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Deciphering the soil virome: Viral drivers of microbiome dynamics and plant health- A comprehensive review

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Abstract

The dynamics of microbial communities, nutrient cycling and plant health are all significantly impacted by soil viruses, a prevalent but little-studied aspect of terrestrial ecosystems. Advances in high-throughput sequencing, metagenomics, and viromics have uncovered a remarkable diversity of soil viruses, including bacteriophages, mycoviruses, archaeal viruses, and plant-associated viruses, which were previously disregarded due to technological difficulties in isolation and identification. These viral communities affect the turnover of carbon, nitrogen, phosphorus, and sulfur by modulating microbial populations through lytic and lysogenic infection cycles, horizontal gene transfer, and the viral shunt. Viral-mediated lysis affects microbial metabolism, soil fertility, and greenhouse gas emissions by releasing nutrients and organic matter into the soil matrix. In addition to their function in the cycling of nutrients, soil viruses have an indirect impact on plant health by controlling helpful microorganisms like mycorrhizal fungi and rhizobacteria that promote plant growth. They also act as reservoirs for soilborne plant viruses. The composition, diversity, and ecological role of soil viral communities are shaped by agricultural practices, such as tillage, crop rotation, fertilizer, and irrigation, as well as climate change effects. Their potential as phage-based biocontrol agents against bacterial and fungal diseases and as bioindicators of soil health is highlighted by recent study. Significant information gaps still exist despite these developments, especially when it comes to connecting viral sequences to particular host activities and ecosystem processes. The present knowledge on soil viral diversity, interactions with microbial hosts, roles in biogeochemical cycles, and impact on plant health is summarized in this review.

Keywords: Soil virome, microbiome interactions, biogeochemical cycling, plant health,

Introduction

Viruses, the smallest known microorganisms, are widespread across all earth's ecosystems and are essential in determining the dynamics, structure and functional activities of microbial communities (Brum and Sullivan 2015; Paez-Espino *et al.*, 2016; Suttle 2007) [13, 75, 96]. Only a small number of eukaryotic viruses, thermophages (viruses that infect thermophilic hosts), and archaeal viruses have been studied globally to date (Breitbart *et al.*, 2004; Dellas *et al.*, 2014; Peng *et al.*, 2012; Prangishvili *et al.*, 2017; Schoenfeld *et al.*, 2008) [12, 23, 78, 79, 91]. For example, in both marine and terrestrial ecosystems, bacteriophages viruses that infect bacteria play crucial roles in the cycling of nutrients and the lysis of host cells. Auxiliary metabolic genes (AMGs) that affect and control host metabolic processes are also carried by them and expressed (Aylward *et al.* 2017; Lindell *et al.* 2007; Puxty *et al.* 2018; Thingstad 2000; Zhou and Zhou 2024) [7, 61, 83, 99, 124, 125]. Similarly, Mycoviruses can cause phenotypic changes in their hosts, such as hypovirulence (reduced virulence) or hypervirulence (increased virulence) in fungi that are harmful to higher organisms (Ghabrial and Suzuki 2009; Pearson *et al.*, 2009; Zhou *et al.*, 2024) [30, 76, 124, 125]. Mycoviruses are found in almost all major fungal lineages. More than 25% of Earth's biodiversity is found in soils, which are home to creatures from several kingdoms of life (Bach *et al.*, 2020). The soil viral microbiome, or virome, has gotten very little attention, despite the fact that soil bacterial and fungal microbiomes have been thoroughly investigated (Compant *et al.*, 2025; Jansson *et al.*, 2023; Turner *et al.*, 2013) [20, 42, 105]. In recent years, however, virome research has

begun to investigate a wide range of soil habitats, including thawing permafrost (Trubl *et al.*, 2018)^[104], mud volcanoes (Yu *et al.*, 2019), deserts (Adriaenssens *et al.*, 2015; Scola *et al.*, 2018)^[3, 92], mangroves (Jin *et al.*, 2019)^[43], glaciers (Han *et al.*, 2017)^[36], and Antarctic soils (Adriaenssens *et al.*, 2017)^[2]. The impact of viruses on the rhizosphere is still mostly unknown, despite the fact that the roles of bacteria in this area have been thoroughly studied. Viruses can control host population numbers and the dynamics of the rhizosphere microbial community by acting as microbial predators, which may contribute to sustainable crop production (Pratama *et al.*, 2020). Soil viromes have been successfully studied using metagenomic and metatranscriptomic techniques (Ma *et al.*, 2024). Furthermore, the systematic characterization of soil viral communities has been made easier by recent advancements in de novo viral identification techniques and soil viromic procedures (Göller *et al.*, 2020; Guo *et al.*, 2021; Kieft *et al.*, 2020; Ren *et al.*, 2020)^[33, 35, 48, 85]. All things considered, HTS (high-throughput sequencing) technologies have significantly improved our knowledge of viral diversity, ecology, and epidemiology as well as virus discovery. Microbial diversity in agricultural soils can be altered by rhizosphere mechanisms that selectively promote or inhibit the establishment of specific microbial species (Edwards *et al.*, 2018; Peiffer *et al.*, 2013)^[25, 77]. This review focuses on the the diversity, structure, and ecological functions of soil viruses as well as their interactions with microbial communities. It demonstrates how viruses control the dynamics of microbial populations through lytic and lysogenic cycles, affecting the cycling of carbon, nitrogen, and phosphorus. The paper also looks into soil bacteria' metabolic reprogramming and viral-mediated horizontal gene transfer. It also covers how soil viruses affect plant health, stress tolerance, and productivity both directly and indirectly.

Abundance and diversity of viruses in soils

Current estimations of soil virus abundances indicate that they are either more abundant than or equal to their hosts. Most of the information about the quantity of viruses in soil has come from counting bacterial viruses (bacteriophages) that can be identified by microscopy and/or produced with their bacterial hosts (Williamson *et al.*, 2013)^[114]. There were around 10^8 - 10^{10} virus-like particles (VLPs) per gram dry weight of soil, according to direct microscopic counts of VLPs from different soil types (Williamson *et al.*, 2017)^[115]. VLP counts were higher in forest soils than in agricultural soils (Williamson *et al.*, 2005). However, the real number of soil viruses may be significantly higher than that found by microscopy because many viruses are intracellular and cannot be seen separately from their hosts. Many viruses' subcellular size has made it more difficult to see them directly in soil, and even free viruses are often difficult to distinguish from the backdrop of soil particles. DNA viruses, however, come in a wide range of sizes, from 20 nm to massive viruses with a diameter of up to 500 nm. A virus's size and form are determined by the quantity of its DNA and the protein clusters that surround it. Although certain enormous viruses found in permafrost soil are larger than normal bacteria, they are usually 20-50 times smaller than bacterial cells (Kuzakov and Mason Jones, 2018; Legendre *et al.*, 2014)^[57]. As sequencing depth increased, ever-better coverage of DNA viral sequences could be obtained.

The soil virome: composition

Types of soil viruses

Bacteriophages: Bacteriophages, commonly referred to as phages (derived from the Greek *phagein*, meaning "to eat"), constitute a major fraction of the viral population and specifically infect bacteria. Their ability to target and lyse bacterial cells endows phages with a distinctive antibacterial potential

(Jamalludeen *et al.* 2009)^[41]. Phages are considered to be the most diverse and abundant entity on earth and are thought to exist in every ecosystem (Maranger and Bird 1995; Hendrix 2002; Hanlon 2007)^[37, 38, 68]. Forest soils and agricultural soils typically contain phage abundances of approximately 10^8 - 10^9 particles per gram of dry soil (Williamson *et al.*, 2003^[117]; Williamson *et al.*, 2005). In addition, phages are known to encode and express a diverse array of auxiliary metabolic genes that enable them to perform important ecological functions (Breitbart, 2012; Weitz and Wilhelm, 2012)^[11]. A single phage exhibits high host specificity, typically targeting a particular bacterial species or closely related strains, and replicates within the host by utilizing its cellular machinery. Phage propagation occurs either via the lytic cycle, resulting in host cell lysis and release of progeny viruses, or through the lysogenic cycle, in which the phage genome integrates into the host and is inherited during cell division, often imparting new traits to the bacterium (Young *et al.*, 2000; Brock *et al.*, 1988)^[121]. Phages are classified based on characteristics such as host range, morphology, genome type, infection strategy, and phylogeny (Abeles *et al.*, 1984)^[1]. Nearly all bacterial groups, including cyanobacteria, archaea, and mycoplasmas, are susceptible to phage infection.

Fungal Viruses (Mycoviruses): Mycoviruses are widely associated with fungal species, with substantial evidence documenting their presence in ascomycetes. One of the earliest reports described the isolation of a mycovirus from a mushroom (Hollings and Stone, 1971)^[39]. Viral infections in fungi can disrupt host metabolic processes, particularly in diseased hosts. Although mycoviruses share certain features with plant and animal viruses, they also exhibit unique characteristics, such as strictly intracellular transmission, propagation through sporulation without the need for protein-mediated movement, the ability to persist in dividing and fusing cells, and the absence of an extracellular infection stage (Deng *et al.*, 2022)^[24]. Studies by Ioli Kotta-Loizou have further demonstrated that mycovirus-induced effects on fungal hosts arise from alterations in host cell metabolism or the expression of virus-encoded gene products (Kotta-Loizou and Coutts, 2017)^[52]. The ability of these viruses to persist and spread within natural pathogen populations is essential for their successful application in disease control strategies. Mycoviruses are primarily transmitted between fungal isolates through hyphal anastomosis and are also vertically passed from parent to offspring via conidia (Myers and James, 2022)^[71].

Archaeal Viruses: Early pioneering work by Zillig *et al.*, 1996^[126] led to the discovery of the first archaeal viruses. Initial observations indicated that viruses infecting euryarchaea, particularly halophiles and methanogens, resembled classical head-tail bacteriophages. In contrast, subsequent investigations of viruses infecting hyperthermophilic crenarchaea revealed unique morphologies, pointing to the existence of previously unknown viral families. These viruses possess double-stranded DNA genomes ranging from approximately 13.7 to 75.3 kilobase pairs. While many of them package circular genomes, the filamentous *Lipothrixviridae* and rod-shaped *Rudiviridae* are distinct exceptions, as they uniquely encapsidate linear double-stranded DNA. Most crenarchaeal viruses are enveloped; however, members of the *Rudiviridae* lack a lipid envelope. With the exception of *Fuselloviridae*, these viruses generally follow a lytic replication strategy, although cell lysis has been conclusively demonstrated only for STIV and ATV (family *Bicaudaviridae*) (Prangishvili *et al.*, 2006)^[80].

Soilborne plant viruses: Plant viruses present in soil originate from decaying roots, infected plant debris, or vectors such as

fungi, nematodes, and protists. Many of these are RNA viruses (e.g., Tobamoviruses, Potyviruses) (Rush, 2003)^[90]. Soil serves as a reservoir, enabling virus transmission to emerging roots.

Some soilborne viruses depend on fungal vectors (e.g., *Plasmodiophorales* transmit benyviruses and furoviruses).

Table 1: Composition of the Soil Virome and Estimated Relative Abundance

Viral Group	Proportion in Soil Viromes (%)	Ecological Role and Key Features	References
Bacteriophages (Phages)	50-90	Dominant soil viral fraction; primarily dsDNA Caudoviricetes; regulate bacterial turnover, gene exchange and nutrient flux via lysis	Williamson <i>et al.</i> , 2017; Emerson <i>et al.</i> , 2018 ^[26, 115] .
Archaeal Viruses	1-10	Infect soil archaea involved in nitrification and methanogenesis; often display unique spindle- or bottle-shaped morphologies	Prangishvili <i>et al.</i> , 2017 ^[79] .
Fungal Viruse (Mycoviruses)	5-20	dsRNA/ssRNA viruses infecting saprophytic and pathogenic fungi; influence decomposition, soil aggregation and fungal virulence	Ghabrial <i>et al.</i> 2015; Nibert <i>et al.</i> , 2014 ^[72] .
Soilborne plant Viruses	<1-5	RNA viruses from decaying roots and residues; some transmitted via fungal vector (e.g., <i>Plasmodiophorales</i>)	Rush, 2003 ^[90] .

Soil virome-microbiome interactions

Viral predation and microbial mortality

Phages that replicate exclusively through the lytic pathway are termed virulent phages. In the lytic cycle, the phage infects a bacterial cell, multiplies extensively within it, and ultimately causes host cell death by rupturing the cell to release newly formed viral particles (Fig. 1). The lytic process begins with phage attachment to the bacterial surface via specific protein interactions, followed by injection of the phage genome into the host cell (Karlsson *et al.*, 2003)^[46]. Once inside, the phage hijacks the host’s metabolic machinery to replicate its nucleic acid and synthesize viral proteins. DNA phages directly transcribe their genomes into mRNA, whereas RNA phages, such as retroviruses, first convert their RNA into DNA using reverse transcriptase before proceeding through a DNA-like transcription pathway. Newly synthesized components assemble into complete phage particles, which are released upon host cell lysis.

In some instances, fragments of the host chromosome are mistakenly packaged into phage capsids, facilitating horizontal gene transfer among bacteria through transduction (Madigan and Martinko 2006). Because lytic phages efficiently destroy bacterial cells, they are increasingly explored as promising agents for controlling antibiotic-resistant pathogenic bacteria.

In contrast to the lytic cycle, the lysogenic phase is characteristic of temperate phages and involves integration of the viral genome into the bacterial chromosome, forming a prophage (Campbell and Reece 2005)^[15]. (Fig 1). This integration allows the viral genetic material to be replicated along with the host genome without causing immediate harm to the infected cell (Inal, 2003)^[40]. However, insertion of viral DNA often leads to phenotypic alterations in the host bacterium, a process known as lysogenic conversion, which can enhance bacterial pathogenicity in many species (Keen, 2012)^[47].

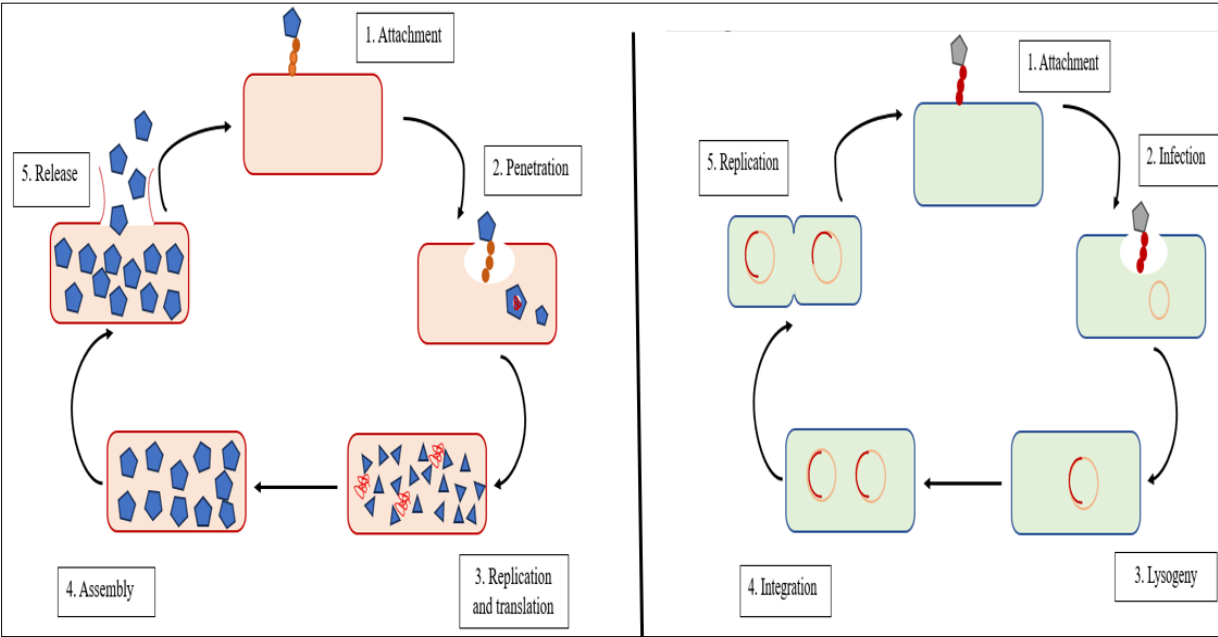


Fig 1: Schematic representation of lytic and lysogenic cycle of phage

Such lysogenic conversion may be inhibited through mechanisms involving hydrogen peroxide-induced reactive oxygen species, glutathione production, and overexpression of transcriptional repressors (Wagner *et al.*, 2001; Liu *et al.*, 2005; Keen, 2012)^[47, 109].

Viral modulation of microbial metabolism (AMGS)

Recent virus-host interaction models predict that viruses exert strong control over actively growing microorganisms, thereby regulating fluctuations in host population abundance. Although these concepts were initially developed from marine studies

(Bouvier *et al.*, 2007; Våge *et al.*, 2013) ^[10]. comparable patterns have also been observed in soil ecosystems. For example, a laboratory wetting experiment on biological soil crusts demonstrated that rewetting stimulated a bloom of Firmicutes, which was subsequently accompanied by a sustained increase in Bacillus-infecting Caudovirales phages; metagenome-assembled genomes confirmed active phage infection within the expanding Firmicutes populations (Goethem *et al.*, 2025). Notably, Firmicutes entered dormancy within two days of rewetting, and analysis of auxiliary metabolic genes (AMGs) in Caudovirales genomes revealed the presence of sporulation-related genes, indicating a potential viral role in regulating bacterial sporulation in soils. Similar sporulation-associated AMGs have been identified in soil viral communities from permafrost (Trubl *et al.*, 2018) ^[104], and grassland ecosystems (Wu *et al.*, 2021). Given the exceptionally high abundance of both viruses and dormant microbes in soils, it is plausible that viral infections contribute to widespread microbial dormancy. Consequently, dormancy as a bet-hedging strategy against viral attack, along with other antiviral responses, should be incorporated into virus-microbe interaction models to improve understanding of ecosystem functioning. Nonetheless, the extent of virus-induced dormancy in natural environments remains unclear, and the mechanistic links between viral infection and host dormancy are still not fully resolved.

Viral shunt

There is substantial evidence that bacterivores, especially protozoa and nematodes, play a crucial role in regulating microbial survival and turnover in soils. Their function in channeling nutrients through the soil micro-food web- known as the microbial loop- was first proposed by Marianne Clarholm (1985) ^[18], and later expanded upon by (Zwart *et al.*, 1994) ^[127]. Plant roots exude carbon-rich compounds into the rhizosphere, stimulating microbial proliferation, enzyme activity, and enhanced nitrogen mineralization from soil organic matter (SOM). Microorganisms assimilate this root-derived carbon and SOM-derived nitrogen to support their growth. The resulting

increase in microbial biomass attracts protozoa and other soil fauna, which graze on the rhizosphere microbiota and release mineral nitrogen back into the soil. Plants subsequently absorb part of this mineral nitrogen, promoting plant growth and further root development. This process establishes a positive feedback loop that intensifies organic carbon inputs into the rhizosphere. The concept of the viral shunt provides a mechanistic explanation for how plant roots can effectively compete with microorganisms for nitrogen (Jover *et al.*, 2014) ^[44]. Soil microorganisms are highly efficient nitrogen competitors (Kuzayakov and Xu, 2013) and rapidly immobilize nitrogen in the vicinity of actively growing roots that release carbon substrates. However, viral infection can quickly induce microbial cell lysis, leading to rapid turnover of microbial biomass and the release of nitrogen in mineral form, thereby making it available for plant uptake.

Horizontal gene transfer

Horizontal gene transfer (HGT) is a key driver of bacterial evolution, involving the transfer of genetic material between a donor and a recipient organism. In addition to vertical inheritance, bacteria acquire new traits and adapt through HGT-mediated genetic exchange (Thomas *et al.*, 2005) ^[101]. Transferred genetic material is commonly organized into syntenic regions known as genomic islands (GIs) (Juhas *et al.*, 2009) ^[45]. The movement of genetic material between organisms occurs predominantly via three principal mechanisms: transformation, conjugation, and transduction. This process can be further facilitated by structures such as outer membrane vesicles (OMVs) (Fulsundar *et al.*, 2014; Fischer *et al.*, 2016) ^[28, 29], virus-like particles (McDaniel *et al.*, 2010) ^[69], and phage-like particles (Bárdy *et al.*, 2020) ^[9]. Numerous studies have highlighted the widespread occurrence and high frequency of HGT. For instance, analysis of 7,781 genomes isolated from gut microbiomes of 48 individuals across 15 populations showed that approximately 90% of these genomes are involved in HGT events (Groussin *et al.*, 2021) ^[34]. Similarly, examination of 827 Enterobacteriaceae genomes obtained from 14 livestock farms identified up to 2,364 putative HGT events (Shaw *et al.*, 2021) ^[94].

Table 2: Key Mechanisms of Soil Virome-Microbiome Interactions

Mechanism	Description	Ecological Outcomes	References
Viral Predation (Lytic Cycle)	Viruses infect and lyse bacterial, archaeal, and fungal hosts, releasing cellular contents into soil.	Microbial mortality; nutrient release; stimulation of heterotrophic activity; altered community abundance.	Weinbauer (2004); Jover <i>et al.</i> , (2014)
Lysogeny and Prophage Integration	Viral genomes integrate into microbial hosts, affecting phenotype, stress tolerance, and gene expression.	Enhanced host fitness; modulation of metabolism; response to environmental stress.	Touchon <i>et al.</i> , (2017); Koonin and Wolf (2012) ^[50, 103] .
Viral Shunt	Microbial biomass converted to dissolved/particulate organic matter through viral lysis.	Increased carbon, nitrogen, and phosphorus turnover; enhanced nutrient bioavailability.	Wilhelm and Suttle (1999); Kuzyakov and Mason-Jones (2018) ^[113] .
Auxiliary Metabolic Genes (AMGs)	Viruses encode functional genes that modify host metabolic pathways during infection.	Enhanced C, N, S cycle processes; accelerated decomposition	Coutinho <i>et al.</i> , (2017); Roux <i>et al.</i> , (2021) ^[89] .
Horizontal Gene Transfer (HGT)	Virus-mediated transduction moves genes among microbial communities.	Spread of metabolic, virulence, and adaptation-related genes; rapid microbial evolution.	Touchon <i>et al.</i> , (2017) ^[103] .

Roles of soil viruses in nutrient cycling

Carbon cycling

Viruses influence carbon cycling through both direct and indirect interactions with the microbial loop and the broader food web in terrestrial and aquatic ecosystems, operating through three primary mechanisms.

(i) Infection and cell lysis: Viruses (particularly bacteriophages) enhance the rapid transfer of carbon from microbial biomass to

the surrounding environment through host cell lysis, a process referred to as the viral shunt. This mechanism primarily affects soil bacteria (Kuzyakov *et al.*, 2018; Emerson *et al.*, 2018; Williamson *et al.*, 2017) ^[26, 54, 115], and planktonic microorganisms in aquatic ecosystems (Aguirre *et al.*, 2015; Wommack and Colwell, 2000) ^[4, 118].

(ii) Gene transfer: Viruses indirectly influence soil carbon cycling by modifying the genetic and metabolic capacities of their

microbial hosts through gene transfer mechanisms (Rohwer and Thurber, 2009) ^[86]. By reprogramming host cellular metabolism—often described as acting as a “puppet master”—viruses alter key biogeochemical functions such as carbon metabolism and sporulation (Charney *et al.*, 2016; Mann *et al.*, 2003 ^[16]), thereby regulating carbon and associated nutrient cycling processes (López-Bueno *et al.*, 2009; Meunier and Jacquet, 2015) ^[63, 66, 67m, 70]. This regulation is mediated in part by auxiliary metabolic genes (AMGs) carried by viruses, which can modulate host photosynthesis, carbon metabolic pathways (Thompson *et al.*, 2011) ^[102], and other physiological processes. Such viral-mediated genetic control can ultimately influence microbial abundance, community composition, and functional activity within ecosystems (Weinbauer *et al.*, 2004) ^[111].

(iii) Altered community structure: Viruses influence microbial abundance, diversity, and community organization by reshaping

species dominance patterns, including through mechanisms such as kill-the-winner dynamics (Thingstad and Lignell, 1997). By regulating host mortality, viruses modify the quantity and quality of organic matter inputs into ecosystems. While viral infections of plants and animals within the broader food web may initially enhance organic inputs through increased host mortality, prolonged infections can ultimately reduce these inputs by lowering host abundance; for example, viral diseases in green plants can decrease photosynthetic rates by up to 50% (Swiech *et al.*, 2001) ^[98]. In addition, virus-mediated gene transfer can modify the spectrum of available organic substrates by promoting carbon source diversification (Thingstad and Lignell, 1997; Kolbasov *et al.*, 2018) ^[49], a process that contributes to the maintenance of microbial species richness and the overall pool of functional genetic information within ecosystems (Weinbauer *et al.*, 2004) ^[111].

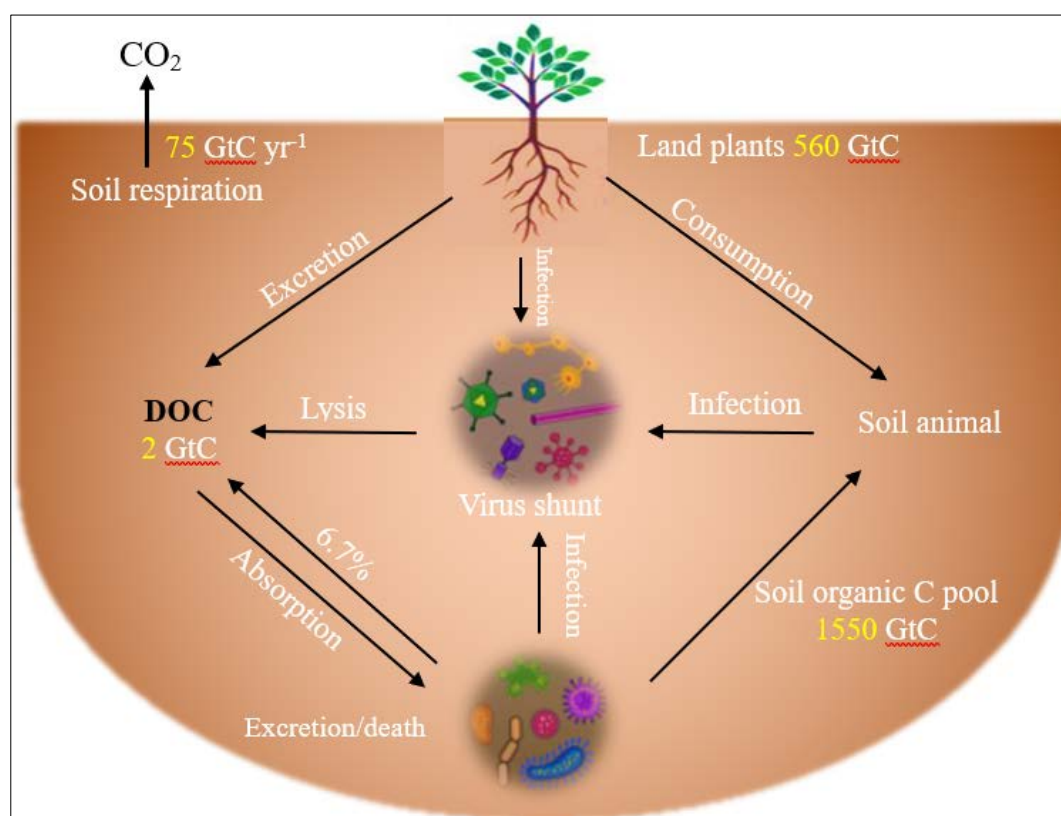


Fig 2: Role of Viruses in Soil Carbon Cycling

Nitrogen cycling

Soil viruses influence nitrogen cycling by infecting key functional microbes, including nitrifiers and denitrifiers (Emerson *et al.*, 2018; Trubl *et al.*, 2018) ^[26, 104]. Viral lysis releases intracellular nitrogen compounds such as ammonium and amino acids, enhancing nitrogen mineralization and altering substrate availability (Kuzakov and Blagodatskaya, 2015) ^[53]. Through kill-the-winner dynamics, viruses exert top-down control on dominant nitrifying and denitrifying populations, thereby regulating nitrification rates, nitrate accumulation, and

denitrification-driven N_2O emissions (Roux *et al.*, 2016; Emerson *et al.*, 2018) ^[26]. In addition, soil viruses carry auxiliary metabolic genes (AMGs) involved in nitrogen metabolism, including genes linked to ammonium assimilation, nitrate reduction, and nitrogen stress responses (Roux *et al.*, 2016; Trubl *et al.*, 2018) ^[104]. Expression of these AMGs during infection temporarily reprograms host nitrogen pathways, enhancing host metabolism and redirecting nitrogen fluxes, positioning soil viruses as active regulators of soil nitrogen availability and ecosystem nitrogen balance (Fig. 3).

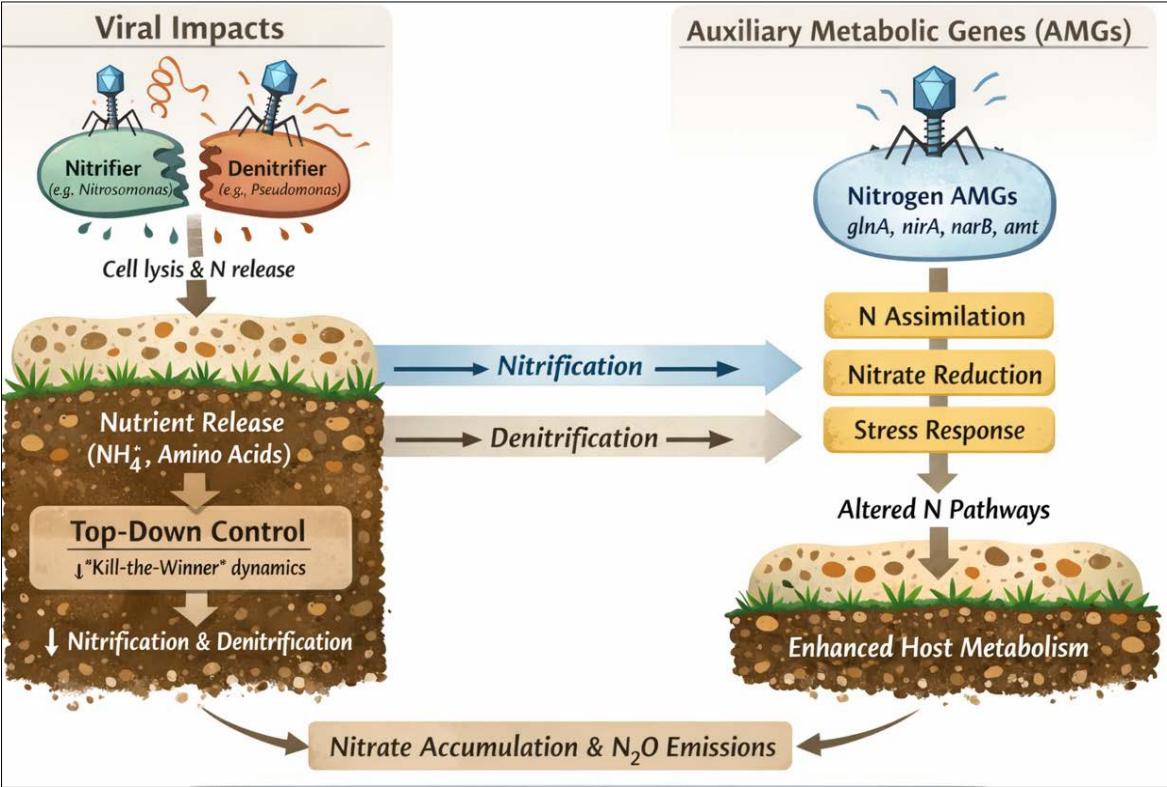


Fig 3: Conceptual model illustrating viral regulation of soil nitrogen cycling

Phosphorus cycling

Agricultural soils may be rich in nitrogen from fertilizer and dissolved organic matter from photosynthetic activity, but these increased inputs of carbon and nitrogen might result in phosphorus limitation. In these circumstances, viral infection may cause host cells to quickly absorb inorganic phosphorus (Pi), with viral genes like *phoH* promoting this uptake to aid in viral reproduction. Together with *phoH*, the four auxiliary metabolic potentials linked to nucleotide synthesis dUTPase, *MazG*, *Thy1*, and *RNR* were discovered to operate as a P metabolism module (Rohwer *et al.*, 2000; Angly *et al.*, 2009) [5, 9, 87]. According to studies, *MazG* is a nucleoside triphosphate pyrophosphohydrolase that can hydrolyze all eight canonical ribonucleoside and deoxynucleoside triphosphates to their

corresponding monophosphates and PP(i), preferring deoxynucleotides. All four ribonucleotide diphosphates (rNDPs) are converted by ribonucleoside diphosphate reductase (*RNR*) to the corresponding deoxynucleoside diphosphates (dNDPs), which are subsequently quickly transformed into dNTP (Rohwer *et al.*, 2000). In addition to providing a substrate (dUMP) for thymidylate synthase, the dUTPase can catalyze dUTP to dUMP and release diphosphate (Chen *et al.*, 2002) [17]. FAD, NADPH, and 5,10-methylenetetrahydrofolate are necessary for *Thy1* to convert dUMP to dTMP (Ogawa *et al.*, 2019) [74]. According to reports, *PhoH* is a cytoplasmic protein that binds ATP and is thought to be stimulated by P starvation (Goldsmith *et al.*, 2011) [32].

Table 3: Roles of viral families in rhizosphere soils

Virus family	Particular role in soils	Soil processes affected	References
Mimiviridae	Control bacterivorous protists to indirectly regulate bacterial turnover and abundance; host lysis releases nutrients and organic carbon.	Microbial loop, N mineralization, C cycling	Colson <i>et al.</i> , 2017; Jover <i>et al.</i> , 2014 [19, 44].
Phycodnaviridae	Regulate algal biomass; viral lysis releases organic materials produced from algae that affects surface stability and soil aggregation.	Primary production, C inputs, soil structure	Prangishvili <i>et al.</i> , 2009
Poxviridae	Host mortality adds organic wastes and nutrients to the soil, although its direct contribution is limited.	Organic matter inputs (indirect)	Prangishvili <i>et al.</i> , 2009
Iridoviridae	Belowground carbon allocation	soil C fluxes	Cory <i>et al.</i> , 2013
Ascoviridae	Increasing viral biomass and organic debris.	Nutrient recycling	Cory <i>et al.</i> , 2013
Microviridae	Lytic infection releases C, N, and P into the rhizosphere.	Microbial turnover, nutrient recycling, microbial loop	Trubl <i>et al.</i> , 2018 [104].;
Myoviridae	Control bacterial dominance via kill-the-winner dynamics; mediate transduction of metabolic and stress-response genes	Microbial diversity, carbon metabolism, nutrient availability	Jover <i>et al.</i> , 2014; Pratama and van Elsas, 2018 [44, 81].

Influence of soil viruses on plant health

Direct effect

Certain plant viruses can directly colonize root tissues, usually through natural apertures or through soil-dwelling vectors like

nematodes and insects. However, actual infection of living plant root cells by soil viruses is rather uncommon compared to viral infections of microorganisms. Root exudates, which are complex mixtures of sugars, organic acids, amino acids, and secondary

metabolites released into the rhizosphere that function as both nutritional resources and signaling molecules for soil microbes, can be affected by these direct plant virus-root interactions (Roossinck, 2015) ^[88]. In addition to altering local nutrient gradients, root exudates actively interact with and attract particular microbial taxa, influencing the structure and function of rhizosphere communities in ways that benefit plant growth and health (Liang *et al.*, 2025) ^[60]. Exudate composition, which varies dynamically with plant developmental stage and environmental conditions, has been demonstrated to regulate microbial colonization patterns, attracting beneficial microbes like plant growth-promoting rhizobacteria (PGPR) and mycorrhizal fungi while discouraging pathogens (Upadhyay *et al.*, 2022) ^[106].

Indirect effect via microbial hosts

By infecting the microbial hosts that comprise the rhizosphere microbiome, such as nitrogen-fixing bacteria, PGPR, and fungal symbionts like mycorrhizal fungi, soil viruses have far more ubiquitous indirect interactions with plant roots (Wang *et al.*, 2024; Pratama and van Elsas, 2020; Núñez-Muñoz *et al.*, 2025) ^[73, 82, 110]. These microbial communities' abundance, activity, and community composition are all impacted by viral predation, which has a cascading effect on nutrient cycling processes crucial to plant nutrition (Pratama and van Elsas, 2020) ^[82]. For instance, lytic infection of nitrogen-fixing bacteria might momentarily decrease nitrogen fixation while simultaneously releasing nitrogen-rich cellular contents into the soil by virus-mediated lysis. This process is theoretically similar to the "viral shunt" discussed in microbial ecology. Similar to this, microbial production of phytohormones like auxins and cytokinins, which are important regulators of plant root growth and architecture, is impacted by viral control of PGPR abundance. In mutualistic relationships, viral effects on fungal symbionts can alter the efficiency of water and nutrient exchange, indirectly influencing plant physiological reactions (Núñez-Muñoz *et al.*, 2025) ^[73].

Influence on root exudates

Root exudates are essential to rhizosphere communication networks that control community assembly and function, microbial signaling and root exudates are at the core of soil virus-microbe-plant interactions (Liang *et al.*, 2025; Núñez-Muñoz *et al.*, 2025) ^[60]. In addition to serving as sources of carbon and energy, the chemicals released by roots also function as chemoattractants, repellents, and signaling cues that control the recruitment and activity of microorganisms, including pathogens and beneficial PGPR (Liang *et al.*, 2025) ^[60]. These substances affect microbial metabolic pathways, biofilm formation, quorum sensing and community organization in response to environmental stress or plant physiological condition (Upadhyay *et al.*, 2022) ^[106]. According to Núñez-Muñoz *et al.*, (2025) ^[73], microbial populations generate signaling molecules and metabolites that influence plant defensive responses and hormonal balance, which in turn affects root exudation patterns. Viral infections alter the biochemical signals plants receive from their microbiome because they alter the makeup and functional potential of microbial communities (Wang *et al.*, 2024; Pratama and van Elsas, 2020; Núñez-Muñoz *et al.*, 2025) ^[73, 82, 110]. Therefore, the root exudation profile and plant stress physiology are affected by changes in microbial community structure, which can be brought about by viral predation, lysogeny, or horizontal gene transfer. These changes have consequences for root growth, immune priming, and nutrient acquisition (Wang *et al.*, 2024; Núñez-Muñoz *et al.*, 2025) ^[73, 110].

Impacts on plant health

Given the structural and functional similarities between the rhizosphere and gut microbiomes, the phage community should react to the rhizosphere microbiome and plant health similarly (Koskella *et al.*, 2018) ^[51]. The soil bacterial community may be modulated by rhizosphere phages. They are therefore intimately linked to the functioning of the soil and rhizosphere due to their structure and organic matter cycling. In particular, a variety of active viral populations were found in deep terrestrial ecosystems, where they were crucial in determining the structure of microbial communities and the turnover of nutrients (Daly *et al.*, 2018; Koskella *et al.*, 2018) ^[51]. Studies conducted in permafrost soil that found many AMGs in viral populations involved in C cycling further bolster the significance of soil phages in soil functioning (Trubl *et al.*, 2018) ^[104]. Crucially, by affecting nutrient inputs (from organic matter deposition to the cycling of soil nutrients like N, P, and S) and the qualitative/quantitative changes in rhizodeposits, these effects may produce plant-soil feedback (Li *et al.*, 2019). However, it has recently been suggested that the soil bacterial population is not significantly impacted by viral predation (Fierer, 2017) ^[27]. According to earlier research, VLPs were less common than rhizosphere bacteria, which may indicate that they are less vulnerable to phages (Swanson *et al.*, 2009) ^[97]. On the other hand, comparable ratios would suggest that the viromic population is primarily lysogenic because of the large number of bacterial hosts (Pratama and van Elsas, 2020). From an ecological standpoint, the virome probably contributes to the rhizosphere's resilience.

Conclusion

Soil viruses are integral components of terrestrial ecosystems, playing pivotal roles in microbial community structure, nutrient cycling, and plant health. Viruses control microbial populations and biogeochemical processes, affecting soil fertility and ecosystem sustainability through mechanisms such as the viral shunt, horizontal gene transfer, and lytic and lysogenic infection cycles. By regulating helpful microorganisms and acting as reservoirs for plant diseases, they also have an indirect and direct impact on plant health. Viral families like *Mimiviridae*, *Phycodnaviridae*, *Poxviridae*, *Iridoviridae*, *Ascoviridae*, *Microviridae*, *Myoviridae* play significant roles in soil nutrient cycling by regulating microbial populations and mediating organic matter turnover. This opened up possibilities for exploiting viruses as bioindicators of soil health and as biocontrol agents in agriculture. Despite these discoveries, there are still a lot of unanswered questions, especially when it comes to connecting viral sequences to host functions and ecological implications.

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