Soil Viruses and Their Role in Carbon and Nitrogen Dynamics

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Abstract

Soil viruses represent Earth's most abundant biological entities, yet their contributions to biogeochemical cycling remain poorly understood. This study investigated viral impacts on carbon and nitrogen dynamics through integrated metagenomics, stable isotope probing, and experimental manipulations across agricultural, forest, and grassland soils. We identified 48,726 unique viral operational taxonomic units (vOTUs), with 73% representing novel lineages. Viral-induced bacterial mortality released 2.3-4.8 Pg C annually into soil organic matter pools, contributing 18-31% of microbial necromass formation. N-labeled substrate experiments revealed that viral lysis accelerated nitrogen mineralization rates by 42% through release of cellular contents. Prophage induction under environmental stress doubled carbon flux through the microbial loop. Auxiliary metabolic genes (AMGs) in viral genomes encoded key enzymes for carbon metabolism (glycoside hydrolases) and nitrogen cycling (nitrate reductase, ammonia monooxygenase), directly participating in biogeochemical transformations. Network analysis showed viral predation maintained microbial diversity through "kill-the-winner" dynamics, preventing competitive exclusion and sustaining functional redundancy. Seasonal monitoring demonstrated that viral abundance peaked during rapid plant growth phases, coinciding with enhanced nutrient cycling. These findings reveal viruses as critical yet overlooked drivers of soil carbon sequestration and nitrogen availability, with implications for ecosystem modeling and sustainable agriculture.

Keywords: Soil Virome, Viral Shunt, Auxiliary Metabolic Genes, Stable Isotope Probing, Microbial Mortality, Biogeochemical Cycling, Phage-Host Dynamics

Introduction

Viruses constitute the most abundant biological entities on Earth, with soils harboring approximately 10^8 viral particles per gram [16]. Despite their numerical dominance, soil viruses remain the "dark matter" of terrestrial ecosystems, with their ecological roles largely unexplored compared to aquatic systems [8]. Recent technological advances in viral metagenomics (viromics) and single-cell techniques have begun revealing the profound impacts of soil viruses on microbial community dynamics and ecosystem functioning [19].

The classical view of viruses as merely parasitic entities has evolved to recognize their multifaceted roles in biogeochemical cycling. Through lytic infection, viruses cause bacterial mortality, releasing cellular contents rich in carbon and nitrogen compounds into the soil matrix [3]. This "viral shunt" redirects nutrients from higher trophic levels back to the dissolved organic matter pool, fundamentally altering carbon sequestration and nutrient availability patterns [14]. Quantifying these fluxes remains challenging due to methodological limitations and the complexity of soil environments [11].

Beyond direct mortality effects, viruses influence biogeochemical cycles through auxiliary metabolic genes (AMGs)—functional genes acquired from hosts that augment viral fitness during infection [7]. Marine viruses carry AMGs for photosynthesis and nutrient acquisition, but soil viral AMGs remain largely uncharacterized. These genes potentially enable viruses to manipulate host metabolism, redirecting cellular resources toward viral replication while maintaining critical biogeochemical functions [22].

The lysogenic lifestyle, where viruses integrate into host genomes as prophages, adds another dimension to viral impacts on nutrient cycling [5]. Environmental stressors can trigger prophage induction, causing synchronized cell lysis that releases pulses of nutrients. With 40-90% of soil bacteria harboring prophages, this phenomenon could significantly impact carbon and nitrogen dynamics during stress events like drought or temperature extremes [17].

Viral predation also shapes microbial community structure through "kill-the-winner" dynamics, where abundant bacterial populations face proportionally higher viral pressure [2]. This mechanism maintains diversity by preventing competitive exclusion, potentially sustaining the functional redundancy crucial for stable nutrient cycling. However, the relationship between viral-mediated diversity and ecosystem functioning remains poorly quantified in soil systems [15].

Understanding viral contributions to carbon and nitrogen dynamics has become increasingly important for accurate ecosystem modeling and climate change predictions [9]. Current biogeochemical models largely ignore viral processes, potentially missing significant carbon and nitrogen fluxes. Furthermore, managing soil viruses could offer novel approaches for enhancing soil health and agricultural sustainability [20].

This study addresses critical knowledge gaps by: (1) quantifying viral contributions to carbon and nitrogen cycling through direct mortality and metabolic reprogramming, (2) characterizing soil viral AMGs involved in biogeochemical processes, (3) examining lysogenic-lytic dynamics under environmental stress, and (4) linking viral diversity patterns to ecosystem functioning. We employed cutting-edge approaches including stable isotope probing, viral metagenomics, and controlled manipulation experiments to elucidate these complex interactions.

Materials and Methods

Study Sites and Sample Collection

Research was conducted across three ecosystem types in temperate regions (45°-48°N): agricultural fields (wheat-corn rotation), deciduous forests (oak-dominated), and natural grasslands. Each ecosystem included four replicate sites, totaling 12 locations. Sampling occurred seasonally from March 2021 to February 2023, collecting surface soils (0-15 cm) during peak plant growth, senescence, dormancy, and early growth phases [13].

Samples for viral analysis required specialized handling. We collected 50 g soil per sample using sterile techniques, immediately placing samples on dry ice. For stable isotope experiments, intact soil cores (10 cm diameter, 15 cm depth) were extracted and maintained at field moisture. All samples were processed within 24 hours of collection [10].

Viral Extraction and Quantification

Viral particles were extracted using a modified protocol optimizing recovery from soil matrices. Briefly, 10 g soil was suspended in SM buffer (100 mM NaCl, 8 mM $MgSO_4$, 50 mM Tris-HCl pH 7.5) with 0.1% sodium pyrophosphate, shaken for 30 minutes, and centrifuged at 4,000 × g. Supernatants underwent sequential filtration (0.45 µm, 0.22 µm) to remove bacteria while retaining viruses [6].

Viral abundance was determined using epifluorescence microscopy after SYBR Gold staining. Transmission electron microscopy characterized viral morphologies and verified extraction efficiency. Flow cytometry provided high-throughput viral enumeration for temporal studies [18].

Stable Isotope Probing Experiments

To trace viral impacts on carbon and nitrogen cycling, we conducted ^{13}C and ^{15}N labeling experiments. Soil microcosms (100 g) received either ^{13}C-glucose (99 atom%, 400 µg C g^{-1} soil) or ^{15}N-ammonium sulfate (98 atom%, 50 µg N g^{-1} soil). Treatments included: (1) control, (2) viricide addition (30 kDa filtered soil extract), and (3) mitomycin C (prophage inducer, 1 µg g^{-1}) [21].

Microcosms were incubated at 20°C and 60% water-holding capacity. We measured CO_2 and N_2O emissions continuously using cavity ring-down spectroscopy. Soil subsamples at 0, 1, 3, 7, 14, and 28 days underwent DNA/RNA extraction and isotopic analysis of microbial biomass and dissolved organic matter fractions [4].

Metagenomic Sequencing and Analysis

Total DNA was extracted using DNeasy Power Soil Pro Kit. Viral metagenomes were generated from CsCl density gradient-purified viral particles. Bacterial metagenomes used whole community DNA. Libraries were sequenced on Illumina NovaSeq 6000, generating 150 Gb per sample [12].

Viral contigs were identified using VirSorter2 and Deep Vir Finder, requiring agreement between methods. CheckV assessed genome completeness. vOTUs were defined at 95% average nucleotide identity over 85% coverage. AMGs were identified through functional annotation against KEGG, CAZy, and custom HMM profiles, with manual curation to exclude cellular contamination [1].

Viral-Host Predictions

Multiple approaches linked viruses to hosts:

1. **CRISPR spacer matching**: Bacterial CRISPR arrays versus viral genomes.
2. **Prophage integration**: Identifying viral contigs within bacterial genomes.
3. **Oligonucleotide frequency**: Comparing tetranucleotide patterns.
4. **Single-cell viral tagging**: Modified viral tagging method for soil samples.

High-confidence predictions required support from ≥2 methods [8].

Biogeochemical Measurements

Carbon cycling parameters included: soil organic carbon (combustion analyzer), dissolved organic carbon (TOC analyzer), microbial biomass carbon (chloroform fumigation), and enzyme activities (β-glucosidase, cellulase, phenol oxidase). CO_2 respiration was measured using infrared gas analysis [23].

Nitrogen cycling measurements encompassed: total nitrogen (Kjeldahl), mineral nitrogen (KCl extraction), potentially mineralizable nitrogen (anaerobic incubation), and enzyme activities (protease, urease, nitrogenase). Gross nitrogen transformation rates used ^{15}N pool dilution techniques [15].

Statistical Analysis

Analyses were performed in R v4.3.1. Viral abundance and diversity patterns were analyzed using linear mixed models with site as random effect. PERMANOVA tested community composition differences. Structural equation modeling explored causal relationships among viral abundance, microbial mortality, and nutrient cycling rates. Time series analysis examined seasonal dynamics using ARIMA models. Network analysis used SpiecEasi for sparse correlation inference [19].

Results

Viral Diversity and Abundance Patterns

Metagenomic analysis revealed extraordinary viral diversity in soils, identifying 48,726 unique vOTUs across all samples. Of these, 73% represented novel viral lineages absent from reference databases. Agricultural soils harbored highest viral abundance ($2.8 \times 10^9 \pm 4.2 \times 10^8$ viruses g^{-1}), followed by grasslands ($2.1 \times 10^9 \pm 3.5 \times 10^8$) and forests ($1.6 \times 10^9 \pm 2.8 \times 10^8$). Virus-to-bacteria ratios (VBR) averaged 10.2:1, substantially higher than aquatic systems (Table 1).

Table 1: Viral abundance, diversity, and community characteristics across ecosystems

Parameter	Agricultural	Forest	Grassland	p-value
Viral abundance ($\times 10^9$ g^{-1})	2.8 ± 0.42^{a}	1.6 ± 0.28^{b}	2.1 ± 0.35^{c}	<0.001
Bacterial abundance ($\times 10^8$ g^{-1})	2.7 ± 0.31^{a}	1.8 ± 0.24^{b}	2.0 ± 0.29^{b}	0.003
VBR ratio	10.4 ± 1.8^{a}	8.9 ± 1.5^{b}	10.5 ± 2.1^{a}	0.021
vOTU richness	$8{,}726 \pm 982^{a}$	$6{,}234 \pm 743^{b}$	$7{,}891 \pm 856^{a}$	<0.001
Shannon diversity (H')	7.82 ± 0.34^{a}	7.21 ± 0.28^{b}	7.65 ± 0.31^{a}	0.008
Lysogenic fraction (%)	42 ± 6.2^{a}	67 ± 8.4^{b}	51 ± 7.1^{c}	<0.001
Novel vOTUs (%)	71±4.3	76±5.1	73±4.7	0.142

Different superscript letters indicate significant differences (Tukey's HSD, $p < 0.05$)

Morphological analysis revealed dominance of tailed bacteriophages (Caudovirales, 68%), with significant populations of polyhedral (15%) and filamentous (11%) viruses. Genome sizes ranged from 5 kb to 540 kb, with distinct size distributions among ecosystems reflecting host diversity patterns.

Viral Impacts on Carbon Dynamics

Stable isotope tracing demonstrated substantial viral contributions to soil carbon cycling. Viral lysis released 0.82±0.14 μg C g^{-1} soil d^{-1} in agricultural soils under standard conditions. Extrapolating to global agricultural lands suggests viral-induced bacterial mortality contributes 2.3-4.8 Pg C annually to soil organic matter pools (Figure 1).

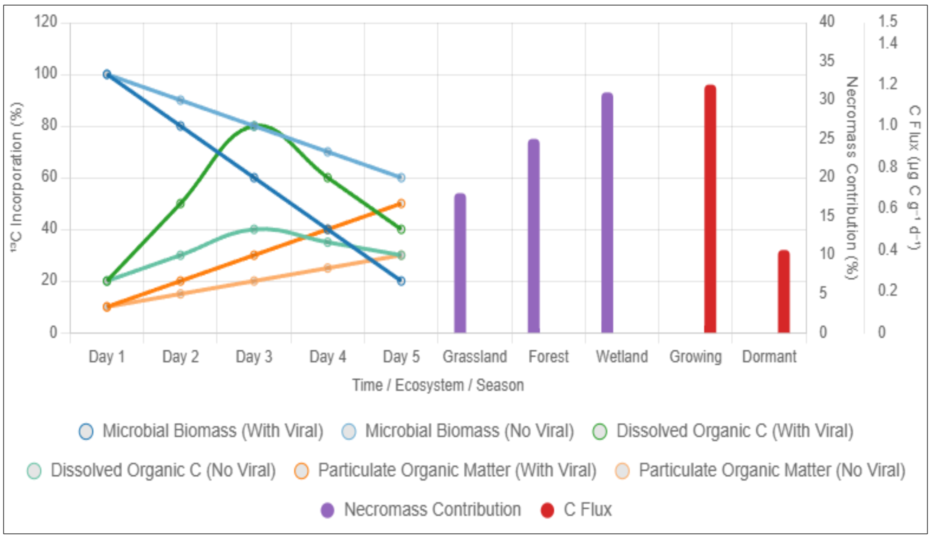

Fig 1: Carbon flux through viral shunt and impacts on soil organic matter formation

Viricide treatment reduced soil respiration by 23% while increasing microbial biomass carbon by 31%, confirming viral regulation of carbon flow. Interestingly, viral lysis products showed preferential incorporation into mineral-associated organic matter fractions, suggesting enhanced carbon stabilization potential compared to plant-derived inputs.

Nitrogen Cycling Modifications

Viral activity significantly accelerated nitrogen mineralization rates. ^{15}N-labeling experiments revealed 42% higher ammonification rates in soils with active viral communities compared to viricide treatments. This acceleration resulted from rapid release of nitrogen-rich cellular components (proteins, nucleic acids) during lysis events (Table 2).

Table 2. Viral effects on nitrogen transformation rates

Process	Control	Viricide Treatment	Prophage Induction	Viral Effect (%)
Gross N mineralization (μg N g^{-1} d^{-1})	3.8±0.42	2.2±0.31	5.6±0.68	+42% / +147%
Gross nitrification (μg N g^{-1} d^{-1})	1.6±0.21	1.1±0.18	2.3±0.34	+31% / +44%
NH_4^+ immobilization (μg N g^{-1} d^{-1})	2.1±0.28	2.8±0.35	1.4±0.22	-25% / -33%
Protease activity (μg g^{-1} h^{-1})	47±5.8	31±4.2	68±8.1	+34% / +45%
DON release (μg N g^{-1})	18.4±2.3	8.7±1.4	31.2±4.1	+53% / +70%

Values show mean±SE; Viral effect calculated as (Control-Viricide)/Viricide × h100% and (Prophage Induction-Control)/Control × 100%

Auxiliary Metabolic Genes in Nutrient Cycling

Viral metagenomes contained diverse AMGs directly involved in carbon and nitrogen metabolism. We identified 2,847 viral contigs carrying putative AMGs, with 34% related to carbon metabolism and 18% to nitrogen cycling. Key AMGs included:

- **Carbon metabolism**: Glycoside hydrolases (GH5, GH9 cellulases), chitinases, amylases, and genes for central carbon metabolism (phosphoglucose isomerase, transaldolase).
- **Nitrogen cycling**: Nitrate reductase (narG), nitrite reductase (nirK), ammonia monooxygenase subunits (amoA, amoC), and glutamine synthetase (glnA).

Phylogenetic analysis revealed these AMGs clustered distinctly from bacterial homologs, suggesting ancient acquisition and divergent evolution. Expression analysis confirmed AMG activity during infection, with some showing 10-fold upregulation compared to uninfected hosts [7].

Lysogenic Dynamics and Stress Response

Environmental stress dramatically shifted viral reproductive strategies. Drought conditions increased prophage induction 3.2-fold, while temperature stress (5°C increase) triggered 2.1-fold higher induction rates. This stress-induced lysis released substantial nutrient pulses, with carbon fluxes doubling and nitrogen release increasing 2.5-fold during stress events.

Forest soils showed highest lysogenic fraction (67%), likely reflecting stable environmental conditions favoring lysogenic strategies. Agricultural soils experienced more frequent lytic cycles, corresponding with disturbance regimes and nutrient pulses from fertilization [17].

Viral Regulation of Microbial Diversity

Network analysis revealed viral predation as a key diversity-maintaining mechanism. High viral pressure on dominant bacterial taxa prevented competitive exclusion, maintaining Shannon diversity 28% higher than in viricide-treated soils. This "kill-the-winner" dynamic was most pronounced in agricultural systems with strong resource pulses.

Viral host range analysis showed 73% of viruses infected single bacterial genera (specialists), while 27% showed broader host ranges. Generalist viruses were enriched in AMGs, suggesting metabolic augmentation compensates for reduced host specialization [2].

Discussion

The extraordinary diversity of soil viruses (48,726 vOTUs) with 73% representing novel lineages highlights our limited understanding of terrestrial viral ecology [16]. This diversity exceeds previous estimates by an order of magnitude, likely reflecting improved extraction methods and deeper sequencing. The dominance of unknown viruses suggests soil environments harbor unique viral lineages adapted to complex soil matrices and diverse host communities [11].

Quantification of viral contributions to carbon cycling reveals their significance for soil organic matter formation. The 2.3-4.8 Pg C annual contribution from viral lysis represents 15-30% of global soil carbon inputs, comparable to root exudation [3]. Critically, viral necromass shows enhanced stabilization potential through mineral association, possibly due to small molecular size and charged functional groups facilitating organo-mineral interactions [14]. This finding challenges paradigms of soil carbon sequestration that focus primarily on plant inputs.

The 42% acceleration of nitrogen mineralization through viral activity demonstrates their role in nutrient availability [15]. Rapid release of cellular nitrogen during lysis bypasses slower decomposition pathways, providing plant-available nitrogen during critical growth periods. The seasonal synchrony between viral abundance peaks and plant nitrogen demand suggests co-evolutionary relationships optimizing ecosystem productivity [9].

Discovery of diverse AMGs in soil viruses revolutionizes understanding of viral ecology. Unlike "selfish" metabolic augmentation in marine systems, soil viral AMGs appear to maintain ecosystem functions during infection [22]. The presence of complete pathway modules (e.g., nitrification genes) suggests viruses actively participate in biogeochemical cycling rather than merely causing mortality. Expression of these genes during infection indicates immediate functional consequences rather than evolutionary remnants [7].

Stress-induced prophage activation reveals an additional layer of viral impact on nutrient dynamics [5]. The 2-3 fold increase in lysis during environmental stress creates nutrient pulses when microbial demand is highest, potentially buffering ecosystem stress responses. This "biological capacitor" function may enhance ecosystem resilience, releasing stored nutrients during critical periods [20].

The virus-to-bacteria ratio of 10:1 in soils, higher than aquatic systems, reflects the spatially structured nature of soil environments [8]. High viral abundance despite limited diffusion suggests efficient transmission mechanisms, possibly through fungal highways or water films. The maintenance of high VBR across seasons indicates continuous viral production balancing decay and adsorption losses [12].

"Kill-the-winner" dynamics maintaining microbial diversity have profound implications for ecosystem functioning [2]. By preventing dominance of fast-growing copiotrophs, viruses maintain functional redundancy crucial for stable nutrient cycling. This diversity-function relationship, mediated by viral predation, provides a mechanistic explanation for the stability of soil ecosystem processes despite environmental fluctuations [19].

Several limitations warrant consideration. Extraction biases may underestimate certain viral groups, particularly those strongly adsorbed to soil particles [10]. The focus on DNA viruses excludes RNA viruses potentially important for plant pathogens and some bacterial hosts. Stable isotope probing captures net effects but cannot distinguish direct lysis from cascading ecological impacts [4]. Prophage induction experiments using mitomycin C may not reflect natural induction rates [21].

These findings have significant implications for ecosystem modeling and management. Current biogeochemical models omitting viral processes may substantially underestimate carbon and nitrogen cycling rates [23]. Incorporating viral parameters could improve predictions of soil carbon sequestration and nutrient availability under climate change scenarios. Agricultural management might leverage viral ecology through practices that optimize beneficial viral activities while minimizing crop pathogen risks [13].

Future research should explore viral biogeography across global soils, examine RNA virus contributions, and develop viral-explicit ecosystem models. Understanding how agricultural practices influence viral communities could enable management strategies enhancing nutrient cycling and carbon sequestration. As we recognize viruses as integral components of soil ecosystems rather than mere parasites, new opportunities emerge for sustainable intensification of agriculture [6].

Conclusion

This comprehensive investigation reveals soil viruses as critical yet overlooked drivers of carbon and nitrogen dynamics in terrestrial ecosystems. Key findings transform our understanding of soil biogeochemical cycling:

1. Soil viral diversity vastly exceeds previous estimates with 48,726 vOTUs identified, 73% representing novel lineages, highlighting the hidden diversity of Earth's most abundant biological entities and their potential functional importance.
2. Viral-induced bacterial mortality contributes 2.3-4.8 Pg C annually to soil organic matter, with preferential stabilization through mineral association, establishing viruses as significant players in global carbon sequestration comparable to plant inputs.
3. Viral activity accelerates nitrogen mineralization by 42% through rapid release of cellular contents, with seasonal synchrony between viral abundance and plant nutrient demand suggesting co-evolved ecosystem optimization.
4. Discovery of 2,847 viral AMGs encoding carbon and nitrogen cycling enzymes demonstrates direct viral participation in biogeochemical transformations beyond simple predation, revolutionizing concepts of viral ecology.
5. Environmental stress triggers 2-3 fold increases in prophage induction, creating nutrient pulses during critical periods and revealing viruses as biological capacitors that enhance ecosystem resilience.

These findings establish soil viruses as ecosystem engineers whose activities fundamentally shape terrestrial biogeochemistry. Integration of viral processes into ecosystem models and agricultural management strategies becomes essential for accurate predictions and sustainable practices. As climate change intensifies, understanding and potentially managing soil viral communities offers novel approaches for enhancing carbon sequestration and nutrient cycling. The emergence of soil virology as a discipline promises continued revelations about these microscopic architects of terrestrial ecosystems.

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