

UC Davis

UC Davis Previously Published Works

Title

Soil Virus Life-Strategy Conversion and Implications for Ecosystem and Soil Functions

Permalink

<https://escholarship.org/uc/item/6js3187w>

Journal

Global Change Biology, 31(8)

ISSN

1354-1013

Authors

Tong, Di

Ma, Bin

Hu, Lingfei

et al.

Publication Date

2025-08-01

DOI

10.1111/gcb.70460

Peer reviewed

REVIEW

Soil Virus Life-Strategy Conversion and Implications for Ecosystem and Soil Functions

Di Tong^{1,2} | Bin Ma^{1,2}  | Lingfei Hu^{1,2} | Yong Li^{1,2} | Randy A. Dahlgren³ | Jianming Xu^{1,2} 

¹State Key Laboratory of Soil Pollution Control and Safety, College of Environmental and Resource Sciences, Zhejiang University, Hangzhou, China | ²Zhejiang Provincial Key Laboratory of Agricultural Resources and Environment, Zhejiang University, Hangzhou, China | ³Department of Land, Air and Water Resources, University of California, Davis, Davis, California, USA

Correspondence: Jianming Xu (jmxu@zju.edu.cn)

Received: 16 April 2025 | **Revised:** 28 July 2025 | **Accepted:** 11 August 2025

Funding: This work was supported by National Natural Science Foundation of China, 42330711; National Key R&D Program of China, 2024YFD1501801; Fundamental Research Funds for the Central Universities, 226-2025-00004; Earmarked Fund for China Agriculture Research System, CARS-01; China Postdoctoral Science Foundation, GZC20251623.

Keywords: environmental thresholds | one health | soil functions | soil nutrient cycling | soil virus | viral life strategy conversion

ABSTRACT

Both viral abundance and life state vary across contrasting soil environments and are crucial for mediating microbial metabolism and soil functions. Yet, why soil viruses favor the lytic or lysogenic cycle in a given soil environment, and to what extent they affect soil functions, remains unclear. In this review, we constructed a soil virus abundance dataset containing 691 samples, which for the first time included the lysogenic fraction index to quantify the proportion of soil viruses in the lysogenic state. Moreover, we have assessed the distribution and key drivers of soil viral properties based on 21 soil physicochemical indicators. We also systematically summarized three molecular mechanisms regulating viral lysis–lysogenic transformations that are believed to be widespread in soil environments. We propose a conceptual framework for a transition threshold of viral life strategies based on existing experimental evidence. When environmental stress falls below the critical tolerance level of soil microbes, soil viruses facilitate stress relief. However, once stress exceeds the microbial tolerance threshold, the soil viruses transition to another life cycle, such as from the lysogenic to lytic state. This transition results in completely different effects on microbial metabolic systems and associated soil functions. Further, we documented the role of soil viruses in soil ecosystem functions, highlighting in particular, the importance of the “viral shuttle” and “virovory” mechanisms for soil carbon sequestration and complementary One Health functions. Finally, we provide our perspective on future research needs to advance our understanding of soil virology and its impact on soil functions, particularly in the context of global climate change.

1 | Introduction

Viruses, the most abundant biological entity on Earth, are increasingly recognized for their important ecological roles due to the close relationship between viruses and almost all living organisms (Jansson and Wu 2023). It has been estimated that viral abundance (VA) in soils is much higher than in the marine environment (4.88×10^{30} VLPs in soil vs. 1.29×10^{30} VLPs in marine), assuming that all soil ecosystems have the same virus-to-microbe ratio (VMR) (Guemes et al. 2016). Clearly, using the same VMR

cannot accurately depict the complexity and heterogeneity of the real-world soil environment. This is because highly variable soil properties, such as pH, moisture, clay, and nutrient content, significantly influence microbial and viral communities (Li et al. 2019; Lee et al. 2022; Nicolas et al. 2023; Philippot et al. 2023).

Although previous attempts were made to assess significant differences in the abundance of soil viruses across different ecosystems, the sample size was too small ($N=52$) and did not include other important indicators, such as the lysogenic

fraction (LF) and relationships with soil physicochemical properties (Williamson et al. 2017). Due to recent advances in soil virus research, additional data on soil viral dynamics have been elucidated, especially data concerning the use of the lysogenic fraction to assess viruses in the lysogenic state (Liang, Zhang, et al. 2020). Therefore, it is an appropriate time to update the soil virus dataset and investigate the key differences and drivers of viruses in different soil ecosystems at the global scale. It is also warranted to address the role of viruses in nutrient cycling processes, given the changing global climate and land-use patterns. Both the “viral shunt” and “viral shuttle” mechanisms, as well as interactions that couple carbon, nitrogen, and phosphorus cycling, have been documented in soil environments (Li et al. 2013; Tong et al. 2023, 2025). However, the extent to which these mechanisms affect soil carbon cycling and associated nutrient cycling functions remains unclear.

Viruses can be divided into virulent and temperate categories according to their life strategies. The former can only lyse hosts, whereas the latter can choose between a lytic or lysogenic cycle depending on host density and environmental conditions (Howard-Varona et al. 2017; Kuzyakov and Mason-Jones 2018; Bruce et al. 2021). Different viral life cycles can significantly impact host metabolic activities. In the lysogenic cycle, the virus has minimal impact on host metabolism, whereas the virus in the lytic cycle reprograms the host's resource acquisition and central carbon and energy metabolism (Howard-Varona et al. 2020). These changes may further alter the ability of soil microbes in contaminant bioremediation (Zheng et al. 2022). Models such as kill-the-winner (Chen, Weinbauer, et al. 2021), piggyback-the-winner (Knowles et al. 2016), or cull-the-winner (Santos-Medellin et al. 2023) have been proposed to explain the dynamics between viruses and their hosts. But why do virus-host relationships follow different models in different soil environments? What are the molecular mechanisms involved in these relationships? And what are the associated effects on soil properties and soil functions? Furthermore, soil microbiomes, including soil viruses, have been proposed as an important component of the One Health concept that provides an integrated and unifying approach to sustainably balance and optimize the health of people, animals, and ecosystems (Singh et al. 2023).

Significant progress has been achieved in soil virology research, including the discovery of novel soil viruses (Schulz et al. 2018), improvements to the global soil virus databases and viral biogeographic patterns (Schulz et al. 2020; Ma et al. 2024), the optimization of soil virus extraction methods (Williamson et al. 2005; Narr et al. 2017; Yu et al. 2023), and the elucidation of mechanisms for virus-host mutualism in different soil environments (Lee et al. 2023; Lopez-Garcia et al. 2023; Ma et al. 2023; Ter Horst et al. 2023; Cheng et al. 2024). However, there is a lack of systematic summaries assessing the mechanisms driving soil viral lysis–lysogenic transitions and viral properties among different soil ecosystems. Thus, this review aims to summarize the molecular mechanisms of soil viral lysis–lysogenic transition and viral properties, including VA, VMR, and LF, the fraction of microbial mortality caused by soil viruses, and their distribution among global soil ecosystems. Moreover, we propose a new concept: the viral threshold response to soil environmental stressors, such as the threshold-based role of temperature, moisture, and contaminants, in viral lysis–lysogenic transformation.

Further, we systematically demonstrate the impact of soil viruses on soil ecological functions in terms of food security/safety, secondary source of pathogenic viruses, maintenance of soil biodiversity in harsh environments, and sustainable pathogen killers/suppressors in the context of the One Health concept.

2 | Distribution of Soil Viruses in Different Terrestrial Ecosystems

Estimates of soil virus abundance can reach up to 4.88×10^{30} VLPs (virus-like particles) gdw^{-1} soil, accounting for nearly 10% of the global virus inventory (Guemes et al. 2016). As such, soil viral dark matter has attracted considerable attention and become a hot topic of research, especially in terms of soil virome metagenomics. However, it remains unclear how many soil viruses actually exist in different soil ecosystems, how/why they may differ, and how they affect ecological and soil functions. To address these unknowns, we expanded the soil virus abundance dataset of Williamson et al. (2017), increasing the sample size from 52 to 691. From the newly updated soil virus abundance dataset (Table S1 and Figure 1A), soil virus abundance (VA) ranges from 2.70×10^3 VLPs gdw^{-1} soil in hot deserts to 1.76×10^{10} VLPs gdw^{-1} soil in wetlands. Moreover, the ecosystem type purported to have the highest soil virus abundance was not the previously reported forest soils, but follows the order: wetland (mean/median: $5.87 \times 10^9/3.97 \times 10^9$ VLPs gdw^{-1} soil) > agricultural land ($2.47 \times 10^9/1.39 \times 10^9$ VLPs gdw^{-1} soil) > grassland ($1.36 \times 10^9/7.81 \times 10^8$ VLPs gdw^{-1} soil) $\approx$ forest ($1.22 \times 10^9/7.94 \times 10^8$ VLPs gdw^{-1} soil) > tundra ($5.84 \times 10^8/4.95 \times 10^8$ VLPs gdw^{-1} soil) > cold desert ($3.30 \times 10^8/2.90 \times 10^8$ VLPs gdw^{-1} soil) > hot desert ($3.76 \times 10^6/1.05 \times 10^5$ VLPs gdw^{-1} soil) (Figure 1). Due to the disturbance caused by human agricultural activities, the range of VA in agricultural soil is greater than in other land-use types.

In addition to extracellular free virus particles, intracellular viruses in a lysogenic state can be detected and referred to as the lysogenic fraction (LF) (Liang, Zhang, et al. 2020). The LF can facilitate a more intuitive and precise comprehension of soil viral population dynamics and life-history strategies. Furthermore, LF can be utilized to infer the extent to which viruses function via AMGs without lysing their hosts in soil. To our knowledge, this is the first time that the LF in different soil ecosystems has been systematically assessed (Figure 1C). The results showed that the highest LF was found in grassland (mean/mediation: 56.4/59.2%) and agricultural (52.8/59.2%) soils, followed by forest soil (48.0/50.9%), wetlands (44.4/44.4%), and cold desert (15.5/19.3%). The LF in hot deserts and tundra soils has not been reported at this time.

The virus-to-microbe ratio (VMR) has been proposed as a proxy for the relationship between viral and microbial communities (Parikka et al. 2017). For many years, research has attempted to predict the rate of host viral infection by estimating the VMR. A consensus has emerged that viral abundance is typically tenfold higher than microbial abundance (Guemes et al. 2016). However, the VMR is more complex than expected, especially in soils (Liang et al. 2023). The VMR in soils is highly variable across different ecosystems, ranging from 0.002 to 8200, with an average value of ~ 153 , more than an order of magnitude higher

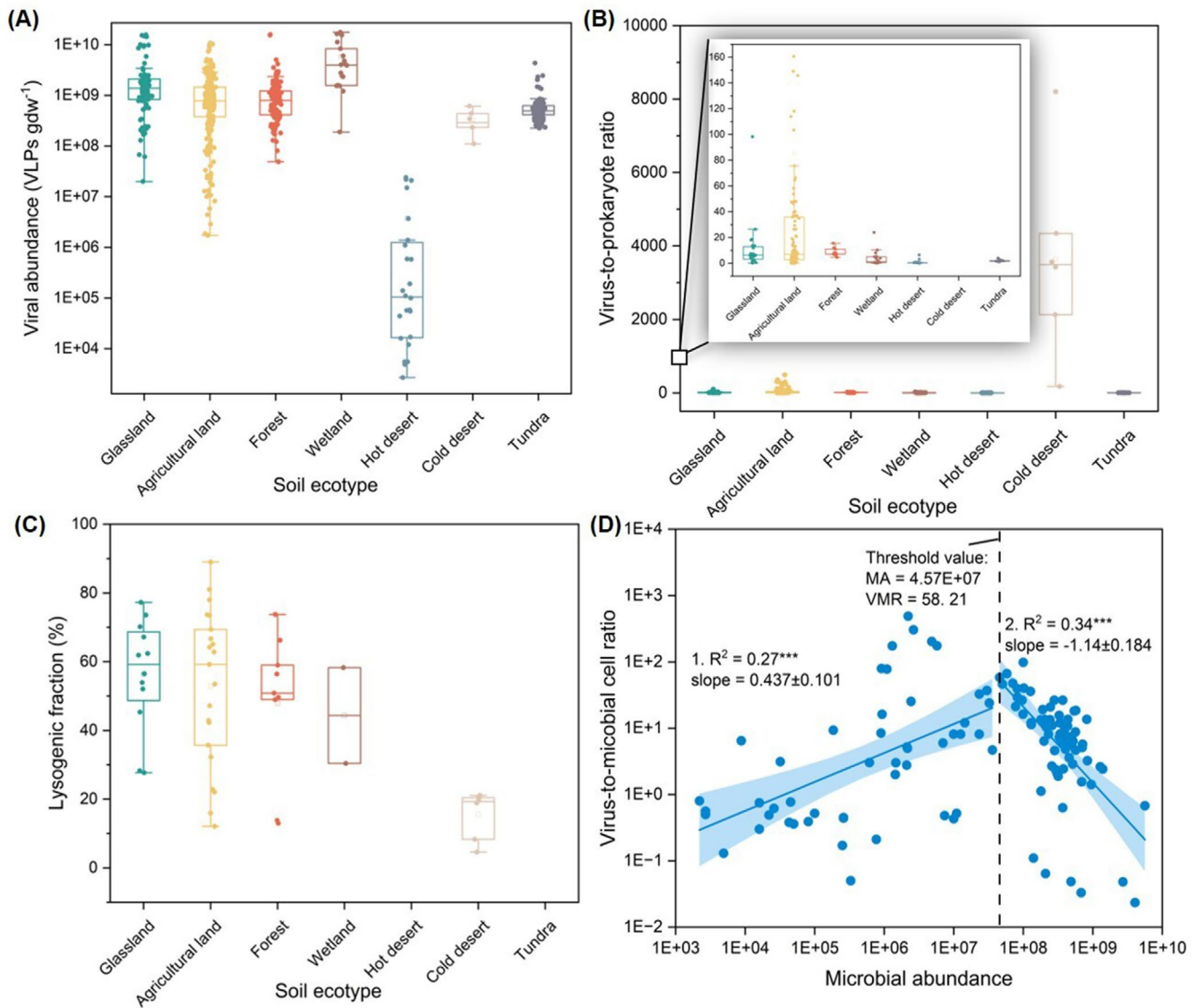


FIGURE 1 | Variation of viral properties in different soil ecosystems. (A) Viral abundance grouped by soil ecotypes: Grassland ($N=97$), agricultural ($N=255$), forest ($N=121$), wetland ($N=18$), hot desert ($N=24$), cold desert ($N=6$) and tundra ($N=150$) (See Table S1 for more details). (B) Virus-to-microbe ratio (VMR) and (C) the LF (lysogenic fraction) of different soil ecosystems. (D) Relationship between VMR and microbial abundance.

than the consensus value of 10 (Table S1). This would imply that the total viral abundance in soils is much higher than previously estimated based on the VMR of 10.

The VMRs in different soil ecosystems were compared to better estimate the viral abundance and the rate of virus infection of hosts. As shown in Figure 1B, the highest VMR occurred in the cold desert (mean/median: 3638/3493), followed by agricultural soil (85.6/7.1) and grassland soil (12.1/6.3), and then forest soil (8.4/7.2), wetlands (3.9/1.2), tundra (2.1/2.0) and hot desert (0.8/0.5). Notably, the VMR does not always increase with microbial abundance, but decreases sharply at higher microbial abundances. Hence, a higher microbial abundance does not always mean a higher virus-induced host mortality (Wigington et al. 2017; Liang et al. 2023). More specifically, there appears to be a threshold value (microbial abundance $\approx 4.57 \times 10^7 \text{ g}^{-1}$ soil and VMR ≈ 58.2) between the relationship of VMR and microbial abundance. The VMR increases with microbial abundance below this threshold value, whereas VMR decreases at

higher microbial abundances (slope = -1.14 vs. slope = 0.437 ; Figure 1D). This threshold tendency for VMR suggests that both the kill-the-winner (KtW) and piggyback-the-winner (PtW) models exist in the soil environment. That is to say that the KtW strategy is transformed to PtW as the microbial abundance increases, with a threshold value corresponding to a microbial abundance of $\sim 4.57 \times 10^7 \text{ g}^{-1}$ soil.

If only endogenous factors are considered, without considering exogenous factors (e.g., soil physicochemical properties) that are too complex to explain, the threshold trend in VMR versus microbial abundance can be attributed to the trade-off between the capacity for effective viral infection and host defense. This has been confirmed by a long-term field experiment that found the higher the microbial abundance, the stronger the resistance to viruses (Wu et al. 2020). Another potential factor is the prevalence of a viral lysogenic state with a high microbial density under microbially favorable environmental conditions, such as a nutrient-rich environment (Knowles et al. 2016;

Chen, Weinbauer, et al. 2021; Liang et al. 2023). In addition to total viral abundance, the composition of viral communities is compiled in Figures S1 and S2. Despite the large variation in viral abundance between different soil ecosystems, the most abundant viral species in soil were similar and included DNA viruses of *Siphoviridae*, *Myoviridae*, and *Podoviridae*, and RNA viruses of *Narnavirales*, *Tolivirales*, and *Picornavirales* (Emerson et al. 2018; Cao et al. 2022; Chen et al. 2022; Liao et al. 2022b).

Soil virus abundance was correlated with a total of 21 soil physicochemical properties (Figures S3–S5) to assess potential drivers of virus abundance. Soil viral abundance showed a significant positive relationship with clay content, SOC, and TP, whereas a negative correlation was found with sand content and C/N (Figure S3). A systematic consideration of the effects of soil physicochemical properties on soil virus abundance, VMR, and LF leads to the following conclusions: (1) The same properties affecting viral abundance also affect VMR, but in an opposite manner (Figures S3 and S4). This suggests that both clay content and SOC can stimulate the growth of microbes and viruses (Liang et al. 2023), with the microbial growth rate being higher than that of soil viruses. The response of the soil virus community to the soil environment may lag behind that of its host, which has also been observed during the rewetting of grassland soils (Nicolas et al. 2023). (2) Soil nitrogen content can induce the transformation of soil viruses from the lysogenic to lytic state (indicated by the negative relationship between inorganic N and LF, and the negative correlation between virus abundance and C/N; Figures S3 and S5). (3) Microbes are more sensitive to pH than viruses. There was no clear relationship between pH and viral abundance; however, significant relationships between pH with VMR and LF were found (Figures S4 and S5). In addition, pH appears to stimulate the bloom of free virus abundance by inducing prophages, which results in decreased FL and increased VMR (Figures S4 and S5).

3 | Viral Lytic-Lysogenic Transition Mechanisms

Despite numerous papers documenting the two dominant viral life cycles (lysis versus lysogeny) and the co-evolution of viruses and their hosts (Obeng et al. 2016; Pratama and van Elsas 2018; Correa et al. 2021; Chevallereau et al. 2022), the mechanism triggering the life cycle switch in the soil environment remains elusive. Here, we divide the decision pathway of lysis-lysogeny into three parts according to their molecular basis: host SOS trigger factor (signals from hosts to viruses; B to V), quorum sensing systems (B to V), and arbitrium systems (signals from viruses to viruses; V to V). These three mechanisms are described in more detail in the [Supporting Information](#).

Both lytic and temperate phages can successfully infect their host, but dramatically differ in their ability to reprogram the host's metabolism (Ankrah et al. 2014; Rosenwasser et al. 2016; Howard-Varona et al. 2020). During infection, temperate phages tend to conserve energy by repressing energy-consuming processes, such as motility and translation processes, and utilizing the host's translational machinery to replicate. In contrast, lytic phages are likely to reprogram central carbon and energy metabolism processes by overexpressing the related genes and hijacking the host's tRNAs for translating their progeny

(Howard-Varona et al. 2020). The vastly different influence of host metabolisms by different state phages implies different effects on ecosystem and soil functions. Although the three lytic-lysogenic transition mechanisms are widespread in soil environments (Ghosh et al. 2009; Stokar-Aviñal et al. 2019; Liang, Wagner, et al. 2020), it remains unclear how soil viruses favor the lytic or lysogenic cycle in a given soil environment, let alone how the transformation affects soil functions (Figure 2).

4 | Environmental Thresholds of Soil Viral Life-Cycle Transformation

4.1 | Soil Temperature Threshold

All steps of viral infection are temperature dependent, such as host encounter, absorption, injection of genetic material into host cells, synthesis of viral progeny, and assembly/release of virions (Wieczynski et al. 2023). Elucidating the effect of temperature on soil viruses is crucial to understanding the interactions between soil viruses and their hosts, and thus the impacts on soil functions. To date, there is no unifying concept concerning how temperature affects the interactions between soil viruses and their hosts. During an 8-year study of warming at the field scale, the higher temperature increased microbial activities, which in turn stimulated viral lysing, with more lytic viruses at higher temperatures as assessed by screening CRISPR-Cas marker genes (Wu et al. 2020). However, other studies suggest that warmer temperatures reduce viral proliferation and activity (Straub et al. 1992; Nasser and Oman 1999). For instance, in hot deserts, extracellular viral abundance is too low to detect, and only when mitomycin C is added to soils do viral particles increase (Prigent et al. 2005; Adriaenssens et al. 2015). In contrast, soil viruses are abundant in cold deserts, ranging from 2.3×10^8 to 6.4×10^8 VLPs per gram of soil (Williamson et al. 2007). The lysogenic cycle appears to be more prevalent at higher temperatures, with 4.6%–21.1% bacterial lysogens in cold desert soils compared to 84% bacterial lysogens in hot desert soils (Fierer et al. 2007; Williamson et al. 2007).

Coupled with the results of a pure *Micromonas* virus culture experiment, we posit that a temperature threshold exists that regulates the transition of viral life strategies (Figure 3 and Table S3), with the threshold being close to the host's optimal growth temperature (T_{opt}) (Demory et al. 2017). At temperatures below T_{opt} , viruses replicate in the classical lytic cycle, with efficiency increasing with temperature until T_{opt} is approached. At T_{opt} , the shortest latent period, largest burst size, and fastest virus production rate occur due to the high host metabolic activities, protein biosynthesis rates, and enhanced membrane permeability for virus absorption (Demory et al. 2017). As temperatures rise above T_{opt} , even by 1°C, host resistance to viruses is dramatically increased, and viral lytic infection strategies rapidly turn to lysogenic cycles (Wu et al. 2020; Liao et al. 2023).

Based on these findings, the results from the 8-year soil warming experiment are consistent with temperature conditions below T_{opt} , whereas the results of the desert soils are consistent with conditions above T_{opt} . Of course, virus-host interactions in desert soils may be jointly influenced by other factors, such as hyperaridity and extreme oligotrophy (Zablocki et al. 2016; Hwang et al. 2021). Another interesting finding is that viruses

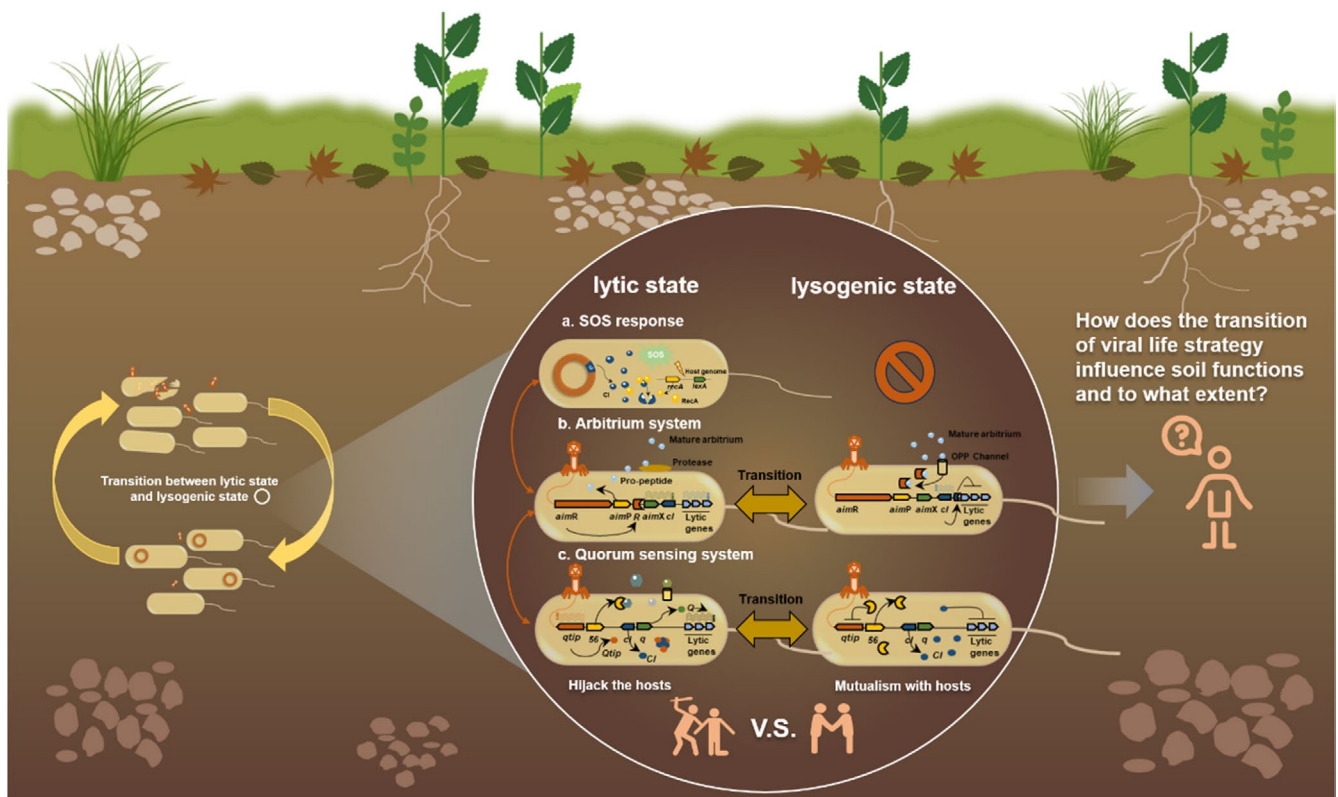


FIGURE 2 | Three mechanisms regulating virus lysis-lysogenic transformation. (A) The SOS response only occurs when host DNA is irreversibly damaged (Wegrzyn and Wegrzyn 2005). This regulatory mechanism is unidirectional from the lysogenic state to the lytic state. The regulators of the SOS response influence virus and host metabolism and community structure in soil environments (Ghosh et al. 2009; Liang, Wagner, et al. 2020; Xia et al. 2023). (B) The arbitrium system involves peptide communication from viruses to progeny viruses. (C) The quorum sensing system involves peptide communication from hosts to viruses. Both the arbitrium system and the quorum sensing system are common in soils and can promote the interconversion of the lysogenic and lytic cycles, depending on the concentration of peptides (Erez et al. 2017; Stokar-Aviail et al. 2019; Liang, Wagner, et al. 2020).

retained lytic properties (61% of detected viruses were lytic) and soil viral communities changed with their shifting host communities during hyperthermophilic composting from 32°C to > 90°C (Liao et al. 2023). These findings provide important insights as to how viral life strategy and virus-host interactions might respond to temperature.

4.2 | Soil Moisture Threshold

Changing soil moisture conditions, regulated by precipitation and evapotranspiration patterns, shape the connectivity and activity of microbes, which in turn affect virus-microbe interactions (Cao et al. 2022). Soil viruses change dynamically with the bloom and decline of their hosts under different soil moisture conditions (Van Goethem et al. 2019). Recent studies revealed a consistent soil virus life strategy as a function of soil moisture: the drier the soil, the more lysogenic phages, and the wetter the soil, the more lytic phages. These relationships hold regardless of whether the results are from laboratory or field conditions (Hwang et al. 2021; Wu, Davison, Gao, et al. 2021; Wu, Davison, Nelson, et al. 2021; Cao et al. 2022; Santos-Medellin et al. 2022). For instance, the transcripts of lysogenic markers increased 20-fold under drier conditions, and the richness of auxiliary metabolic genes (AMGs) and related pathways showed a remarkable increase (Wu, Davison, Gao, et al. 2021; Wu, Davison, Nelson,

et al. 2021). The AMGs can enable microbial resilience to low water stress and aid in the survival of their hosts under extremely dry conditions, thereby protecting viral life in a mutualist relationship (Hwang et al. 2021). Despite the higher number of viral contigs detected in drier soils, the total number of viral transcriptional activities decreased by nearly 50%, indicating that most of the viruses in dry soils are dormant (Wu, Davison, Gao, et al. 2021). In sum, drier soils contained more dormant viruses selected for lysogenic cycles and have a greater abundance and richness of AMGs, consistent with the PtW model, whereas in wetter soils, soil viruses bloom with their hosts, consistent with the KtW model (Hwang et al. 2021; Jansson and Wu 2023). This suggests that microbial density increases with reduced VMR and enhanced lysogeny in drier soils, which gives the dominant microbes a competitive advantage and reduces the growth opportunity of less abundant microbes, thereby resulting in lower microbial community diversity. However, in wetter soils, the higher microbial density and VMR resulted in enhanced lytic infections that persistently killed the numerically dominant microbes, which promoted the growth of relatively less active species and increased microbial diversity. In addition to these two classical models, the interactions between soil viruses and microbes can demonstrate “Cull-the-Winner” dynamics during the rewetting process (Santos-Medellin et al. 2023). This indicates that, while viruses infect and cull dominant host populations, they do not decimate them (Zhao, Liang, et al. 2025).

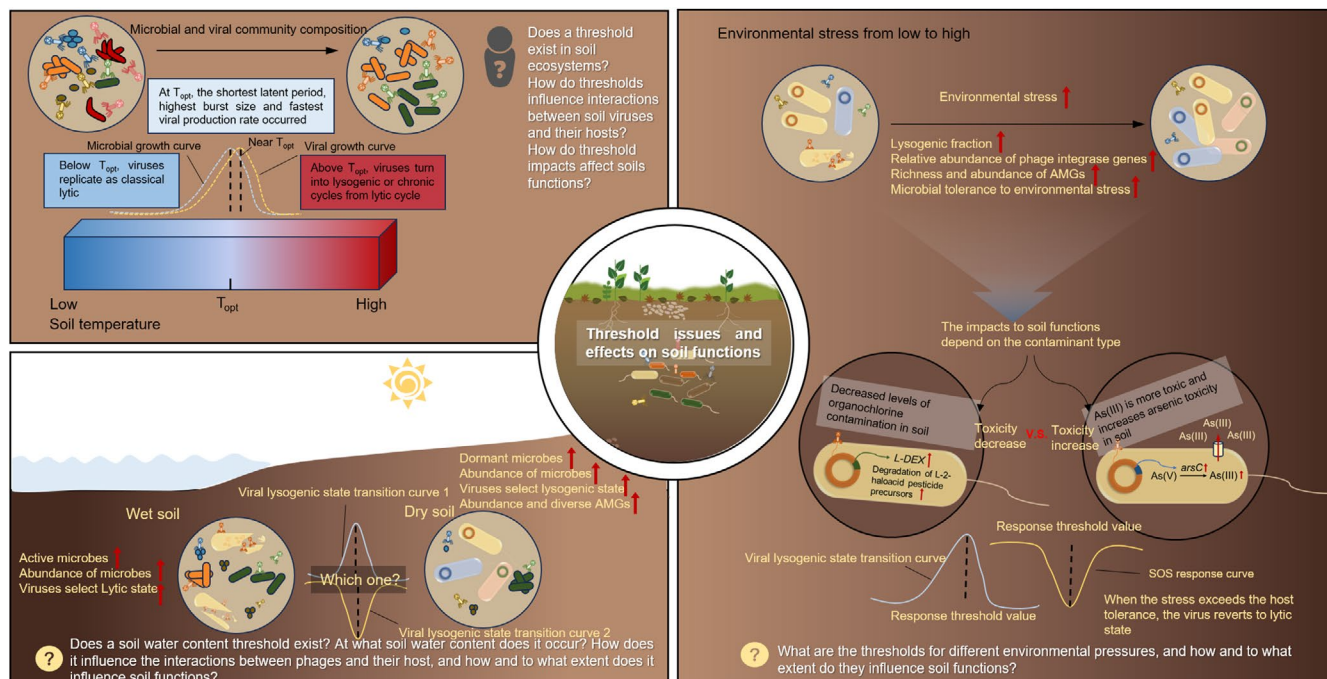


FIGURE 3 | Examples of environmental thresholds inducing soil viral life-cycle transformations. When the temperature is less than an assumed temperature threshold of $\sim 30^{\circ}\text{C}$, viral lytic infections increase with increasing temperature. Once the temperature exceeds this threshold, the viral life cycle transforms from the lytic cycle to the chronic cycle. Assumed soil moisture thresholds range from 29.5% to 39.1%. Below the threshold, viral AMGs increase with soil moisture, whereas above the threshold, AMGs decrease. Soil viruses turn to the lysogenic cycle when facing contaminant stress to help their hosts survive via AMGs. Once above the stress threshold, viruses may decide to lyse their hosts. Table S3 provides additional details concerning environmental thresholds.

Across a soil water gradient, AMGs of viruses in intermediate moisture treatments were either the highest or the lowest among all treatments (Wu, Davison, Nelson, et al. 2021; Cao et al. 2022). Although the results appear inconsistent, they may imply that there is a soil water content threshold that directly affects phages or indirectly affects soil viruses by altering soil biogeochemical conditions related to soil moisture (Figure 3 and Table S3). This inference follows from research results indicating that phage activity was completely lost when SWC decreased to $<5\%$ (Straub et al. 1992, 1993), whereas other studies demonstrate that viral abundance was positively correlated with SWC (Williamson et al. 2005; Roux and Emerson 2022). Further studies are warranted to assess whether there is a soil water content threshold and how it mechanistically affects interactions between phages and their hosts, as well as the extent to which these results impact soil functions.

4.3 | Soil Contaminant Thresholds

With rapid urban and industrial development, soils are under increasing anthropogenic pressure, exposing soil biomes to extreme environmental stress (e.g., heavy metal pollution, pesticide contamination, acid mine drainage). Soil microbial tolerance mechanisms in response to unfavorable soil environments have been extensively studied (Griffiths and Philippot 2013; Epelde et al. 2015). However, there is minimal research examining how soil viruses adapt to survive elevated levels of soil contaminants. How do viruses respond to soil contamination gradients? Does a contaminant threshold response exist for

viruses? To this end, we compiled related research results to address these questions, including stress induced by chromium (Cr), arsenic (As), organochlorine pollution (OCP), copper (Cu), and acidic mine tailings (Jacquiod et al. 2018; Tang et al. 2019; Gao et al. 2020; Huang et al. 2021; Zheng et al. 2022).

Regardless of soil contamination type, all soil viruses select for lysogenic cycles and encode various AMGs to help their host survive. More specifically, both the relative abundance of phage integrase genes (0.1%–0.7%) and the lysogenic fractions of the bacterial community (1.54 to 22.84 VLPs/cell) significantly increased along a Cr pollution gradient (0.11 to 465 mg Cr/kg). These responses help their hosts to survive under Cr stress, as most of the membrane transporter genes ($>77.0\%$) and reductase genes ($>61.7\%$) were detected in lysogenic viromes (Huang et al. 2021). Similarly, the lysogenic viral lifestyle was more prevalent in extremely acidic sulfidic mine tailings and OCP-contaminated soils (Gao et al. 2020; Zheng et al. 2022). Moreover, pesticide degradation genes were enriched in viral AMGs under OCP exposure. The AMGs can help bacteria degrade OCP and survive by transferring proteins that actively degrade monochloroacetate (MCA) and S(L)-2-chloropropionic acid (S(L)-2-CPA) haloacid precursors into *E. coli* after cloning virus-encoded L-2-haloacid dehalogenase (Zheng et al. 2022).

Under some extreme environmental stresses, lysogenic phages revert to lytic cycles, which may imply the existence of a response threshold. For example, the average abundance of lysogenic phages in As-contaminated soil followed: highly As-contaminated (4.96%) $>$ very highly As-contaminated

(3.93%) > moderately As-contaminated (2.52%) (Gao et al. 2023). A similar trend of first increasing and then decreasing lysogenic phages was found along a benzo[a]pyrene environmental stress gradient. This research further clarified that changes in SOS response genes (e.g., *recA* and *lexA*) were responsible for the shift in lysogenic phage abundance (Xia et al. 2023). The down-regulation of the SOS response and DNA metabolism in semi-contaminated plots and up-regulation in hotspot plots were compared to control plots in a century-long soil Cu contamination study. This research documented that under low environmental stress, viruses switch to a lysogenic state to help their host survive, whereas, when the stress exceeds the host's tolerance, the virus reverts to the lytic state (Jacquiod et al. 2018).

Although lysogenic cycles are favored under environmental stress and response thresholds may exist (Figure 3 and Table S3), the impact of soil phage-host interactions on soil ecosystem functions depends on the type and degree of soil contamination. For instance, viral AMGs can assist bacteria in degrading OCPs, which may reduce the level of pesticide contamination in soil (Zheng et al. 2022). However, lysogenic viruses may increase soil toxicity to a greater extent and threaten other soil biomes if they help their host to survive under As stress, as the reduction of As(V) to As(III) is a common defense mechanism for bacteria (Tang et al. 2019).

5 | Effects of Soil Viruses on Food Webs and the One Health Concept

The above discussion addressed the distribution of soil viruses in different soil ecosystems and relationships with their hosts from the molecular to cellular level. We now address how these widespread viral impacts on their hosts affect ecological and soil functions. We have summarized the relevant literature and discuss three primary aspects: nutrient cycling, environmental stress, and selected aspects of the One Health concept.

5.1 | Impacts on Nutrient Cycling

Viral lysis affects soil carbon cycling through two primary mechanisms, namely the “viral shunt” and “viral shuttle”. The viral shunt mechanism refers to lysate organic matter being recycled into the microbial food web and reutilized by the surviving microbes. In contrast, the viral shuttle mechanism describes the cell debris and other lysis products that are aggregated and retained in the environment for an extended period of time (Zimmerman et al. 2020). While these two mechanisms undoubtedly influence the fate of soil carbon, the quantitative extent of each mechanism remains unknown, especially across contrasting soil ecosystem types. Stable isotope labeling techniques have been applied to demonstrate that soil viruses can successfully exploit host metabolic processes for the assembly of progeny phage particles (Li et al. 2013). This causes carbon flows to different trophic levels of soil microbial food webs (Lee et al. 2021), even involving cross-kingdom interactions in the overarching soil food web (Starr et al. 2021). Nevertheless, the carbon flux associated with viral lysing requires further assessment to quantify the role that viruses play and to eliminate the noise created by cross-feeding among microorganisms.

Scientists have not yet reached a consensus concerning how lysate DOM influences the fate of soil carbon, whether stimulating soil carbon efflux due to the priming effect or promoting soil carbon storage via the retention of recalcitrant compounds. For example, viral lysis has been shown to significantly increase soil carbon mineralization, based on the viral shunt mechanism (Bonetti et al. 2021; Albright et al. 2022; Wang, Yu, et al. 2022), whereas other studies found that active viruses suppress CO₂ release by causing microbial cell mortality (Wei et al. 2021). More recently, Tong et al. (2023) ascribed the effect of viruses on soil carbon mineralization to the tradeoff between the rate of bacterial mortality caused by viruses and the utilization of the nutrients released by the surviving microbial community. They were the first to demonstrate that the “viral shuttle” is active in soil, as documented by the accumulation of recalcitrant DOM. In addition to the DOM fraction, soil viruses can also influence mineral-associated organic C, which is intimately coupled with the N cycle (Tong et al. 2025). For example, Wu, Wan, et al. (2022) demonstrated that virus-bacteria interactions can augment the retention of microbial necromass carbon (increased by 19.8%–47.4%) and nitrogen (increased by 43.6%–57.7%) in soil ecosystems, which has been recognized as an effective mechanism for soil carbon sequestration (Liang et al. 2017). Due to the viral impact on soil microbial necromass and the complex interactions between lysate DOM and minerals, the concepts of a virus-mediated soil microbial carbon pump and soil mineral carbon pump have been proposed (Tong and Xu 2024). However, additional systematic studies examining soil viruses and carbon cycling are required to determine whether soil viruses provide a net “carbon sink” or “carbon source” across a variety of soil environments.

In addition to organic C, inorganic C can be an important carbon pool in soils (Huang, Song, et al. 2024). It has been demonstrated that viruses can directly participate in mineral precipitation processes, such as by forming magnesium carbonate nanospheres (80–200 nm) during diagenesis through amorphous magnesium silicate permineralization (Pacton et al. 2014; Xie et al. 2023). This opens the field of “geovirology” to address the extent to which soil viruses influence the cycling of soil inorganic C. Moreover, autotrophic bacteria and enhanced rock weathering have been shown to reduce atmospheric CO₂ via contrasting reactions. The former mainly fix CO₂ based on the Calvin-Benson-Bassham cycle, with C assimilation rates reaching 0.6–4.9 Pg yr⁻¹ (Pg = 10¹⁵ g), whereas the latter chemically degrade silicate rocks, removing 6–30 Mt CO₂ yr⁻¹ (Beerling et al. 2020, 2025; Li et al. 2021). Understanding how soil viruses participate in these two CO₂ removal processes may enrich our understanding of virus-triggered soil C sink processes and provide new strategies for attenuating atmospheric CO₂ concentrations (Figure 4).

The inherent heterogeneity of soils makes ascertaining the interactions between soil viruses and their hosts difficult to assess in time and space (Pratama and van Elsas 2018). Many soil factors and their interactions can alter the abundance and communities of viruses and their hosts, such as temperature (Liao et al. 2023), soil water content (Nicolas et al. 2023), soil depth (Liang et al. 2019), and soil nutrient status (Liang et al. 2021). Integrating the functions of soil viruses into soil carbon biogeochemical models will improve the precision and accuracy of these models. As an example, the strong positive correlation between viral abundance and CO₂ production as opposed to

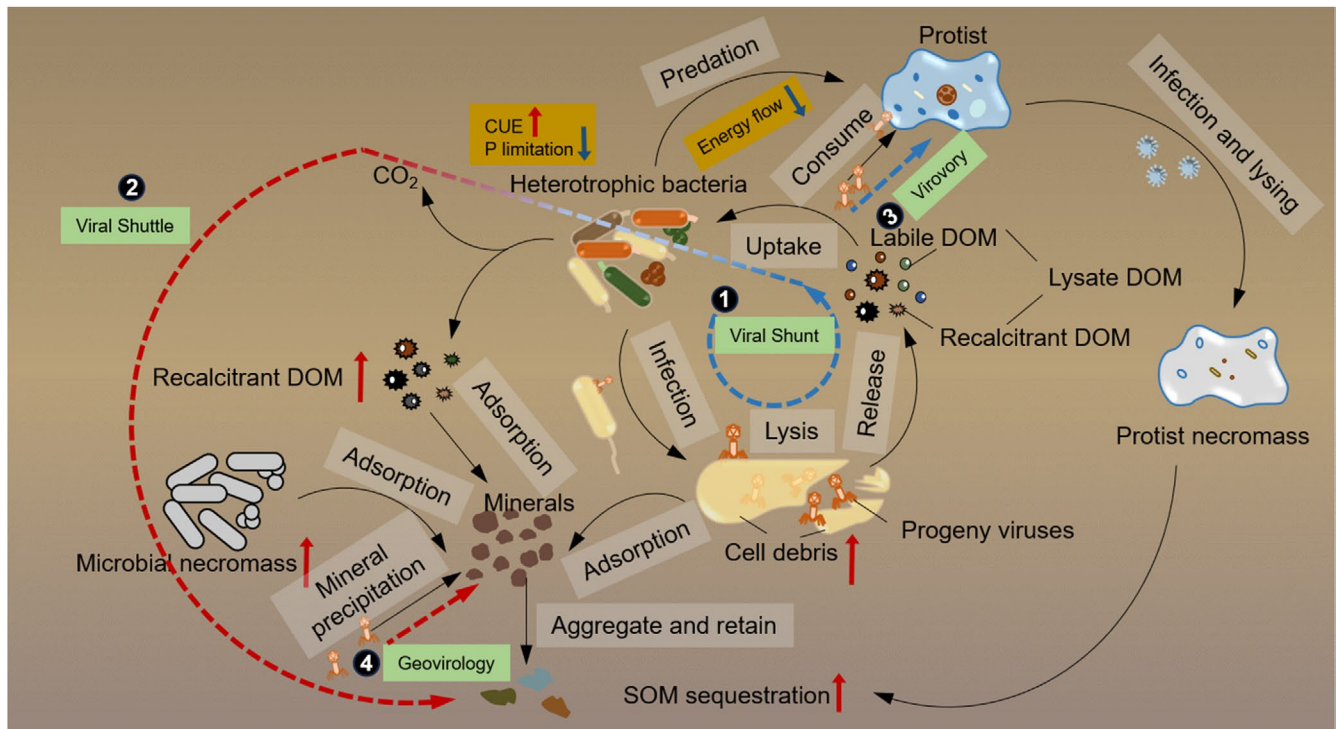


FIGURE 4 | The impact of viruses on soil carbon and nutrient cycling. 1. The “viral shunt” mechanism refers to lysate cellular matter being recycled/reutilized by the surviving heterotrophic microbes. This reduces the energy flow to higher trophic levels and increases microbial carbon-use efficiency (CUE). 2. The “viral shuttle” mechanism describes the cell debris, recalcitrant DOM, microbial necromass and other biological necromass (e.g., protist necromass) that adsorbs to soil minerals or forms aggregates, thereby attenuating carbon/nutrient mineralization and promoting soil organic matter sequestration.

bacterial abundance could considerably affect the source/sink dynamics of soil C (Pan et al. 2014).

Soil viruses can further affect soil N and P cycling (Huang, Zhou, et al. 2024). Multiple pathways within the soil nitrogen cycle are purported to be affected by soil viruses, including ammonification (Lee et al. 2023), nitrification (Lee et al. 2023), nitrogen fixation (Wang, Liu, et al. 2022), and nitrate reduction (Pan et al. 2014). These interactions resulted in a 55% decrease in nitrogen fixation capacity and a nearly 10-fold increase in ammonium concentrations (Braga et al. 2020; Wang, Liu, et al. 2022). Soil viruses may also contribute to soil microbial and plant P limitation as P is recycled by viruses for the synthesis of virion nucleic acids, rendering it inaccessible to microbes and plants (Kuzakov and Mason-Jones 2018). Alternatively, microbial P limitation can be alleviated by P recycling through viral lysis (Tong et al. 2023). Phosphorus cycling and alteration of the soil C/N/P stoichiometry require further investigation to better understand the overall effects of soil viruses on nutrient cycling.

Soil viruses can reprogram their hosts' nutrient metabolism with AMGs, which may confer enhanced substrate utilization capabilities to dominant copiotrophs (Wang et al. 2024). This increases the host's competitiveness and adaptability to harsh environments, akin to the “piggyback the winner” model (Xu et al. 2024; Liu et al. 2025). In addition to virus effects on SOC turnover, 23.7% of the identified AMGs carried by paddy soil viruses were associated with carbon fixation (Zhu et al. 2024). Nearly all the related research concerning soil virus domains place viruses as the top “predator” in their food chains, however,

viruses also can serve as a food source, namely “virovory” (DeLong et al. 2023). It is estimated that 33%–85% of viruses can be removed by bacterial breakdown and protist grazing (Gonzalez and Suttle 1993; Martinez et al. 2024). These processes transfer viral C and N back into the microbial loop.

5.2 | Effects of Viruses on Soil Functions

5.2.1 | Food Security, Safety and Quality

Soil viruses are a key component of soil health and One Health concepts, but often receive little or no attention (Figure 5). Yet, integrating viruses is critical to successfully achieving the goals of soil health and One Health (Singh et al. 2023). The role of soil viruses in soil health/functions remains largely unclear at this time. For example, the urgent need to improve crop yields and quality to feed a growing global population is of critical societal importance (Carvajal-Yepes et al. 2019). Soil viruses can dramatically threaten food security, safety, and quality by notably reducing plant height, fresh biomass, and nitrogen content by enhancing the pathogenicity of soil pathogens (e.g., *Fusarium* and *Rhizoctonia*) (Wang et al. 2018; Abdoulaye et al. 2019; Sutela et al. 2019; Wang, Liu, et al. 2022). Moreover, soil viruses were implicated in increasing As(III) concentrations by as much as 214%, which further signifies an increased soil ecotoxicity and ecological risk (Tang et al. 2019).

Even though soil viruses increase the potential risk of ARG dissemination, ARGs integrated by viral genomes in soil are much

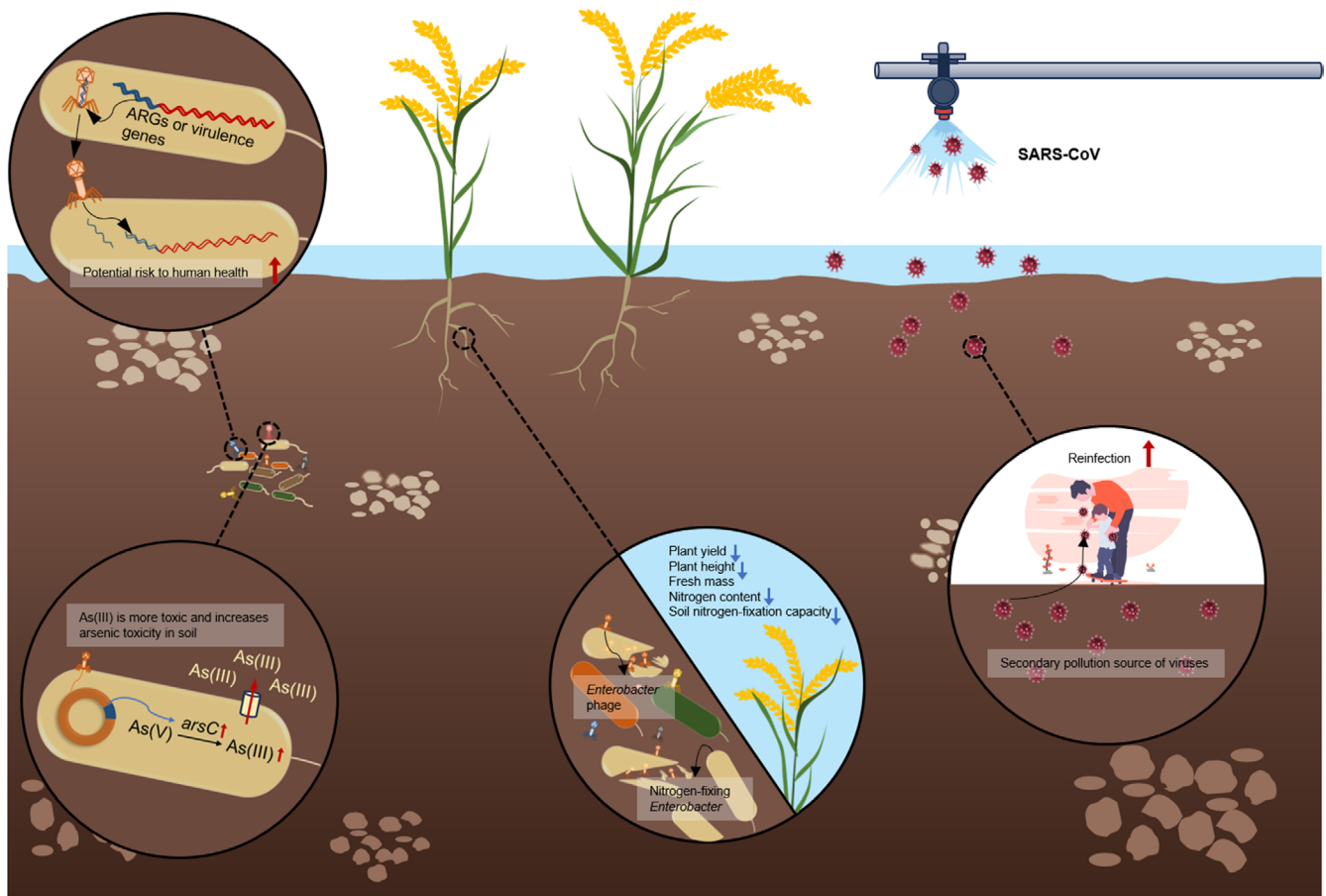


FIGURE 5 | Viral hazards in the soil environment. Soil viruses can increase the spread of ARGs and virulence genes, thereby threatening human and ecological health. Soil viruses can increase arsenic toxicity and reduce food production and quality. Exotic viruses in soil, such as SARS-CoV, can become a secondary source of infection.

lower than those in other ecosystems (e.g., marine and freshwater) (Debroas and Siguret 2019; Chen, An, et al. 2021; Liao et al. 2022a). Intriguingly, soil viruses harbor the greatest richness of ARGs, and a higher proportion of predicted ARGs occur in prophages rather than in free viruses, which contrasts with other ecosystems (Debroas and Siguret 2019). Compared to the low percentage of virus-encoded ARGs in soil, soil viruses may be a major reservoir of virulence factors, with 4.0% of ARGs encoding at least one virulence gene and nearly 89% of virulence genes detectable from soil viruses (Bi et al. 2023). In addition, the potential risk for the viral spread of virulence genes across biomes may increase risks to human health via food chain transfers (Bi et al. 2023). There are also growing concerns about pathophoresis as permafrost thaws, especially as more viruses are being detected in permafrost. Although the viruses viable in ancient permafrost do not necessarily pose a threat to humans, some RNA viruses have yet to enter potentially infectious eukaryotes, including humans (Wu, Wan, et al. 2022; Wu, Bottos, et al. 2022; Jansson and Wu 2023).

5.2.2 | Secondary Source of Pathogenic Viruses

Although the likelihood of autochthonous viral pathogens infecting humans or other animals appears to be low (Wu, Trubl, et al. 2022), soil can serve as a secondary source for spreading

pathogenic viruses, including vertebrate viruses and SARS-CoV-2 (Zhang et al. 2021; Wu, Bottos, et al. 2022; Zhao, Wang, et al. 2025). Pathogenic viruses such as SARS-CoV can be introduced into soils through the disposal of municipal and hospital wastes, including the irrigation and fertilization of food crops with infected wastewater and sewage sludge (Zand and Heir 2020; Iyer et al. 2021). The survival time of pathogenic viruses in the soil environment can range from 15–25 days to 60–90 days, depending on soil type, temperature, moisture, pH, clay content, organic matter, and other soil physicochemical properties (Gutierrez and Buchy 2012; Anand, Adelodun, et al. 2021; Anand, Bianco, et al. 2021). Further, crops can internalize soil viruses, allowing them to remain viable for 3–5 weeks (Badawy et al. 1990; Anand, Bianco, et al. 2021), as well as accelerate disease transmission and the risk of human reinfection via food chain exposure. Given these ecosystem and public health concerns, further studies are strongly warranted to monitor the possible spread of the pathogenic viruses in the soil and determine the possible routes of contamination.

5.2.3 | Maintaining Soil Microbial Youth and Diversity

Through viral lysis predation, regenerating soil bacterial cells remain in a young state, helping to maintain the stability of the entire community structure over long periods (Kuzayakov

and Mason-Jones 2018). Soil viruses can also help their hosts survive in stressful environments, such as burnt soil (Nelson et al. 2022), permafrost (Ettinger et al. 2023) and deep soils (Liang, Zhang, et al. 2020). The frequency and severity of wildfires are rapidly increasing with climate change, which has profound effects on terrestrial ecosystems, such as extreme soil temperature/moisture dynamics, altered nutrient cycles, and soil erosion (Benavides-Solorio and MacDonald 2005; Parks and Abatzoglou 2020; Higuera and Abatzoglou 2021; Jansson and Wu 2023). The reduced soil microbial biomass and community diversity caused by wildfires can inhibit post-fire recovery (Ibanez et al. 2022). However, soil viruses facilitate microbial growth in this harsh environment by encoding AMGs and manipulating cell growth (e.g., pyrimidine ribonucleotide biosynthesis), which stimulates biological recovery after severe wildfires (Nelson et al. 2022).

Lysogeny becomes the main viral reproduction strategy in organic carbon and oxygen depleted subsoil horizons, as indicated by a lysogenic fraction of more than 50% (Liang, Zhang, et al. 2020). Additionally, subsurface soil viruses may interact more closely with their hosts to become more involved in microbial-mediated processes. This is reflected by the increased relative abundance of phage infection cycle proteins and functional protein-coding genes (Liang et al. 2019).

5.2.4 | Green and Sustainable Bacteriophage Therapies

Bacteriophage therapies exploit the specific lytic properties of virulent phages to treat pathogenic bacterial infections and are especially attractive for inactive super-pathogenic bacteria with multidrug resistance (Ye et al. 2019). Compared to antibiotics, phage therapy is safer and more environmentally friendly, not only because of its specific targeting, but also because phage abundance declines as hosts diminish, thereby maintaining the stability and diversity of microbiomes (Watts 2017; Wang et al. 2019). Single phage therapy has been extended to phage cocktails and polyvalent phage therapies to better control bacterial plant pathogens (e.g., *Ralstonia solanacearum* and antibiotic-resistant bacteria) (Sun et al. 2019; Wang et al. 2019; Zhao et al. 2019; Yang et al. 2023). In terms of pathogen-eradication efficiency, phage cocktails have proven the most effective, followed by polyvalent phage and single phage treatments (Yu et al. 2017; Zhao et al. 2019). However, when ecological disturbance is taken into account, polyvalent phages are considered the most advantageous technique (Ye et al. 2019). Limitations of phage treatments include a time-consuming and difficult-to-control isolation process, as well as their inability to infect a wide range of pathogenic strains.

To date, only strictly lytic phages have been selected for phage therapy. Temperate phages are not favored for phage therapies due to their inherent ability to integrate their genomes into hosts, which may increase the transmission of bacterial virulence and ARGs. This is unfortunate since lysogenic phages are so abundant in nature and could provide a tremendous asset in phage therapies (Touchon et al. 2016). With the development of advanced synthetic biology approaches, the use of abundantly available temperate phages in phage therapies could provide broad application prospects (Monteiro et al. 2019). For instance,

engineered temperate phages can interfere with bacterial intracellular processes, causing bacterial cell death, re-sensitize the bacteria to antibiotics, or even reconstitute them to the lytic phase, such as strictly lytic phages (Yosef et al. 2015; Kilcher et al. 2018; Monteiro et al. 2019). Genetic engineering-based phage therapy for both lytic and lysogenic phages still requires further investigation and extensive trials.

6 | Conclusions and Future Perspectives

In this review, we have extended the soil virus abundance dataset ($N=691$) and, for the first time, added data on the lysogenic fraction of soil viruses. This expanded dataset showed that soil viruses are most abundant in wetland, grassland, and agricultural soil ecosystems, as opposed to forest soils, previously believed to have the highest abundances. Importantly, we found a threshold (microbial abundance $\approx 4.57 \times 10^7 \text{ g}^{-1}$ soil and VMR ≈ 58.21) relationship between VMR and microbial abundance. Below the threshold, the relationship between viruses and microbes is consistent with the KtW model, whereas above the threshold, the PtW model appears to prevail. Moreover, the molecular mechanisms regulating viral lysis-lysogenic transformation were grouped into three categories: SOS response, quorum sensing system, and arbitrium system. Remarkably, all three mechanisms were shown to be widespread in the soil environment.

By coupling the results of microcosmic incubation experiments and bioinformatic analysis in response to soil environmental stressors, we propose the concept of a response threshold and suggest that environmental thresholds may induce the conversion between the viral lytic and lysogenic states, which may subsequently affect several soil functions. Finally, we systematically demonstrated the effects of soil viruses on several soil ecological functions, including crop yield/quality, ARGs and virulence gene spread, soil toxicity, and as a secondary source of pathogenic viruses. This is the first review to highlight the importance of the viral shuttle mechanism for soil carbon sequestration, and the importance of soil viruses to the One Health concept.

Although much has been accomplished in the study of soil viruses, there are many outstanding questions that need to be resolved to further advance the understanding and application of soil viruses to soil management and the One Health concept: (1) How many viruses are there in the global range of soil environments? (2) To what extent can AMGs affect the host and resulting soil functions? (3) All three regulatory mechanisms for transforming the viral lysis-lysogenic state are associated with the KtW model, but their roles under the PtW model remain unclear. Are there new regulatory mechanisms or just different communication peptides? (4) What are the effects of the viral shunt, viral shuttle, and virology on soil nutrient cycling and related soil functions? (5) Can biomarkers of viral residues be found, similar to microbial necromass, to facilitate easy and accurate quantification of virus effects on soil carbon/nutrient pools? (6) Are there widespread viral response thresholds to environmental stresses such as drought, flooding, freezing, pollution, circadian rhythms, etc.? If so, what triggers them, and how do they affect soil functions? (7) How do viruses and hosts

respond in the context of feedback to global climate change? (8) Does the role of soil viruses in the presence of multitrophic organisms (i.e., soil food webs) amplify or diminish in real-world soil environments? (9) How do soil viruses participate in atmospheric CO₂ removal processes (i.e., autotrophic bacteria and rock weathering), and to what extent do they reflect the role of virus-triggered soil C sinks? (10). Is it possible to combine soil viruses into prebiotics or to use genetically engineered phage therapies to reduce pests and diseases for improving soil, plant, and human health? By answering these questions, several knowledge gaps concerning soil virology will be filled and several new questions will emerge, thereby facilitating a deeper understanding of the soil viral dark matter and its potential applications in soil management.

Author Contributions

Di Tong: data curation, formal analysis, resources, software, visualization, writing – original draft, writing – review and editing. **Bin Ma:** writing – review and editing. **Lingfei Hu:** writing – review and editing. **Yong Li:** writing – review and editing. **Randy A. Dahlgren:** writing – review and editing. **Jianming Xu:** conceptualization, writing – original draft, writing – review and editing.

Acknowledgments

This study was supported by the National Natural Science Foundation of China (42330711), the National Key R&D Program of China (2024YFD1501801), the Fundamental Research Funds for the Central Universities (226-2025-00004), Earmarked Fund for China Agriculture Research System (CARS-01), and China Postdoctoral Science Foundation (GZC20251623).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in DRYAD at <https://doi.org/10.5061/dryad.jdfn2z3px>.

References

- Abdoulaye, A. H., M. F. Foda, and I. Kotta-Loizou. 2019. "Viruses Infecting the Plant Pathogenic Fungus *Rhizoctonia Solani*." *Viruses* 11, no. 12: 1113. <https://doi.org/10.3390/v11121113>.
- Adriaenssens, E. M., L. Van Zyl, P. De Maayer, et al. 2015. "Metagenomic Analysis of the Viral Community in Namib Desert Hypoliths." *Environmental Microbiology* 17: 480–495. <https://doi.org/10.1111/1462-2920.12528>.
- Albright, M. B. N., L. V. Gallegos-Graves, K. L. Feaser, K. Montoya, J. B. Emerson, and M. S. a. J. Dunbar. 2022. "Experimental Evidence for the Impact of Soil Viruses on Carbon Cycling During Surface Plant Litter Decomposition." *ISME Communications* 2: 1–8. <https://doi.org/10.1038/s43705-022-00109-4>.
- Anand, U., B. Adelodun, A. Pivato, et al. 2021. "A Review of the Presence of SARS-CoV-2 RNA in Wastewater and Airborne Particulates and Its Use for Virus Spreading Surveillance." *Environmental Research* 196: 110929. <https://doi.org/10.1016/j.envres.2021.110929>.
- Anand, U., F. Bianco, S. Suresh, V. Tripathi, A. Nunez-Delgado, and M. Race. 2021. "SARS-CoV-2 and Other Viruses in Soil: An Environmental Outlook." *Environmental Research* 198: 111297. <https://doi.org/10.1016/j.envres.2021.111297>.
- Ankrah, N. Y. D., A. L. May, J. L. Middleton, et al. 2014. "Phage Infection of an Environmentally Relevant Marine Bacterium Alters Host Metabolism and Lysate Composition." *ISME Journal* 8: 1089–1100. <https://doi.org/10.1038/ismej.2013.216>.
- Badawy, A. S., J. B. Rose, and C. P. Gerba. 1990. "Comparative Survival of Enteric Viruses and Coliphage on Sewage Irrigated Grass." *Journal of Environmental Science and Health Part A-Environmental Science and Engineering & Toxic and Hazardous Substance Control* 25: 937–952. <https://doi.org/10.1080/10934529009375610>.
- Beerling, D. J., E. P. Kantzas, M. R. Lomas, et al. 2020. "Potential for Large-Scale CO₂ Removal via Enhanced Rock Weathering With Croplands." *Nature* 583: 242–248.
- Beerling, D. J., E. P. Kantzas, M. R. Lomas, et al. 2025. "Transforming US Agriculture for Carbon Removal With Enhanced Weathering." *Nature* 638: 425–434.
- Benavides-Solorio, J. D. D., and L. H. MacDonald. 2005. "Measurement and Prediction of Post-Fire Erosion at the Hillslope Scale, Colorado Front Range." *International Journal of Wildland Fire* 14: 457–474. <https://doi.org/10.1071/wf05042>.
- Bi, L., L. Han, S. Du, et al. 2023. "Cross-Biome Soil Viruses as an Important Reservoir of Virulence Genes." *Journal of Hazardous Materials* 442: 130111. <https://doi.org/10.1016/j.jhazmat.2022.130111>.
- Bonetti, G., S. M. Trevathan-Tackett, P. E. Carnell, and P. I. Macreadie. 2021. "The Potential of Viruses to Influence the Magnitude of Greenhouse Gas Emissions in an Inland Wetland." *Water Research* 193: 116875. <https://doi.org/10.1016/j.watres.2021.116875>.
- Braga, L. P. P., A. Spor, W. Kot, et al. 2020. "Impact of Phages on Soil Bacterial Communities and Nitrogen Availability Under Different Assembly Scenarios." *Microbiome* 8: 52. <https://doi.org/10.1186/s40168-020-00822-z>.
- Bruce, J. B., S. Lion, A. Buckling, E. R. Westra, and S. Gandon. 2021. "Regulation of Prophage Induction and Lysogenization by Phage Communication Systems." *Current Biology* 31: 5046–5051. <https://doi.org/10.1016/j.cub.2021.08.073>.
- Cao, M., S. Liu, L. Bi, et al. 2022. "Distribution Characteristics of Soil Viruses Under Different Precipitation Gradients on the Qinghai-Tibet Plateau." *Frontiers in Microbiology* 13: 848305. <https://doi.org/10.3389/fmicb.2022.848305>.
- Carvajal-Yepes, M., K. Cardwell, A. Nelson, et al. 2019. "A Global Surveillance System for Crop Diseases." *Science* 364: 1237–1239. <https://doi.org/10.1126/science.aaw1572>.
- Chen, M., X. An, H. Liao, K. Yang, J. Su, and Y. Zhu. 2021. "Viral Community and Virus-Associated Antibiotic Resistance Genes in Soils Amended With Organic Fertilizers." *Environmental Science & Technology* 55: 13881–13890. <https://doi.org/10.1021/acs.est.1c03847>.
- Chen, X., M. G. Weinbauer, N. Jiao, and R. Zhang. 2021. "Revisiting Marine Lytic and Lysogenic Virus-Host Interactions: Kill-The-Winner and Piggyback-The-Winner." *Science Bulletin* 66: 871–874. <https://doi.org/10.1016/j.scib.2020.12.014>.
- Chen, Y., S. Sadiq, J. Tian, et al. 2022. "RNA Viromes From Terrestrial Sites Across China Expand Environmental Viral Diversity." *Nature Microbiology* 7: 1312–1323. <https://doi.org/10.1038/s41564-022-01180-2>.
- Cheng, Z., Y. He, Y. Wang, et al. 2024. "Interactive Dynamics Between Rhizosphere Bacterial and Viral Communities Facilitate Soybean Fitness to Cadmium Stress Revealed by Time-Series Metagenomics." *Soil Biology and Biochemistry* 190: 109313. <https://doi.org/10.1016/j.soilbio.2024.109313>.
- Chevallereau, A., B. J. Pons, S. van Houte, and E. R. Westra. 2022. "Interactions Between Bacterial and Phage Communities in Natural Environments." *Nature Reviews Microbiology* 20: 49–62. <https://doi.org/10.1038/s41579-021-00602-y>.

- Correa, A. M. S., C. Howard-Varona, S. R. Coy, A. Buchan, M. B. Sullivan, and J. S. Weitz. 2021. "Revisiting the Rules of Life for Viruses of Microorganisms." *Nature Reviews Microbiology* 19: 501–513. <https://doi.org/10.1038/s41579-021-00530-x>.
- Debroas, D., and C. Siguret. 2019. "Viruses as Key Reservoirs of Antibiotic Resistance Genes in the Environment." *ISME Journal* 13: 2856–2867. <https://doi.org/10.1038/s41396-019-0478-9>.
- DeLong, J. P., J. L. V. Etten, Z. Al-Ameeli, I. V. Agarkova, and D. D. Dunigan. 2023. "The Consumption of Viruses Returns Energy to Food Chains." *Proceedings of the National Academy of Sciences of the United States of America* 120: e2215000120.
- Demory, D., L. Arsenieff, N. Simon, et al. 2017. "Temperature Is a Key Factor in Micromonas-Virus Interactions." *ISME Journal* 11: 601–612. <https://doi.org/10.1038/ismej.2016.160>.
- Emerson, J. B., S. Roux, J. R. Brum, et al. 2018. "Host-Linked Soil Viral Ecology Along a Permafrost Thaw Gradient." *Nature Microbiology* 3: 870–880. <https://doi.org/10.1038/s41564-018-0190-y>.
- Epelde, L., A. Lanzen, F. Blanco, T. Urich, and C. Garbisu. 2015. "Adaptation of Soil Microbial Community Structure and Function to Chronic Metal Contamination at an Abandoned Pb–Zn Mine." *FEMS Microbiology Ecology* 91: 1–11. <https://doi.org/10.1093/femsec/fiu007>.
- Erez, Z., I. Steinberger-Levy, M. Shamir, et al. 2017. "Communication Between Viruses Guides Lysis-Lysogeny Decisions." *Nature* 541: 488–493. <https://doi.org/10.1038/nature21049>.
- Ettinger, C. L., M. Saunders, L. Selbmann, et al. 2023. "Highly Diverse and Unknown Viruses may Enhance Antarctic Endoliths' Adaptability." *Microbiome* 11, no. 1: 103. <https://doi.org/10.1186/s40168-023-01554-6>.
- Fierer, N., M. Breitbart, J. Nulton, et al. 2007. "Metagenomic and Small-Subunit rRNA Analyses Reveal the Genetic Diversity of Bacteria, Archaea, Fungi, and Viruses in Soil." *Applied and Environmental Microbiology* 73: 7059–7066. <https://doi.org/10.1128/aem.00358-07>.
- Gao, R., B. Ma, M. Hu, et al. 2023. "Ecological Drivers and Potential Functions of Viral Communities in Flooded Arsenic-Contaminated Paddy Soils." *Science of the Total Environment* 872: 162289. <https://doi.org/10.1016/j.scitotenv.2023.162289>.
- Gao, S., A. Schippers, N. Chen, et al. 2020. "Depth-Related Variability in Viral Communities in Highly Stratified Sulfidic Mine Tailings." *Microbiome* 8: 89. <https://doi.org/10.1186/s40168-020-00848-3>.
- Ghosh, D., K. Roy, K. E. Williamson, S. Srinivasiah, K. E. Wommack, and M. Radosevich. 2009. "Acyl-Homoserine Lactones Can Induce Virus Production in Lysogenic Bacteria: An Alternative Paradigm for Prophage Induction." *Applied and Environmental Microbiology* 75: 7142–7152. <https://doi.org/10.1128/aem.00950-09>.
- Gonzalez, J. M., and C. A. Suttle. 1993. "Grazing by Marine Nanoflagellates on Viruses and Virus-Sized Particles - Ingestion and Digestion." *Marine Ecology Progress Series* 94: 1–10. <https://doi.org/10.3354/meps094001>.
- Griffiths, B. S., and L. Philippot. 2013. "Insights Into the Resistance and Resilience of the Soil Microbial Community." *FEMS Microbiology Reviews* 37: 112–129. <https://doi.org/10.1111/j.1574-6976.2012.00343.x>.
- Guemes, A. G. C., M. Youle, V. A. Cantu, B. Felts, J. Nulton, and F. Rohwer. 2016. "Viruses as Winners in the Game of Life." *Annual Review of Virology* 4: 197–214. <https://doi.org/10.1146/annurev-virology-100114-054952>.
- Gutierrez, R. A., and P. Buchy. 2012. "Contaminated Soil and Transmission of Influenza Virus (H5N1)." *Emerging Infectious Diseases* 18: 1530–1532. <https://doi.org/10.3201/eid1809.120402>.
- Higuera, P. E., and J. T. Abatzoglou. 2021. "Record-Setting Climate Enabled the Extraordinary 2020 Fire Season in the Western United States." *Global Change Biology* 27: 1–2. <https://doi.org/10.1111/gcb.15388>.
- Howard-Varona, C., K. R. Hargreaves, S. T. Abedon, and M. B. Sullivan. 2017. "Lysogeny in Nature: Mechanisms, Impact and Ecology of Temperate Phages." *ISME Journal* 11: 1511–1520. <https://doi.org/10.1038/ismej.2017.16>.
- Howard-Varona, C., M. M. Lindback, G. E. Bastien, et al. 2020. "Phage-Specific Metabolic Reprogramming of Virocells." *ISME Journal* 14: 881–895. <https://doi.org/10.1038/s41396-019-0580-z>.
- Huang, D., P. Yu, M. Ye, C. Schwarz, X. Jiang, and P. J. J. Alvarez. 2021. "Enhanced Mutualistic Symbiosis Between Soil Phages and Bacteria With Elevated Chromium-Induced Environmental Stress." *Microbiome* 9: 150. <https://doi.org/10.1186/s40168-021-01074-1>.
- Huang, X., Z. Zhou, H. Liu, et al. 2024. "Soil Nutrient Conditions Alter Viral Lifestyle Strategy and Potential Function in Phosphorous and Nitrogen Metabolisms." *Soil Biology & Biochemistry* 189: 109279. <https://doi.org/10.1016/j.soilbio.2023.109279>.
- Huang, Y., X. Song, Y.-P. Wang, et al. 2024. "Size, Distribution, and Vulnerability of the Global Soil Inorganic Carbon." *Science* 384: 233–239. <https://www.science.org/doi/10.1126/science.adi7918>.
- Hwang, Y., J. Rahlff, D. Schulze-Makuch, M. Schlöter, and A. J. Probst. 2021. "Diverse Viruses Carrying Genes for Microbial Extremotolerance in the Atacama Desert Hyperarid Soil." *MSystems* 6: e00385-21. <https://doi.org/10.1128/mSystems.00385-21>.
- Ibanez, T. S., D. A. Wardle, M. J. Gundale, and M.-C. Nilsson. 2022. "Effects of Soil Abiotic and Biotic Factors on Tree Seedling Regeneration Following a Boreal Forest Wildfire." *Ecosystems* 25: 471–487. <https://doi.org/10.1007/s10021-021-00666-0>.
- Iyer, M., S. Tiwari, K. Renu, et al. 2021. "Environmental Survival of SARS-CoV-2-A Solid Waste Perspective." *Environmental Research* 197: 111015. <https://doi.org/10.1016/j.envres.2021.111015>.
- Jacquiod, S., I. Nunes, A. Brejnrod, et al. 2018. "Long-Term Soil Metal Exposure Impaired Temporal Variation in Microbial Metatranscriptomes and Enriched Active Phages." *Microbiome* 6: 223. <https://doi.org/10.1186/s40168-018-0606-1>.
- Jansson, J. K., and R. Wu. 2023. "Soil Viral Diversity, Ecology and Climate Change." *Nature Reviews Microbiology* 21: 296–311. <https://doi.org/10.1038/s41579-022-00811-z>.
- Kilcher, S., P. Studer, C. Muessner, J. Klumpp, and M. J. Loessner. 2018. "Cross-Genus Rebooting of Custom-Made, Synthetic Bacteriophage Genomes in L-Form Bacteria." *Proceedings of the National Academy of Sciences of the United States of America* 115: 567–572. <https://doi.org/10.1073/pnas.1714658115>.
- Knowles, B., C. B. Silveira, B. A. Bailey, et al. 2016. "Lytic to Temperate Switching of Viral Communities." *Nature* 531: 466–470. <https://doi.org/10.1038/nature17193>.
- Kuzyakov, Y., and K. Mason-Jones. 2018. "Viruses in Soil: Nano-Scale Undead Drivers of Microbial Life, Biogeochemical Turnover and Ecosystem Functions." *Soil Biology & Biochemistry* 127: 305–317. <https://doi.org/10.1016/j.soilbio.2018.09.032>.
- Lee, S., E. T. Sieradzki, G. W. Nicol, and C. Hazard. 2023. "Propagation of Viral Genomes by Replicating ammonia-Oxidising archaea During Soil Nitrification." *ISME Journal* 17: 309–314. <https://doi.org/10.1038/s41396-022-01341-5>.
- Lee, S., E. T. Sieradzki, A. M. Nicolas, et al. 2021. "Methane-Derived Carbon Flows Into Host-Virus Networks at Different Trophic Levels in Soil." *Proceedings of the National Academy of Sciences of the United States of America* 118: e2105124118. <https://doi.org/10.1073/pnas.2105124118>.
- Lee, S., J. W. Sorensen, R. L. Walker, J. B. Emerson, G. W. Nicol, and C. Hazard. 2022. "Soil pH Influences the Structure of Virus Communities at Local and Global Scales." *Soil Biology & Biochemistry* 166: 108569. <https://doi.org/10.1016/j.soilbio.2022.108569>.
- Li, Y., H. Y. Liu, H. Pan, et al. 2019. "T4-Type Viruses: Important Impacts on Shaping Bacterial Community Along a Chronosequence

- of 2000-Year Old Paddy Soils." *Soil Biology & Biochemistry* 128: 89–99. <https://doi.org/10.1016/j.soilbio.2018.10.007>.
- Li, Y., T. Watanabe, J. Murase, S. Asakawa, and M. Kimura. 2013. "Identification of the Major Capsid Gene (g23) of T4-Type Bacteriophages That Assimilate Substrates From Root Cap Cells Under Aerobic and Anaerobic Soil Conditions Using a DNA-SIP Approach." *Soil Biology & Biochemistry* 63: 97–105. <https://doi.org/10.1016/j.soilbio.2013.03.026>.
- Li, Z., D. Tong, X. Nie, et al. 2021. "New Insight Into Soil Carbon Fixation Rate: The Intensive Co-Occurrence Network of Autotrophic Bacteria Increases the Carbon Fixation Rate in Depositional Sites." *Agriculture Ecosystems & Environment* 320: 107579. <https://doi.org/10.1016/j.agee.2021.107579>.
- Liang, C., J. P. Schimel, and J. D. Jastrow. 2017. "The Importance of Anabolism in Microbial Control Over Soil Carbon Storage." *Nature Microbiology* 2: 17105. <https://doi.org/10.1038/nmicrobiol.2017.105>.
- Liang, X., M. Radosevich, J. M. DeBruyn, S. W. Wilhelm, R. McDearis, and J. Zhuang. 2023. "Incorporating Viruses Into Soil Ecology: A New Dimension to Understand Biogeochemical Cycling." *Critical Reviews in Environmental Science and Technology* 54: 117–137. <https://doi.org/10.1080/10643389.2023.2223123>.
- Liang, X., R. E. Wagner, B. Li, N. Zhang, and M. Radosevich. 2020. "Quorum Sensing Signals Alter In Vitro Soil Virus Abundance and Bacterial Community Composition." *Frontiers in Microbiology* 11: 1287. <https://doi.org/10.3389/fmicb.2020.01287>.
- Liang, X., R. E. Wagner, J. Zhuang, et al. 2019. "Viral Abundance and Diversity Vary With Depth in a Southeastern United States Agricultural Ultisol." *Soil Biology & Biochemistry* 137: 107546. <https://doi.org/10.1016/j.soilbio.2019.107546>.
- Liang, X., Y. Wang, Y. Zhang, B. Li, and M. Radosevich. 2021. "Bacteriophage-Host Depth Distribution Patterns in Soil Are Maintained After Nutrient Stimulation In Vitro." *Science of the Total Environment* 787: 147589. <https://doi.org/10.1016/j.scitotenv.2021.147589>.
- Liang, X., Y. Zhang, K. E. Wommack, et al. 2020. "Lysogenic Reproductive Strategies of Viral Communities Vary With Soil Depth and Are Correlated With Bacterial Diversity." *Soil Biology & Biochemistry* 144: 107767. <https://doi.org/10.1016/j.soilbio.2020.107767>.
- Liao, H., H. Li, C.-S. Duan, et al. 2022a. "Metagenomic and Viomic Analysis Reveal the Anthropogenic Impacts on the Plasmid and Phage Borne Transferable Resistome in Soil." *Environment International* 170: 107595. <https://doi.org/10.1016/j.envint.2022.107595>.
- Liao, H., H. Li, C.-S. Duan, et al. 2022b. "Response of Soil Viral Communities to Land Use Changes." *Nature Communications* 13: 6027. <https://doi.org/10.1038/s41467-022-33771-2>.
- Liao, H., C. Liu, C. Ai, et al. 2023. "Mesophilic and Thermophilic Viruses Are Associated With Nutrient Cycling During Hyperthermophilic Composting." *ISME Journal* 17: 916–930. <https://doi.org/10.1038/s41396-023-01404-1>.
- Liu, M., G. Zhou, C. Zhang, et al. 2025. "Impact of Virus-Mediated Modifications in Bacterial Communities on the Accumulation of Soil Organic Carbon." *Advanced Science* 12: e06449. <https://doi.org/10.1002/advs.202506449>.
- Lopez-Garcia, P., A. Gutierrez-Preciado, M. Krupovic, et al. 2023. "Metagenome-Derived Virus-Microbe Ratios Across Ecosystems." *ISME Journal* 17: 1552–1563. <https://doi.org/10.1038/s41396-023-01431-y>.
- Ma, B., C. Y. Lu, Y. L. Wang, et al. 2023. "A Genomic Catalogue of Soil Microbiomes Boosts Mining of Biodiversity and Genetic Resources." *Nature Communications* 14: 7318. <https://doi.org/10.1038/s41467-023-43000-z>.
- Ma, B., Y. Wang, K. Zhao, et al. 2024. "Biogeographic Patterns and Drivers of Soil Viromes." *Nature Ecology & Evolution* 8: 717–728. <https://doi.org/10.1038/s41559-024-02347-2>.
- Martinez, J. M., D. Talmy, J. A. Kimbrel, P. K. Weber, and X. Mayali. 2024. "Coastal Bacteria and Protists Assimilate Viral Carbon and Nitrogen." *ISME Journal* 18: wrac231. <https://doi.org/10.1093/ismejo/wrac231>.
- Monteiro, R., D. P. Pires, A. R. Costa, and J. Azeredo. 2019. "Phage Therapy: Going Temperate?" *Trends in Microbiology* 27: 368–378. <https://doi.org/10.1016/j.tim.2018.10.008>.
- Narr, A., A. Nawaz, L. Y. Wick, H. Harms, and A. Chatzinotas. 2017. "Soil Viral Communities Vary Temporally and Along a Land Use Transect as Revealed by Virus-Like Particle Counting and a Modified Community Fingerprinting Approach (fRAPD)." *Frontiers in Microbiology* 8: 1975. <https://doi.org/10.3389/fmicb.2017.01975>.
- Nasser, A. M., and S. D. Oman. 1999. "Quantitative Assessment of the Inactivation of Pathogenic and Indicator Viruses in Natural Water Sources." *Water Research* 33: 1748–1752. [https://doi.org/10.1016/s0043-1354\(98\)00380-7](https://doi.org/10.1016/s0043-1354(98)00380-7).
- Nelson, A. R., A. B. Narro, C. C. Rhoades, et al. 2022. "Wildfire-Dependent Changes in Soil Microbiome Diversity and Function." *Nature Microbiology* 7: 1419–1430. <https://doi.org/10.1038/s41564-022-01203-y>.
- Nicolas, A. M., E. T. Sieradzki, J. Pett-Ridge, et al. 2023. "A Subset of Viruses Thrives Following Microbial Resuscitation During Rewetting of a Seasonally Dry California Grassland Soil." *Nature Communications* 14: 5835. <https://doi.org/10.1101/2022.09.30.510406>.
- Obeng, N., A. A. Pratama, and J. D. van Elsas. 2016. "The Significance of Mutualistic Phages for Bacterial Ecology and Evolution." *Trends in Microbiology* 24: 440–449. <https://doi.org/10.1016/j.tim.2015.12.009>.
- Pacton, M., D. Wacey, C. Corinaldesi, et al. 2014. "Viruses as New Agents of Organomineralization in the Geological Record." *Nature Communications* 5, no. 1: 4298. <https://doi.org/10.1038/ncomms5298>.
- Pan, D., R. Watson, D. Wang, Z. H. Tan, D. D. Snow, and K. A. Weber. 2014. "Correlation Between Viral Production and Carbon Mineralization Under Nitrate-Reducing Conditions in Aquifer Sediment." *ISME Journal* 8: 1691–1703. <https://doi.org/10.1038/ismej.2014.38>.
- Parikka, K. J., M. Le Romancer, N. Wauters, and S. Jacquet. 2017. "Deciphering the Virus-To-Prokaryote Ratio (VPR): Insights Into Virus-Host Relationships in a Variety of Ecosystems." *Biological Reviews* 92: 1081–1100. <https://doi.org/10.1111/brv.12271>.
- Parks, S. A., and J. T. Abatzoglou. 2020. "Warmer and Drier Fire Seasons Contribute to Increases in Area Burned at High Severity in Western US Forests From 1985 to 2017." *Geophysical Research Letters* 47: e2020GL089858. <https://doi.org/10.1029/2020gl089858>.
- Philippot, L., C. Chenu, A. Kappler, M. C. Rillig, and N. Fierer. 2023. "The Interplay Between Microbial Communities and Soil Properties." *Nature Reviews Microbiology* 22: 226–239. <https://doi.org/10.1038/s41579-023-00980-5>.
- Pratama, A. A., and J. D. van Elsas. 2018. "The 'Neglected' Soil Virome – Potential Role and Impact." *Trends in Microbiology* 26, no. 8: 649–662. <https://doi.org/10.1016/j.tim.2017.12.004>.
- Prigent, M., M. Leroy, F. Confalonieri, M. Dutertre, and M. S. DuBow. 2005. "A Diversity of Bacteriophage Forms and Genomes Can Be Isolated From the Surface Sands of the Sahara Desert." *Extremophiles* 9: 289–296. <https://doi.org/10.1007/s00792-005-0444-5>.
- Rosenwasser, S., C. Ziv, S. G. Van Creveld, and A. Vardi. 2016. "Virocell Metabolism: Metabolic Innovations During Host-Virus Interactions in the Ocean." *Trends in Microbiology* 24: 821–832. <https://doi.org/10.1016/j.tim.2016.06.006>.
- Roux, S., and J. B. Emerson. 2022. "Diversity in the Soil Virosphere: To Infinity and Beyond?" *Trends in Microbiology* 30: 1025–1035. <https://doi.org/10.1016/j.tim.2022.05.003>.
- Santos-Medellin, C., S. J. Blazewicz, J. Pett-Ridge, M. K. Firestone, and J. B. Emerson. 2023. "Viral but Not Bacterial Community Successional

- Patterns Reflect Extreme Turnover Shortly After Rewetting Dry Soils." *Nature Ecology & Evolution* 7: 1809–1822. <https://doi.org/10.1038/s41559-023-02207-5>.
- Santos-Medellin, C., K. Estera-Molina, M. Yuan, J. Pett-Ridge, M. K. Firestone, and J. B. Emerson. 2022. "Spatial Turnover of Soil Viral Populations and Genotypes Overlain by Cohesive Responses to Moisture in Grasslands." *Proceedings of the National Academy of Sciences of the United States of America* 119: e2209132119. <https://doi.org/10.1073/pnas.2209132119>.
- Schulz, F., L. Alteio, D. Goudeau, et al. 2018. "Hidden Diversity of Soil Giant Viruses." *Nature Communications* 9: 1–9. <https://doi.org/10.1038/s41467-018-07335-2>.
- Schulz, F., S. Roux, D. Paez-Espino, et al. 2020. "Giant Virus Diversity and Host Interactions Through Global Metagenomics." *Nature* 578: 432–436. <https://doi.org/10.1038/s41586-020-1957-x>.
- Singh, B. K., Z.-Z. Yan, M. Whittaker, R. Vargas, and A. Abdelfattah. 2023. "Soil Microbiomes Must Be Explicitly Included in One Health Policy." *Nature Microbiology* 8: 1367–1372. <https://doi.org/10.1038/s41564-023-01386-y>.
- Starr, E. P., S. Shi, S. J. Blazewicz, et al. 2021. "Stable-Isotope-Informed, Genome-Resolved Metagenomics Uncovers Potential Cross-Kingdom Interactions in Rhizosphere Soil." *mSphere* 6: e0085-21. <https://doi.org/10.1128/mSphere.00085-21>.
- Stokar-Aviail, A., N. Tal, Z. Erez, A. Lopatina, and R. Sorek. 2019. "Widespread Utilization of Peptide Communication in Phages Infecting Soil and Pathogenic Bacteria." *Cell Host & Microbe* 25: 746–755. <https://doi.org/10.1016/j.chom.2019.03.017>.
- Straub, T. M., I. L. Pepper, and C. P. Gerba. 1992. "Persistence of Viruses in Desert Soils Amended With Anaerobically Digested Sewage-Sludge." *Applied and Environmental Microbiology* 58: 636–641. <https://doi.org/10.1128/aem.58.2.636-641.1992>.
- Straub, T. M., I. L. Pepper, and C. P. Gerba. 1993. "Virus Survival in Sewage-Sludge Amended Desert Soil." *Water Science and Technology* 27: 421–424. <https://doi.org/10.2166/wst.1993.0384>.
- Sun, M., M. Ye, Z. Zhang, et al. 2019. "Biochar Combined With Polyvalent Phage Therapy to Mitigate Antibiotic Resistance Pathogenic Bacteria Vertical Transfer Risk in an Undisturbed Soil Column System." *Journal of Hazardous Materials* 365: 1–8. <https://doi.org/10.1016/j.jhazmat.2018.10.093>.
- Sutela, S., A. Poimala, and E. J. Vainio. 2019. "Viruses of Fungi and Oomycetes in the Soil Environment." *FEMS Microbiology Ecology* 95: fiz119. <https://doi.org/10.1093/femsec/fiz119>.
- Tang, X., P. Yu, L. Tang, et al. 2019. "Bacteriophages From Arsenic-Resistant Bacteria Transduced Resistance Genes, Which Changed Arsenic Speciation and Increased Soil Toxicity." *Environmental Science & Technology Letters* 6: 675–680. <https://doi.org/10.1021/acs.estlett.9b00600>.
- Ter Horst, A. M., J. D. Fudyma, J. L. Sones, and J. B. Emerson. 2023. "Dispersal, Habitat Filtering, and Eco-Evolutionary Dynamics as Drivers of Local and Global Wetland Viral Biogeography." *ISME Journal* 17: 2079–2089. <https://doi.org/10.1038/s41396-023-01516-8>.
- Tong, D., C. Tang, and J. Xu. 2025. "Impact of Soil Viruses on C Emissions Can Be Enhanced by Viral Shuttle Processes in Soil." *Pedosphere* 35: 617–626. <https://doi.org/10.1016/j.pedsph.2025.03.008>.
- Tong, D., Y. Wang, H. Yu, H. Shen, R. A. Dahlgren, and J. Xu. 2023. "Viral Lysing Can Alleviate Microbial Nutrient Limitations and Accumulate Recalcitrant Dissolved Organic Matter Components in Soil." *ISME Journal* 17: 1247–1256. <https://doi.org/10.1038/s41396-023-01438-5>.
- Tong, D., and J. Xu. 2024. "Element Cycling by Environmental Viruses." *National Science Review* 11: nwae459. <https://doi.org/10.1093/nsr/nwae459>.
- Touchon, M., A. Bernheim, and E. P. C. Rocha. 2016. "Genetic and Life-History Traits Associated With the Distribution of Prophages in Bacteria." *ISME Journal* 10: 2744–2754. <https://doi.org/10.1038/ismej.2016.47>.
- Van Goethem, M. W., T. L. Swenson, G. Trubl, S. Roux, and T. R. Northen. 2019. "Characteristics of Wetting-Induced Bacteriophage Blooms in Biological Soil Crust." *MBio* 10: e02287-19. <https://doi.org/10.1128/mBio.02287-19>.
- Wang, L., H. He, S. Wang, et al. 2018. "Evidence for a Novel Negative-Stranded RNA Mycovirus Isolated From the Plant Pathogenic Fungus *Fusarium graminearum*." *Virology* 518: 232–240. <https://doi.org/10.1016/j.virol.2018.03.008>.
- Wang, L., D. Lin, K. Q. Xiao, et al. 2024. "Soil Viral-Host Interactions Regulate Microplastic-Dependent Carbon Storage." *Proceedings of the National Academy of Sciences of the United States of America* 121: e2413245121. <https://doi.org/10.1073/pnas.2413245121>.
- Wang, S., S. Yu, X. Zhao, et al. 2022. "Experimental Evidence for the Impact of Phages on Mineralization of Soil-Derived Dissolved Organic Matter Under Different Temperature Regimes." *Science of the Total Environment* 846: 157517. <https://doi.org/10.1016/j.scitotenv.2022.157517>.
- Wang, X., Z. Wei, K. Yang, et al. 2019. "Phage Combination Therapies for Bacterial Wilt Disease in Tomato." *Nature Biotechnology* 37: 1513–1520. <https://doi.org/10.1038/s41587-019-0328-3>.
- Wang, Y., Y. Liu, Y. Wu, N. Wu, W. Liu, and X. Wang. 2022. "Heterogeneity of Soil Bacterial and Bacteriophage Communities in Three Rice Agroecosystems and Potential Impacts of Bacteriophage on Nutrient Cycling." *Environmental Microbiomes* 17: 17. <https://doi.org/10.1186/s40793-022-00410-8>.
- Watts, G. 2017. "Phage Therapy: Revival of the Bygone Antimicrobial." *Lancet* 390: 2539–2540. [https://doi.org/10.1016/s0140-6736\(17\)33249-x](https://doi.org/10.1016/s0140-6736(17)33249-x).
- Wegrzyn, G., and A. Wegrzyn. 2005. "Genetic Switches During Bacteriophage λ Development." *Progress in Nucleic Acid Research and Molecular Biology* 79: 1–48.
- Wei, X., T. Ge, C. Wu, et al. 2021. "T4-Like Phages Reveal the Potential Role of Viruses in Soil Organic Matter Mineralization." *Environmental Science & Technology* 55: 6440–6448. <https://doi.org/10.1021/acs.est.0c06014>.
- Wieczynski, J. D., K. M. Yoshimura, E. R. Denison, et al. 2023. "Viral Infections Likely Mediate Microbial Controls on Ecosystem Responses to Global Warming." *FEMS Microbiology Ecology* 99: fiad016. <https://doi.org/10.1093/femsec/fiad016>.
- Wigington, C. H., D. Sonderegger, C. P. D. Brussaard, et al. 2017. "Re-Examination of the Relationship Between Marine Virus and Microbial Cell Abundances." *Nature Microbiology* 1: 15024. <https://doi.org/10.1038/s41564-017-0042-1>.
- Williamson, K. E., J. J. Fuhrmann, K. E. Wommack, and M. Radosevich. 2017. "Viruses in Soil Ecosystems: An Unknown Quantity Within an Unexplored Territory." *Annual Review of Virology* 4: 201–219. <https://doi.org/10.1146/annurev-virology-101416-041639>.
- Williamson, K. E., M. Radosevich, D. W. Smith, and K. E. Wommack. 2007. "Incidence of Lysogeny Within Temperate and Extreme Soil Environments." *Environmental Microbiology* 9: 2563–2574. <https://doi.org/10.1111/j.1462-2920.2007.01374.x>.
- Williamson, K. E., M. Radosevich, and K. E. Wommack. 2005. "Abundance and Diversity of Viruses in Six Delaware Soils." *Applied and Environmental Microbiology* 71: 3119–3125. <https://doi.org/10.1128/aem.71.6.3119-3125.2005>.
- Wu, H., S. Wan, C. Ruan, et al. 2022. "Phage-Bacterium Interactions and Nutrient Availability Can Shape C and N Retention in Microbial Biomass." *European Journal of Soil Science* 73: e13296. <https://doi.org/10.1111/ejss.13296>.

- Wu, R., E. M. Bottos, V. G. Danna, J. C. Stegen, J. K. Jansson, and M. R. Davison. 2022. "RNA Viruses Linked to Eukaryotic Hosts in Thawed Permafrost." *MSystems* 7: e00582-22. <https://doi.org/10.1128/msystems.00582-22>.
- Wu, R., B. Chai, J. R. Cole, et al. 2020. "Targeted Assemblies of cas1 Suggest CRISPR-Cas's Response to Soil Warming." *ISME Journal* 14: 1651–1662. <https://doi.org/10.1038/s41396-020-0635-1>.
- Wu, R., M. R. Davison, Y. Gao, et al. 2021. "Moisture Modulates Soil Reservoirs of Active DNA and RNA Viruses." *Communications Biology* 4: 992. <https://doi.org/10.1038/s42003-021-02514-2>.
- Wu, R., M. R. Davison, W. C. Nelson, et al. 2021. "DNA Viral Diversity, Abundance, and Functional Potential Vary Across Grassland Soils With a Range of Historical Moisture Regimes." *MBio* 12: e02595-21. <https://doi.org/10.1128/mBio.02595-21>.
- Wu, R., G. Trubl, N. Tas, and J. K. Jansson. 2022. "Permafrost as a Potential Pathogen Reservoir." *One Earth* 5: 351–360. <https://doi.org/10.1016/j.oneear.2022.03.010>.
- Xia, R., M. Sun, J. L. Balcazar, P. Yu, F. Hu, and P. J. J. Alvarez. 2023. "Benzo a Pyrene Stress Impacts Adaptive Strategies and Ecological Functions of Earthworm Intestinal Viromes." *ISME Journal* 17: 1004–1014. <https://doi.org/10.1038/s41396-023-01408-x>.
- Xie, S., X. Zhu, T. Algeo, and X. Qiu. 2023. "Geovirology: Viruses and Their Roles in Geological History." *Science Bulletin* 68: 379–382. <https://doi.org/10.1016/j.scib.2023.02.001>.
- Xu, Q., H. Zhang, P. Vandenkoornhuys, et al. 2024. "Carbon Starvation Raises Capacities in Bacterial Antibiotic Resistance and Viral Auxiliary Carbon Metabolism in Soils." *Proceedings of the National Academy of Sciences of the United States of America* 121: e2318160121. <https://doi.org/10.1073/pnas.2318160121>.
- Yang, K., X. Wang, R. Hou, et al. 2023. "Rhizosphere Phage Communities Drive Soil Suppressiveness to Bacterial Wilt Disease." *Microbiome* 11: 16. <https://doi.org/10.1186/s40168-023-01463-8>.
- Ye, M., M. Sun, D. Huang, et al. 2019. "A Review of Bacteriophage Therapy for Pathogenic Bacteria Inactivation in the Soil Environment." *Environment International* 129: 488–496. <https://doi.org/10.1016/j.envint.2019.05.062>.
- Yosef, I., M. Manor, R. Kiro, and U. Qimron. 2015. "Temperate and Lytic Bacteriophages Programmed to Sensitize and Kill Antibiotic-Resistant Bacteria." *Proceedings of the National Academy of Sciences of the United States of America* 112: 7267–7272. <https://doi.org/10.1073/pnas.1500107112>.
- Yu, P., J. Mathieu, Y. Yang, and P. J. J. Alvarez. 2017. "Suppression of Enteric Bacteria by Bacteriophages: Importance of Phage Polyvalence in the Presence of Soil Bacteria." *Environmental Science & Technology* 51: 5270–5278. <https://doi.org/10.1021/acs.est.7b00529>.
- Yu, S., S. Wang, X. Zhao, et al. 2023. "Extraction Optimisation to Measure Viral Abundance in Red Soils." *Biology and Fertility of Soils* 59: 927–937. <https://doi.org/10.1007/s00374-023-01765>.
- Zablocki, O., E. M. Adriaenssens, and D. Cowan. 2016. "Diversity and Ecology of Viruses in Hyperarid Desert Soils." *Applied and Environmental Microbiology* 82: 770–777. <https://doi.org/10.1128/aem.02651-15>.
- Zand, A. D., and A. V. Heir. 2020. "Emerging Challenges in Urban Waste Management in Tehran, Iran During the COVID-19 Pandemic." *Resources, Conservation and Recycling* 162: 105051. <https://doi.org/10.1016/j.resconrec.2020.105051>.
- Zhang, D., X. Zhang, Y. Yang, et al. 2021. "SARS-CoV-2 Spillover Into Hospital Outdoor Environments." *Journal of Hazardous Materials Letters* 2: 100027. <https://doi.org/10.1016/j.hazl.2021.100027>.
- Zhao, K., Y. Wang, R. Xue, X. Liu, B. Ma, and J. Xu. 2025. "Agriculture Increases Potential Health Risks of Vertebrate Viruses in Soils." *iMeta* 4: e70034. <https://doi.org/10.1002/imt2.70034>.
- Zhao, X., X. Liang, Z. Zhu, et al. 2025. "Phages Affect Soil Dissolved Organic Matter Mineralization by Shaping Bacterial Communities." *Environmental Science & Technology* 59: 2070–2081. <https://doi.org/10.1021/acs.est.4c08274>.
- Zhao, Y., M. Ye, X. Zhang, et al. 2019. "Comparing Polyvalent Bacteriophage and Bacteriophage Cocktails for Controlling Antibiotic-Resistant Bacteria in Soil-Plant System." *Science of the Total Environment* 657: 918–925. <https://doi.org/10.1016/j.scitotenv.2018.11.457>.
- Zheng, X., M. T. Jahn, M. Sun, et al. 2022. "Organochlorine Contamination Enriches Virus-Encoded Metabolism and Pesticide Degradation Associated Auxiliary Genes in Soil Microbiomes." *ISME Journal* 16: 1397–1408. <https://doi.org/10.1038/s41396-022-01188-w>.
- Zhu, D., S.-Y. Liu, M.-M. Sun, et al. 2024. "Adaptive Expression of Phage Auxiliary Metabolic Genes in Paddy Soils and Their Contribution Toward Global Carbon Sequestration." *Proceedings of the National Academy of Sciences of the United States of America* 121: e2419798121. <https://doi.org/10.1073/pnas.2419798121>.
- Zimmerman, A. E., C. Howard-Varona, D. M. Needham, et al. 2020. "Metabolic and Biogeochemical Consequences of Viral Infection in Aquatic Ecosystems." *Nature Reviews Microbiology* 18: 21–34. <https://doi.org/10.1038/s41579-019-0270-x>.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** gcb70460-sup-0001-Supinfo.docx. **Table S1:** gcb70460-sup-0002-TablesS1-S4.xlsx.