers influence the responsiveness of microbial communities to perturbations, including the increase in concentrations of nutrient levels or sources of DOM; and the ecosystem functioning of the microbial communities, including promotion of the emission of greenhouse gases such as carbon dioxide and methane. Viral control has an impact on the structure and evolutionary process of microbial communities on the degradation of dissolved organic carbon of either terrestrial or algal origin. The interface between the marine and the terrestrial is changed due to the periodical floods and the influx of marine life. In the later succession of bacteria communities in fresh sediments and estuarine water, the viral activity dictates the fate of salt-marsh vegetation in inner degeneration. Genomic studies have suggested that the regulation of microbial community by the virus in the marine sediments can be associated with the provision of measurable sedimentary carbon substrate by continental weathering [2].

8. Conclusion

Viruses have been recognized as key components of the microbial population and community despite the lack of clear understanding of their regulations of the microbial community and the ecosystem consequences. General tendencies have been observed, showing that the nature of the interaction between viruses and the host and the strength of this interaction depend on the resource environment, host diversity level, and other environmental traits. Viral lysis and infection may facilitate the exchange of carbon, nitrogen and phosphorus between several biogeochemical cycles and also may contribute to the temporal processes of greenhouse gas fluxes. The impacts of viruses on the competitive survival, relative abundance, and persistence of particular taxa over a broad spectrum of environments are well understood, although generalizations on how to predict the impact of viral-regulation effects are deficient. It is, therefore, evident that the further study of ecosystem-specific viral-microbial interactions and their functional implications is a high-priority research question.

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