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The soil microbiome is recognized as an essential component of healthy soils. Viruses are also diverse and abundant in soils, but their roles in soil systems remain unclear. Here we argue for the consideration of viruses in soil microbial food webs and describe the impact of viruses on soil biogeochemistry. The soil food web is an intricate series of trophic levels that span from autotrophic microorganisms to plants and animals. Each soil system encompasses contrasting and dynamic physicochemical conditions, with labyrinthine habitats composed of particles. Conditions are prone to shifts in space and time, and this variability can obstruct or facilitate interactions of microorganisms and viruses. Because viruses can infect all domains of life, they must be considered as key regulators of soil food web dynamics and biogeochemical cycling. We highlight future research avenues that will enable a more robust understanding of the roles of viruses in soil function and health.

Soils provide many ecosystem services that are vital for human wellbeing, such as food production, nutrient and carbon retention, erosion and pest control, and clean water, among others[1,2]. Soils contain at least 59% of the total global species diversity[3], spanning from microorganisms to megafauna, including organisms living aboveground and below. It is this biodiversity that sustains ecosystem services and contributes to the sustainable functioning of soils. Microorganisms are particularly important given their roles in the cycling of organic matter and nutrients, as causative agents or suppressors of plant diseases and in atmospheric nitrogen fixation, among many others. These activities tightly link soil microorganisms to Earth's biogeochemistry and consequently to climate change[4]. For example, it has been suggested that increased soil microbial activity would enhance greenhouse gas sequestration[5] by reducing carbon dioxide (CO_2) emissions and promote processes such as nitrogen fixation and methane oxidation, all of which could help to regulate the climate. In contrast, climate change may decrease soil organic carbon stocks as a result of a changing soil–water–gas equilibrium[1]. For example, elevated temperatures can increase microbial respiration, speeding up the degradation of organic matter and leading to the release of CO_2 into the atmosphere[6]. Understanding the regulation of these dynamics and ensuring good soil health is thus pivotal for maintaining a sustainable future for all life on Earth.

Soil food webs are complex, with many interactions and feedbacks that are still not fully understood[7]. At the base of the food web is organic matter produced by primary producers: mainly plants, along with detritus (Fig. 1). This detritus includes necromass, which is dead biological material originating from plants, animals and microorganisms, as well as faecal material. This organic matter feeds microorganisms (prokaryotes and fungi), which are then consumed by other predators (for example, protists and nematodes). These predators are themselves preyed on by the next trophic level, and so on. Each trophic level releases CO_2 through respiration and returns some organic matter (for example,

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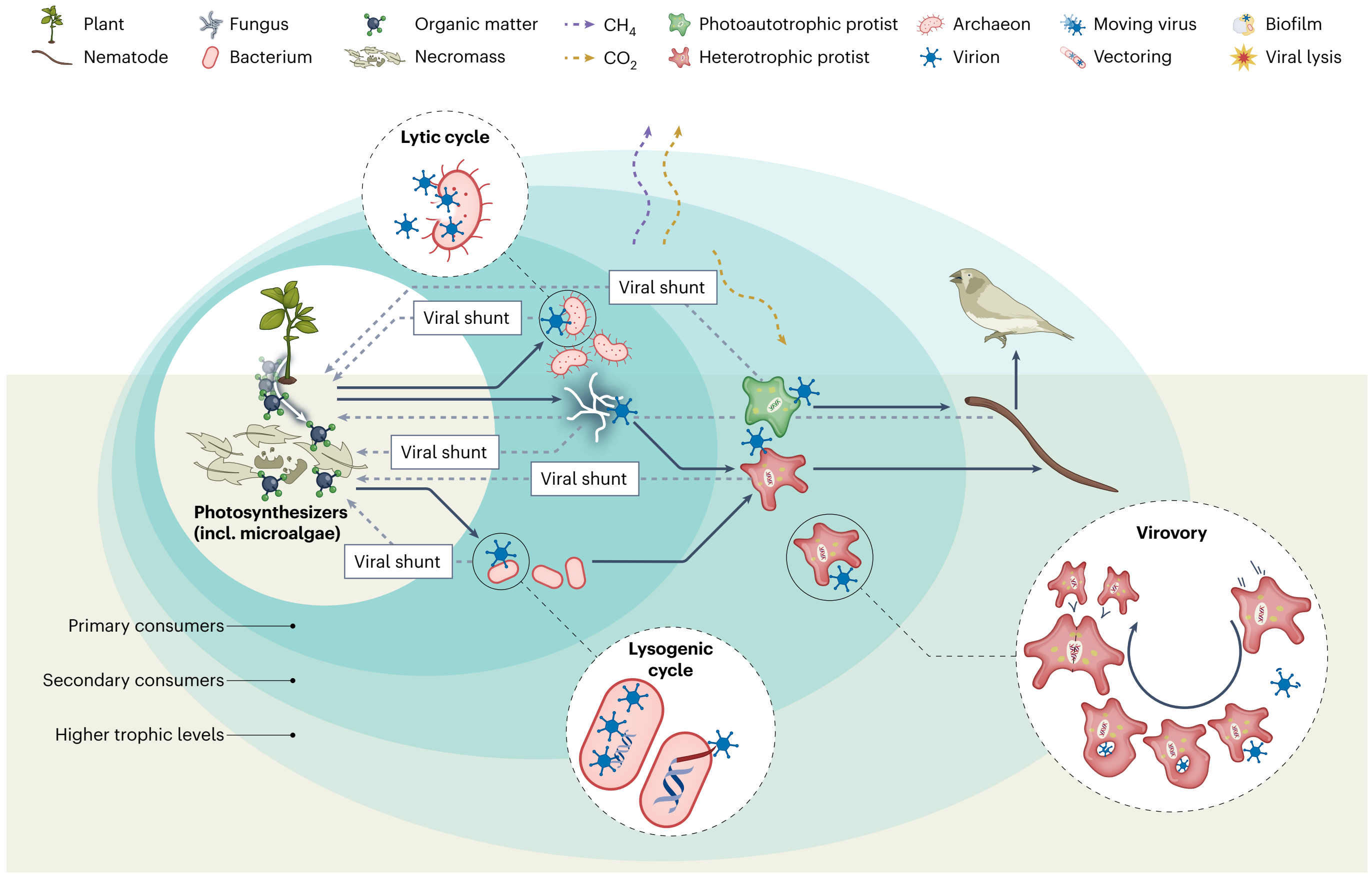

Fig. 1 | Inclusion of viruses in the soil microbial food web. Simplified schematic of the soil microbial food web, including viruses. Plants and microalgae are the photosynthesizers and the source of organic matter, together with the necromass (dead leaves and cells). Organic matter is consumed by archaea, bacteria and fungi (primary consumers). These are consumed by protists (secondary consumers) and then by the higher trophic layers (here represented by a nematode). At each level, organisms produce organic matter that feeds the food web. Viral infection of the microbial community (that is, archaea, bacteria, fungi and protists) traps the organic matter at the lower levels of the food web, essentially creating a viral shunt. Cycling of organic matter by the microorganisms also produces CO_2 (dashed brown arrows) and CH_4 (dashed purple arrows), which can be sequestered or released into the atmosphere. Bacteria and protists can also consume virions—a process described as virovory (here depicted only by the protists)—which would lead to growth and increased abundance of the organisms consuming the virions. Lytic and lysogenic cycles are represented for archaea and bacteria, respectively, although they can be found in several microorganisms. Full arrows point towards consumers, whereas dashed arrows show the production of organic matter. Please note that the organisms are not drawn to scale. Incl., including.

through excretions or death) to feed the microorganisms at the base of the food web (Fig. 1). This recycling of organic matter through microbial activity is referred to as the microbial loop[8]. The microbial loop is vital for ecosystem functioning, converting dead organic matter into more readily usable forms and ensuring a steady supply of organic matter to higher trophic levels. As a process conducted by microorganisms, the efficiency of the microbial loop depends on abiotic conditions (for example, temperature), microbial diversity (both in taxonomy and metabolic potential) and interactions with other players such as viruses and grazers. There are many variables that can determine the number of trophic levels within a soil food web, but the final trophic level can be, for example, a macrofaunal organism such as a centipede. However, the soil food web is not a static and defined compilation of layers; instead, each trophic level can interact at various levels (for example, ingested microorganisms can survive invertebrates' digestive tracts and can thus be transported to new locations across a soil system[9]). The complex network of interactions has made understanding of the soil food web difficult to dissect. Another way to tease apart these complexities is to consider soil food web organization through the lens of functional groups, such as litter transformers (for example, mostly fungi) and the ecosystem engineers (for example, worms and other insects)[7]. More recently, it has been recognized that the soil microbiome is vital to achieving sustainable agricultural practices and healthy soils, given the essential functions microorganisms play in nutrient acquisition or resilience to plant diseases (for example, ref. 10). For example, microbial inoculants (that is, specific functional microorganisms added to crops) have been shown to promote plant growth and confer resistance to pathogens[11], thus enabling a decrease in dependency on agricultural chemicals and more sustainable agricultural practices.

The role of viruses in soil food webs has recently gained traction, with experimental studies showing enhancements of viral abundance that accelerate dissolved organic matter cycling[12] and nitrogen mineralization[13] and viral dominance in the soil food web increasing under experimental warming[14]. Many pressing questions remain. The importance of eukaryotic and temperate prokaryotic viruses is still unknown[15]; the fate of viral particles may have unexplored significance for element retention in soil food webs (notably of phosphorus[16]) and importantly the response of viral trophic interactions to global changes, including warming, may be crucial to understanding how soil systems will respond as a whole[17]. Consequently, the role of viruses in soil function and health is still unclear.

Given that microorganisms are at the base of the soil food web and given their importance to the Earth's biogeochemistry and soil microbial dynamics, this Perspective will describe possible impacts of viruses in the soil microbial food web and more importantly the areas that require further research. Overall, research into the role of viruses in the soil microbial food web lags behind other habitats, such as aquatic environments[18], and for this reason we aim to elevate viruses to the forefront of soil research. We argue that viruses should be integrated into a food web conceptualization of soil environments, similar to what is done for aquatic ecosystems, especially regarding their contribution to biodiversity and biogeochemical cycling. However, we highlight how virus–host interactions are distinct in soils due to the unique physicochemical constraints of the soil environment, such as varying particle sizes and fluctuating water contents. To understand soil viral ecology, it is essential for the scientific community to study virus–host interactions in all microbial members of soil ecosystems, viral impacts on the cycling of organic matter and viral impacts on soil health.

A brief overview of soil viruses

Soil viruses range in estimated abundance from 10^7–10^9 virus-like particles per gram of soil[19]. Observations indicate that viruses are less abundant in desert soils than in environments with high organic matter content, including temperate forests and wetlands[19–21]. Soil viruses show extraordinary genetic diversity in DNA and RNA, infecting all domains of life (for example, refs. 22,23), thus it is expected that they will impact soil biodiversity through viral infection and possibly killing the host. The release of new virions and cell organic matter after a lytic cycle also impacts biogeochemical cycling, with organic matter that is available for other microorganisms to uptake and virions that are able to infect new hosts. Furthermore, auxiliary metabolic genes (AMGs)—host-derived genes in viral genomes that are involved in metabolic processes—have been identified in soil viruses, but the overall impact of these AMGs on biogeochemical cycling remains poorly understood. Although viruses can probably infect every organism living in soils, most viral research in terrestrial ecosystems has focused on virus–plant interactions. These interactions are typically classified as detrimental, as, for example, in the case of many mosaic viruses that cause disease in plants that are essential for food production (see ref. 24), or beneficial, as in the case of viruses that infect plant pathogens and serve as potential biocontrol agents (see ref. 25).

Most notably, evidence of the viral impact on soil biogeochemistry is sparse, indirect and speculative. For example, metagenomic and metatranscriptomic approaches show soil DNA and RNA viruses infecting prokaryotes and fungi that are important for carbon and nitrogen cycling (for example, refs. 26,27) and these approaches have also revealed AMGs related to carbon degradation and acquisition (for example, ref. 28). Several viruses have been isolated that infect rhizobia (bacteria, living as symbionts in plant root nodules, that convert nitrogen gas into ammonium; for example, ref. 29), suggesting their potential importance for nitrogen cycling in the rhizosphere. A recent study has also shown the potential of viral infections to increase microbial biomass consumption and respiration in some soils[30], with the scale of impact depending on the community composition and nutrient availability.

Fitting viruses into soil microbial food webs

The microbial loop describes a way to conceptualize the cycling of carbon by microorganisms, whereby particulate and dissolved organic matter produced from extracellular release and mortality at each trophic level is returned to the food web via microbial incorporation[31]. This concept, initially formulated to explain aquatic food webs, has subsequently been extended to other environments, including soils[8]. Predation is a key process in microbial food webs as it structures the community composition and maintains biodiversity while at the same time producing and transforming organic matter that feeds microorganisms[32]. Viral predation of soil microorganisms is well established (for example, ref. 15), yet at present we still lack enough data from diverse environments or time series to yield estimates of the broader impacts of these interactions. As such, the inclusion of viral dynamics in the microbial soil food web is less developed compared with in aquatic ecosystems, which have historically focused more research on viruses, establishing them as an integral part of the aquatic microbial food web[18].

More recent research has also suggested that viruses are important drivers of soil microbial food webs, in particular because they facilitate trophic interactions that impact both microbial diversity and biogeochemistry[16]. Our understanding of viral infection cycles is typically defined on concepts formulated in phage (viruses infecting bacteria) ecology. Phages are usually characterized as virulent or temperate (although viral infection exists in a continuum between these two, with intermediate strategies such as chronic infection[33]). After infection, strictly lytic (virulent) phages redirect host metabolism to produce more virions, followed by lysis to release their progeny and the dead cell organic matter (Fig. 1). In contrast, temperate phages can integrate into the host genome (lysogeny; Fig. 1), where they can remain for many host generations until—either stochastically or in response to stimuli—they activate lytic reproduction. Lysis has the advantage of exponential replication if the probability of new infection is high, but killing the host is disadvantageous if new hosts cannot be reached[34]. Lysogeny avoids extracellular risks but achieves much slower reproduction, coupled to that of the host cell[34], and in some cases confers protection against other viral infections[35]. Functionally, soil viruses are hypothesized to have similar roles to those established in aquatic environments[18,36]. However, the mechanisms by which soil viruses infect microorganisms are expected to be quite different due to the physicochemical nature of soil systems (that is, soil particle and pore structure) and the variability of environmental conditions (such as water availability), all of which limit the spread of viral progeny relative to aquatic systems. In the following sections, we describe how viruses should be integrated into the conceptualization of the soil microbial food web.

Viral drivers of soil microbial diversity and metabolism

Theories to describe how viruses impact microbial diversity are well documented in aquatic ecosystems (for example, refs. 37,38). For example, the kill the winner hypothesis describes the role of viruses in maintaining microbial diversity in aquatic ecosystems by killing dominant and fast-growing organisms, allowing slower-growing microorganisms to coexist. A similar mechanism is expected in soils, where the dominant members of the soil microbial community are more likely to be lysed by viruses, thus allowing less abundant community members to take over and thrive. Soil viruses can also impact microbial diversity through mutualistic relationships, where both the host and virus benefit[39]. For example, this was demonstrated by a double-stranded RNA mycovirus (that is, a virus that infects fungi) of the fungus *Ustilago maydis*, which encodes a toxin that when expressed during infection can kill competing fungi[40]. These mutualistic interactions are particularly relevant in soils where fungi predominate and are infected by mycoviruses[41]. This specific example highlights how such interactions can influence microbial diversity by giving an advantage to the virus-infected fungi over their competitors. Horizontal gene transfer, where viruses act as vectors of genetic material between cells, can also impact microbial diversity by introducing new genes into different microbial populations, and this has also been suggested as a common mechanism in other environments[42,43]. This genetic exchange increases variability and adaptability among microorganisms, especially under environments of high population density such as soil biofilms, where interactions between viruses and microorganisms are frequent.

Microbial diversity changes resulting from viral infections inevitably modify soil microbial metabolic processes and thus the overall biogeochemistry. During viral lysis, cellular content is released in the form of particulate and dissolved organic matter, which includes larger cell pieces and agglomerates of particulate organic matter that larger grazers can feed on, as well as dissolved organic matter small enough that it is only available to other microorganisms. This lysed organic matter has two possible fates in soil systems: (1) biological (uptake by microorganisms for biomass or released as CO_2 through respiration); or (2) physicochemical (adsorption to soil particles, which may permanently sequester the material; for example, if organic matter is entombed into small soil pores, rendering it inaccessible to microbial degradation). Such physicochemical processes are similar to those in aquatic sediments, but contrast with water column processes where lysed material can float away, making it more difficult to assimilate by microorganisms. If the organic matter is used for microbial growth, progeny cells become potential hosts of subsequent viral infections: a cycle that traps organic matter in lower trophic levels through a process referred to as the viral shunt[44] (Fig. 1). This mechanism not only recycles carbon, but also nutrients essential for microbial growth. Consequently, organic matter does not move up the food web, but is instead sequestered in the soil.

In aquatic ecosystems, bacteria are the main consumers of dissolved organic matter. In soils, fungi are dominant members at the base of the food web as they degrade organic matter, in particular recalcitrant plant-derived compounds such as lignin and cellulose[45]. Fungi are not routinely included in conceptualization of the aquatic microbial loop or viral shunt because of their relatively low abundance in aquatic systems. However, in soil systems, because fungi are more abundant, mycovirus–fungi interactions are probably essential to fully understanding the ecological and biogeochemical dynamics of soil microbial food webs (Fig. 1). How fungi might impact the viral shunt in soil remains largely unknown. Documented mycoviruses are primarily found intracellularly, being passed on to daughter cells during cell division, sporulation or cell fusion, without a known extracellular infection route[41]. Furthermore, intracellular mycoviruses described to date are not necessarily integrated into the hosts genome[46]. For this reason, traditional definitions of either lytic or lysogenic viral lifestyles do not necessarily apply to mycoviral infection cycles. Nonetheless, mycoviruses have been shown to alter fungal growth rates, sporulation, the virulence of plant pathogenic fungi and the secretion of extracellular enzymes[41]. This is quite different from aquatic ecosystems, where fungi are currently neither considered central players nor generally found in high abundances[47]. More work is needed to fully capture the impact of soil mycoviral infections.

Another difference between aquatic and soil systems is the fate of infections. For example, a report indicated that 40% of soil bacteria include inducible prophages[47], whereas most fungi are shown to have intracellular viruses[41]. Assuming this is generally applicable, it would mean that a considerable share of the viral infection cycle in soils is taking place intracellularly, resulting in substantially different virus–host interactions. This is clearly seen in the effects mycoviruses can have on their fungal host, ranging from inhibition to enhancement of growth[46]. Such a scope of mycovirus–fungi relations will inevitably also impact soil biogeochemical cycling. If fungal growth were to decrease due to mycovirus infection it would reduce the fungi's ability to degrade organic matter, but with increased fungal growth the reverse would be true.

Although microbial mobility is restricted in soils relative to in aquatic systems, organisms and organic matter are more concentrated in the soil environment. Integrated across the globe, viruses in the top 30 cm of soils are estimated to contain 1.2×10^6 Mg carbon, 4.4×10^5 Mg nitrogen and 1.5×10^5 Mg phosphorus (see Supplementary Tables 1–5), constituting a minor fraction of the organic carbon found in soil microbial biomass (~0.01%; see Supplementary Table 6). Despite these small standing stocks, it is important to remember that viruses can rapidly replicate and release the cell content into the surrounding environment, whereby they impact the cycling of carbon, nitrogen and phosphorus. Viruses can also be a nutrient source for other microorganisms—a process referred to as virovory (Fig. 1). Although virovory is a relatively well-established mechanism, it has received increased attention recently, with some studies showing the consumption of viral particles by aquatic protists (probably via phagocytosis) and bacteria (probably via extracellular enzymatic degradation) (for example, refs. 48–50). These findings suggest that the energy and nutrients stored in viruses could have been overlooked, along with their biogeochemical importance in soils, especially where resources are scarce and microbial movement might be physically limited. Although some progress has been made towards understanding the roles of viruses in soil biogeochemistry, their concrete function and impact remain poorly resolved. Broadening our understanding of these intricate interactions is crucial to fully comprehending the ecological implications of viruses in soil ecosystems. By delving deeper into these relationships, we can unravel the complex dynamics that shape soil ecology and inform strategies for sustainable soil management and ecosystem preservation. In the following sections, we describe the research priorities for better understanding viruses in the soil microbial food web.

Research directions for the field

Assessing how soil physicochemical conditions impact viruses

Soil virology is a rapidly expanding field and although researchers can borrow some theories and techniques from more established virology subfields, the differences described above necessitate new innovations. Here we outline how microbiologists and virologists could direct their efforts to better gauge the roles of viruses in soil food webs and their impact on biogeochemistry.

A given volume of soil probably has a higher concentration of microorganisms and viruses than the same volume of water from an aquatic ecosystem. However, although water allows dispersal and contact, in soils these interactions are more limited by unique physicochemical properties. Differences in soil texture (clay, sand and silt particles, as well as aggregates), organic matter, moisture and air give rise to diverse, distinct microhabitats. Conditions such as oxygen and water availability, water retention, adsorption and cation exchange capacity, as well as pH and nutrient levels affecting viruses directly and indirectly via host performance, may differ within short distances and temporally. These properties mean that in soils, even though viruses and their hosts might be physically proximal, they may be unable to interact, which can lead to diversification of viruses and favouring of lysogeny or intracellular states over lytic infections[23]. Compared with the relatively more stable and homogeneous nature of aquatic ecosystems, the spatiotemporal shifts in soil properties via disturbances or climatic conditions are more prone to affecting virus–host interactions.

Under dry conditions, we suggest that viruses have several possibilities to ensure their persistence. First, viruses could remain in a lysogenic state[51] protected inside the host, where they could remain until more favourable conditions emerge[15]. Second, virions could persist by being passively encased in biofilms (Fig. 2a). Biofilms are a matrix of microbially produced exopolymeric substances that glue cells together, creating a complex and stable environment protecting microorganisms and by chance also viruses from desiccation while keeping them close together[52]. As such, biofilms are important hot spots of microbial and viral activity. Likewise, pores filled with water could protect microorganisms and viruses from desiccation, prolonging their survival until conditions are more favourable for viral infection (Fig. 2a). Soil systems are overall prone to rapid fluctuations in moisture over short time periods. When dry soils are rewetted, some lysogenic viruses could rapidly revert to a lytic state, release virions and reach new hosts[53] (Fig. 2b), releasing organic matter via viral lysis, which could subsequently stimulate additional microbial metabolic activity and growth across the microbial food web (Fig. 2c). Consequently, the viral shunt would also be stimulated, which would lead to increased production of virions that in turn would infect more microorganisms. The lysogeny of these microorganisms releases particulate and dissolved organic matter that feeds new microbial growth, and these microorganisms can be infected by virions. Such a cyclic turnover means the organic matter is retained in the lower levels of the soil food web. The boom and bust[54] infection dynamics in soils (Fig. 2a–c) is dependent

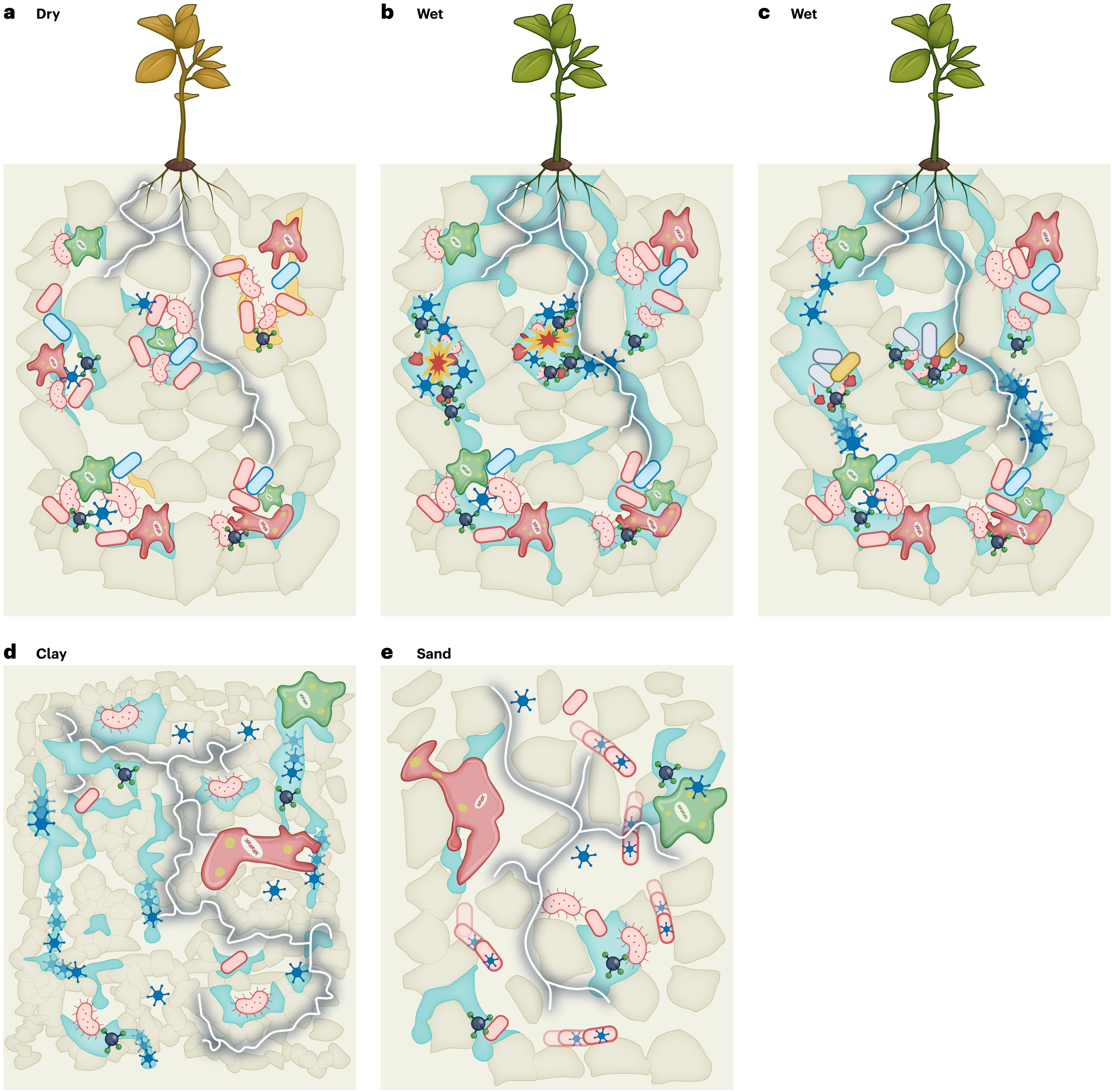

Fig. 2 | Physicochemical conditions of soils. a–**c**, Boom and bust viral infection dynamics between dry and wet soil conditions over time. **a**, Dry soil conditions under which microorganisms, virions and organic matter are found in hotspots with reduced mobility and activity, entrapped in water-filled pores (blue) and biofilms (yellow). **b**, Under wet conditions, virions are more active, replicating and lysing microbial cells and releasing organic matter and new virions. **c**, These virions are now able to find new hosts in other hotspots, while the released microbial organic matter serves as food for other microorganisms to grow and create a new community. **d**,**e**, Difference between clay and sandy soils. **d**, Clay soils with smaller pores can restrict the movement of protists and their ability to find microbial prey, whereas virions are still able to disperse and infect microorganisms. Here, we also show preferential flow paths, with water flowing primarily through macropores and carrying virions as it disperses across the soil. **e**, Sandy soil with larger pores allows the movement of both virions and protists, for example through vectoring where bacterial cells move in the soil while being infected with a virus. It should be noted that preferential flow paths and organismal vectors can be found in all soil types and not just in clay or sand. Please note that the organisms are not drawn to scale. See Fig. 1 for key.

on changes in environmental conditions such as rain and droughts. Given that the frequency and duration of these events are expected to undergo substantial shifts with a changing climate[55], a better insight into virus–host dynamics in soil environments is essential.

In particular, viral and microbial compositions have been shown to shift between dry and wet conditions (for example, refs. 23,53). One study found increased viral richness with wetting, but no substantial change for the microbial community[51], whereas another study found lower diversity in drier soils[26]. Additionally, these studies suggested that there were more temperate viruses in the drier soils, but also more putative AMGs in wetter soils. Together, this suggests higher viral activity under wet conditions, but also that viruses do not decimate dominant populations. Less well understood, however, is the extent to which viruses impact the fate of organic matter under shifting climate and environmental conditions. Open questions include the length of time that viruses remain infectious during adverse conditions, or the rates of virus-induced mortality or lytic–lysogenic switches under different physicochemical conditions. To address these challenging questions, experiments using virus–host model systems should initially be performed under controlled settings with variable physicochemical conditions (for example, wet/dry oscillations with projected temperature increases, altered pH and so on), then changes in organic matter fluxes, nutrient cycles and host physiology should follow over time.

Another unique constraint found in soils is texture and consequent pore size, with clay soils having smaller pore sizes relative to sandy soils. This would restrict larger predators such as protists from reaching microbial prey, whereas smaller predators, including viruses, could still have access (Fig. 2d). In contrast, in sandy soils with larger pores, there are enhanced possibilities for viral movement by vectoring (being carried by biota; Fig. 2e). We propose several mechanisms that could allow viral movement within varying soil textures that should be investigated further, such as preferential flow paths (biotically or abiotically produced macropores through which most of the infiltrating water and compounds flow[56]) (Fig. 2d) and organismal vectors (where active movement of organisms through soil facilitates the migration of viruses[57]) (Fig. 2e). Preferential flow paths as a route for virus dispersal have been studied mainly under laboratory controlled conditions and for specific viral strains[58]. Nematodes and earthworms have also been shown to vector viruses through soils[59,60]. Earthworms rework the soil structure, recreating channels[61] that could be used as preferential flow paths that could also serve to disperse viruses. Movement and dispersion of viruses through microorganisms still needs to be verified; however, it could be achieved either via an infected motile microbial cell (Fig. 2e) or by hitchhiking. Hitchhiking could be achieved either in hyphal-riding bacteria[62] or by virions attached to the microorganism through a biofilm, as was observed in T cells, where biofilms were produced by the infected cells and their synthesis was controlled by viruses inside the host[63]. To study the movement of viruses and microorganisms in soils, we suggest the use of fluorescently labelled viruses and hosts within controlled soil columns[64], or microfluidic techniques, which would allow the study of microbial interactions while mimicking the spatiotemporal variability of soils' physicochemical conditions at appropriate micro- and nanometre scales[65]. Such techniques could help us to understand the time frame over which viruses remain infective under different soil conditions (for example, dry/wet) and soil types (particle sizes). As soil properties are distinct from those of other ecosystems, it will be crucial to examine the impacts of these physicochemical conditions on viral dynamics and how these might vary due to local and global changes.

Assessing viral dynamics in key soil microbial groups

Fungi. Soil fungi are important due primarily to their ability to degrade complex organic matter[45] and facilitate nutrient availability through mycorrhizal associations[66]. A unique feature of fungi is their extensive network of mycelia (estimated to be as much as 100,000 cm per cm^3 of soil), which enhance water retention and prevent erosion but also form fungal highways, enabling the transfer of nutrients and bacteria across networks that can span several hectares[67,68]. Furthermore, fungi engage in complex interactions with bacteria, ranging from mutualistic to antagonistic relationships that profoundly shape soil organic matter dynamics. However, understanding of fungal viruses and their impacts has lagged behind other virus–host systems and because they are undoubtedly important in organic matter cycling they represent a critical gap in our understanding of soil microbial ecology.

One way to progress our understanding of these complex interactions would be to isolate mycoviral–fungal pairs that are typically only found intracellularly but might use extracellular routes. It is important to understand differential impacts between these two viral lifestyles because in addition to obvious differences in viral productivity under the two mechanisms, intracellular viral infection could have countless impacts on fungal host physiology, such as modifying gene expression and fungal growth, and subsequently the cycling of organic matter, with consequences for the overall food web structure. Applying nanoscale secondary ion mass spectrometry would be advantageous to follow viral impacts on metabolic activity, as well as biogeochemical fluxes. As an example, this could help to reveal how viral infection and lysis impact the nutrient assimilation rates and stoichiometry of individual cells. Previously, nanoscale secondary ion mass spectrometry imaging has tracked the transfer of ^{13}C-labelled carbon from the rhizosphere to bulk soils by arbuscular mycorrhizal fungi, which supported bacterial taxa in the bulk soils, thereby influencing the fate of soil organic matter[69]. Given that fungi are key recyclers and nutrient movers in soils, it is crucial to disentangle mycoviral–fungal interactions to understand the cycling of organic matter, with consequences for the health of natural and agricultural soils.

Archaea. Archaea account for only ~2% of all prokaryotes in surface soil layers[66]; however, they are important drivers of soil biogeochemistry and an integral part of the carbon (for example, methanogenesis[70]), nitrogen (for example, nitrification[71]) and sulphur (for example, sulphate reduction[67]) cycles. Archaea also have a higher diversity in soils compared with other environments[68]. Still, virus–archaea interactions are rarely studied, but recently it has been suggested that viruses actively infect soil archaea[72]. Methane (CH_4) production and oxidation are important steps in the carbon cycle; both processes are carried out by anaerobic archaea[73]. Although several archaea have already been isolated from soil environments (for example, rice fields and peat bogs), the role of viruses in controlling the production of climate gases such as CH_4 has not been determined. Soils are the only known biological sink for atmospheric CH_4[74] (Fig. 3a). It could be speculated that disruption by viral infection could impact the rate of greenhouse gas emissions and whether carbon is sequestered or degraded. For example, if archaeal groups that produce CH_4 are targeted by viral infection, it could lead to an accumulation of potentially degradable organic carbon, which might be sequestered or stimulate the growth of other microbial groups (Fig. 3b). In contrast, if archaeal oxidizers were targeted by viruses, it could lead to an accumulation of CH_4 that could be released to the atmosphere, thereby increasing the climate footprint (Fig. 3c).

Archaea also play central roles in the soil nitrogen cycle due to their involvement in a suite of nitrogen metabolisms—nitrogen fixation, ammonia and nitrite oxidation, annamox and denitrification[73]. Many links in the nitrogen cycle could be disrupted by viral–archaeal infection. As an example, it could be speculated that if archaeal nitrogen fixation is interrupted by viral infection it could decrease nitrogen availability (Fig. 3d,e), which in turn could decrease soil fertility and possibly also plant growth and crop yield, but of course other links in the nitrogen cycle could also be disrupted by viral infection with varying effects. A first step towards elucidating the role of viruses in controlling archaea populations and functions would be to focus on extreme soil environments, such as saline or acid/alkaline, where archaea are typically found. Combining molecular techniques with stable isotope probing of membrane lipids specific to certain archaeal groups[75] might help to elucidate specific impacts and interactions of viruses and archaeal populations, and cultivation and manipulation experiments could provide a fruitful avenue for investigating cause and effect relationships in response to specific manipulations.

Protists. Protists are immensely diverse and unique in soils and encompass a variety of metabolic niches, from autotrophs to omnivores[76]. In soils, protists are predominantly consumers; hence, they play a central role in controlling the structure of the soil microbiome by consuming bacteria, fungi, nematodes and other protists[77,78]. Soil protist viruses are underinvestigated, with most soil research focusing on large and

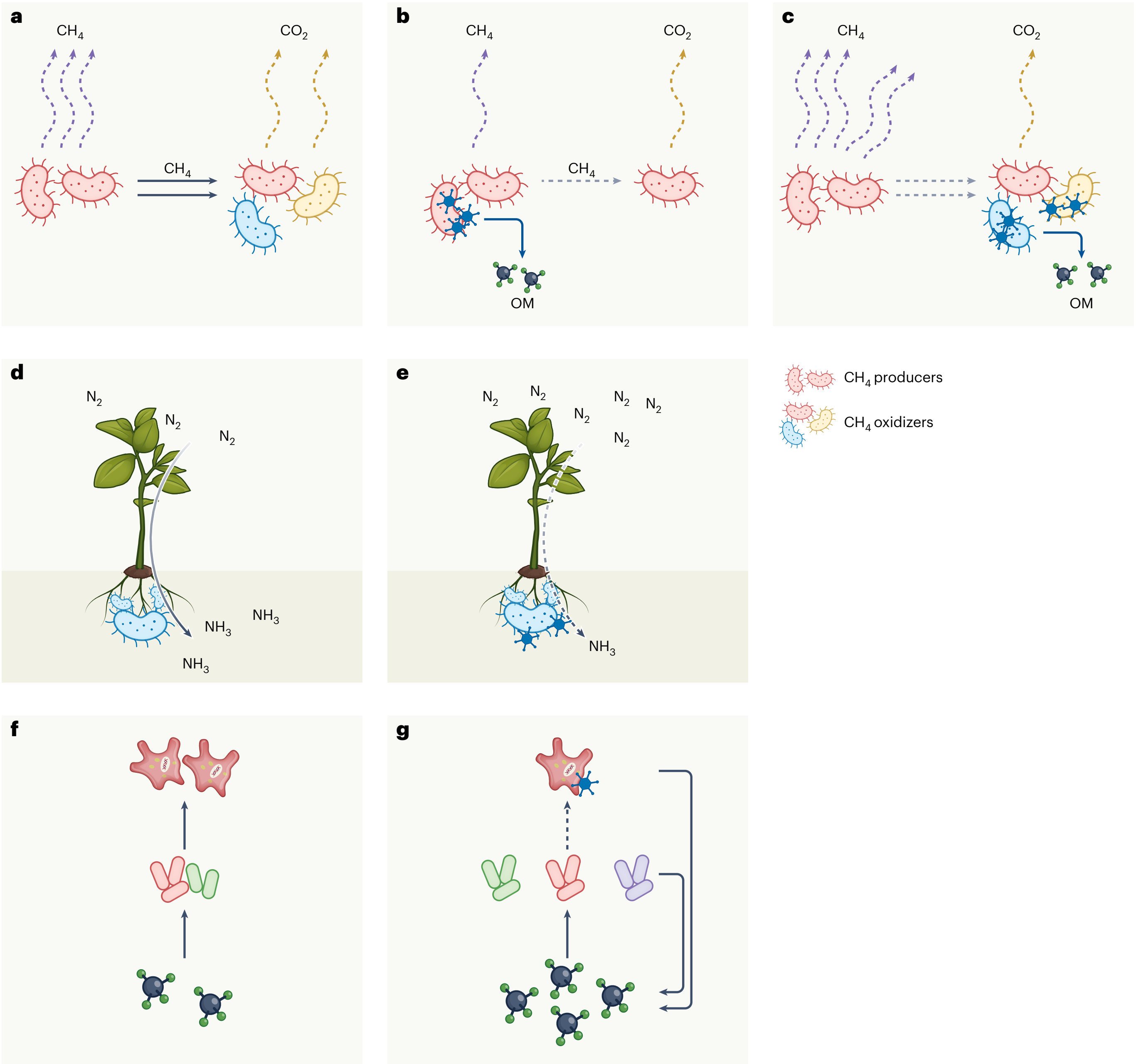

Fig. 3 | Viral–host interactions in soils. a–**g**, Schematics showing several possible mechanisms whereby viral infections of different soil microorganisms can impact biogeochemistry and population dynamics. **a**–**c**, Impact of viral infection on anaerobic archaea and carbon cycling. **a**, Without viral infection, different archaeal groups produce and oxidize CH_4, as well as producing CO_2. **b**, If archaea that produce CH_4 are infected by virions, this could lead to an accumulation of potentially degradable organic carbon and a decrease in CH_4 and CO_2 production. **c**, If CH_4 oxidizers are targeted by viral infection, this could lead to an accumulation and release of CH_4 into the atmosphere. **d**,**e**, Archaea are also important in regulating the nitrogen cycle. For example, they can fix atmospheric dinitrogen (N_2) into ammonia (NH_3), which then becomes available to plants (**d**). However, infection of these archaea by virions could decrease the available nitrogen (here represented as NH_3) to plants (**e**). **f**,**g**, Protists normally predate on bacterial populations (**f**), but if virions infect these protists, it could be speculated that the top-down control would be loosened, potentially increasing bacterial abundance and diversity while trapping the organic matter in the lower trophic levels (**g**). Please note that the organisms are not drawn to scale. OM, organic matter. See Fig. 1 for key.

giant viruses, which are known to infect a range of eukaryotic hosts from the smallest flagellates to multicellular eukaryotes[79]. Giant viruses can be as large as bacteria and are known for reprogramming host metabolism, and future work targeting the impacts of these infections is necessary. Protists are also hosts of many smaller viruses and are even known to predate on viral particles[48]. Although most protists are omnivorous, it is thought that they feed most commonly on bacteria[80] (Fig. 3f), so it could be speculated that if viruses attacked and killed protists it would loosen the predatory control on the bacterial community[81]. This in turn would change the bacterial community composition and activity, potentially increasing bacterial abundance while also retaining the organic matter in the lower levels of the microbial food web (Fig. 3g), essentially creating a soil viral shunt. Furthermore, unlike viruses, protists are generally mobile and can therefore actively seek more favourable prey and environments[82]. Therefore, viral infection of protists could decrease the spatial transfer of material within soils but also reduce the role of protists as prey for larger soil organisms.

Using cultivation techniques together with fluorescence microscopy combined with specific stains or fluorescently labelled probes could allow visualization of virus–protist interactions in situ. For example, virocell fluorescence in situ hybridization using labelled messenger RNA of the virus and host that is detected through imaging flow cytometry would allow the study of viral infection dynamics[83]. Specifically, it would enable observations of real-time viral–protist interactions while also determining the physiological impact of the infection and the numbers of viruses produced.

RNA viruses. Previous research has suggested that prokaryotes are predominantly infected by DNA viruses, whereas RNA viruses infect mainly eukaryotic hosts ranging from unicellular protists and yeasts to multicellular plants, animals, algae and fungi[84,85]. The dominance of soil metagenomic sequencing in particular, which generally cannot recover RNA viral genomes, has led to the notion that soil DNA viruses are more abundant and diverse and thus play a more dominant role in the soil microbial food web. Recently, however, this hypothesis was challenged by studies showing a high diversity of RNA viruses (including phages) in soils[22,26].

Still, there are several methodological challenges to overcome in relation to extraction methods and bioinformatic tools before the entire soil RNA viral community can be explored. An increasing focus on deeply sequenced soil metatranscriptomes would enhance the known diversity of RNA viruses. In addition to sequence-based approaches, it will also be important to isolate more RNA viruses from soil systems to determine the true scope of their infection dynamics compared with DNA viruses and consequently to fully assess their impact on soil food webs.

Assessing the biogeochemical impact of soil viruses

Although several lines of evidence indicate an important role for viruses in regulating soil microbial food webs, little is known about their broader impacts on biogeochemical cycling. It has been shown that organic matter generated during viral cell lysis in aquatic ecosystems is readily available for microorganismss[86]. While the same could be assumed for soils, this has not been robustly determined. In particular, the quantity and properties of new organic matter resulting from virus-induced mortality and the rate at which this material is cycled in soils has yet to be studied. Vital processes such as soil organic carbon and nutrient sequestration depend not only on organic matter production but also on adsorption to mineral particles and the physicochemical environment. Whether or not these properties are altered as a result of viral infection and lysis, and vice versa, is a critical question that must be answered.

Another fundamental gap in our understanding is how the complex interactions between soil properties and viral lysis impact the flow of elements. What are the rates of degradation, availability and proportion allocated to each viral pathway under varying environmental conditions? What is the contribution of viral lysis to soil carbon, nitrogen and phosphorus cycling? How does viral lysis of microorganisms impact soil organic matter stoichiometry? Answering these fundamental questions will require the use of diverse tools and techniques, in particular isolating new virus–host systems and probing how infections impact nutrient dynamics and rates under controlled conditions.

Concluding remarks

Understanding the role of soil viruses has ecological as well as practical implications in terms of food production and soil health. Studies have demonstrated a decrease in soil biodiversity and organic carbon content due to exhaustive agricultural practices[87]. Understanding the roles of viruses in sustaining biodiversity—in the retention of organic matter and their potential as sustainable solutions to crop diseases through pathogen control—could help to provide solutions towards improving soil health. Despite the high abundance of soil viruses, with one estimate suggesting that the top 30 cm of soils globally (except drylands where viral counts are low) contain around 2.3×10^{25} virus-like particles (see Supplementary Tables 1–3), they are not yet robustly considered as part of the soil food web. Soils are essential for a healthy environment, human wellbeing and survival, but our current understanding of the roles and impacts of soil viruses is in its infancy. Therefore, obtaining further knowledge of soil viruses will be pivotal for our understanding of how soils fit into the broader Earth system. By highlighting new directions on the impact of viruses, we hope to provoke new ideas and hypotheses, challenge the research community and, importantly, stimulate further studies on the impact of viruses in soils.

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Author contributions

C.C. conceived of the idea and wrote the first draft of the manuscript. C.C., C.L. and K.M.-J. provided the calculations. C.L., B.A., L.A., Z.B., F.B.C., T.C., C.L.E., J.B.E., L.H., R.B.K., V.L., K.M.-J., T.N., S.S., G.T., A.w.K., R.W., R.A.W., A.W., T.Z. and R.S. read and corrected the manuscript. A.w.K. provided the figures.

Competing interests

The authors declare no competing interests.

Additional information

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