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Estimating the Importance of Viral Contributions to Soil Carbon Dynamics

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ABSTRACT

Biogeochemical models for predicting carbon dynamics increasingly include microbial processes, reflecting the importance of microorganisms in regulating the movement of carbon between soils and the atmosphere. Soil viruses can redirect carbon among various chemical pools, indicating a need for quantification and development soil carbon models that explicitly represent viral dynamics. In this opinion, we derive a global estimate of carbon potentially released from microbial biomass by viral infections in soils and synthesize a quantitative soil carbon budget from existing literature that explicitly includes viral impacts. We then adapt known mechanisms by which viruses influence carbon cycles in marine ecosystems into a soil-explicit framework. Finally, we explore the diversity of virus–host interactions during infection and conceptualize how infection mode may impact soil carbon fate. Our synthesis highlights key knowledge gaps hindering the incorporation of viruses into soil carbon cycling research and generates specific hypotheses to test in the pursuit of better quantifying microbial dynamics that explain ecosystem-scale carbon fluxes. The importance of identifying critical drivers behind soil carbon dynamics, including these elusive but likely pervasive viral mechanisms of carbon redistribution, becomes more pressing with climate change.

1 | Introduction

Microorganisms (including bacteria, archaea, fungi, and protists) are major drivers of terrestrial carbon cycling, controlling the balance between carbon storage in *soil organic matter* (see Box 1 for glossary) and CO_2 release to the atmosphere (Liang, Schimel, and Jastrow 2017 and references therein). A growing body of indirect evidence suggests that the soil *virosphere* is an essential component of soil carbon cycling (Emerson et al. 2018; Graham et al. 2024; Lee et al. 2021; Starr et al. 2019, 2021; Trubl et al. 2018). Microorganisms, like all cellular life on Earth, are subject to viral infection which can significantly impact microbial population dynamics, metabolism, and evolution (Chevallereau et al. 2022; Pratama and van Elsas 2018). As a result, microbially-driven soil processes are undoubtedly altered by viruses, as they are in aquatic ecosystems (Zimmerman et al. 2020). Because microbial growth, metabolism, and turnover have such a strong influence on soil carbon dynamics (reviewed in Sokol et al. 2022), an improved conceptualization of the viral mechanisms that impact microbial processes is required to enable accurate accounting and prediction of soil carbon cycling and sequestration.

BOX 1 | Glossary.

Soil organic matter (*SOM*): The fraction of soil derived from animal, plant, and microbial sources, representing a continuum of decomposing compounds.
Virosphere: the entire complement of viruses; may be applied to all viruses globally or to a pool of viruses associated with a specific host, environment, genome type.
Virome: the metagenome of a viral community (typically from enriching for the virus-size fraction).
Lysis: loss of cell membrane integrity with extracellular release of intracellular material.
Bacteriophage (*phage*): a virus that infects a bacterial host.
Lytic infection: fatal cycle of viral reproduction that disrupts host cell integrity and releases progeny virus particles, typically with a burst of many viruses over a relatively short time interval.
Bioavailable: rapidly degradable compounds; not observed to accumulate (synonymous with "labile"); may or may not be related to chemical reactivity.
Recalcitrant: slowly degradable compounds, whether due to physical, chemical, and/or biological mechanisms; observed to accumulate.
Pseudo/lysogenic infection: non-fatal cycle of viral reproduction where viruses reside inside and replicate with host cells without production of virus particles; viral genome may or may not integrate with host genome.
Necromass: dead microbial biomass, cellular residues, or exuded compounds that accumulates.
Persistent carbon: carbon that resists mineralization and/or oxidation to CO_2 and accumulates (synonymous with "stable" or "durable" carbon).
Latent period: the duration of a viral infection, from adsorption to a host cell until release of new viruses; equivalent to virus generation time.
Burst size: the number of new viruses produced from each virus-infected cell.
Viral Shunt: mechanism of carbon recycling within a microbial community by virus-mediated release of cellular biomass from lytic infection.
Viral Shuttle: mechanism of enhanced carbon storage resulting from lytic viral infection.
Transparent exopolymer particles (*TEP*): gel-like particles formed from extracellular polysaccharides produced by aquatic microorganisms.
Microbial carbon pump (*MCP*): mechanism of carbon storage where microbial metabolism converts a portion of organic material forms that resist further degradation.
Extracellular polymeric substances (*EPS*): hydrated matrix of biopolymers (polysaccharides, proteins, nucleic acids) secreted by some microorganisms.
Inefficient lytic infection: delayed or stalled lytic infection cycle.
Chronic infection: non-fatal cycle of viral reproduction that releases virus particles without loss of host cell integrity, typically with continuous release of few viruses over a relatively long time interval.
Lysogen: host cell with at least one prophage or provirus.
Auxiliary metabolic genes (*AMG*): virally encoded genes that manipulate host metabolism during infection.
Lysogenic conversion: change in host phenotype during lysogenic infection cycle due to expression of prophage- or provirus-encoded gene(s).
Prophage/provirus: viral genome that integrates replicates with host cell genome during lysogeny without production and release of virus particles.

Major conceptual advances regarding the roles of viral infection in carbon cycling have been made in marine and aquatic systems, which we propose can be translated to promote similar progress for terrestrial systems. In oceans, viruses are recognized as significant agents of microbial mortality, on par with protistan grazers (e.g., Fuhrman and Noble 1995). Although empirical virus-induced mortality estimates vary widely across near-shore and off-shore marine ecosystems (Cram, Parada, and Fuhrman 2016; Pasulka, Samo, and Landry 2015; Wilhelm, Brigden, and Suttle 2002), their importance is evident in marine ecology. For example, virus-mediated *lysis* of planktonic cells is estimated to release ~150 Pg carbon per year in marine systems (Fuhrman 1999; Lara et al. 2017; Suttle 2005; Wilhelm and Suttle 1999) an amount that profoundly impacts predictions of global biogeochemical cycling. Virus- and grazer-mediated phytoplankton mortality are now being used to constrain carbon flows in ecosystem-scale marine models (Talmy et al. 2019). Parallels in soil ecology are nascent and have the potential to significantly alter current representations of soil carbon dynamics.

Estimates of viral contributions to soil carbon transformations have been stymied by a range of soil- and virus-specific challenges that have been reviewed thoroughly elsewhere (Bi et al. 2022; Fierer 2017; Jansson and Wu 2022; Pratama and van Elsas 2018; Roux and Emerson 2022; Trubl et al. 2020; Williamson et al. 2017). Briefly, the high diversity and mobility of viral genomes, set against the backdrop of complex microbial communities and microhabitats within the soil matrix, challenge tools typically used for culture-independent investigations and efforts to connect environmental viruses and hosts. Some methodological limitations are now being overcome and the field of soil viral ecology is increasing rapidly. Notable advances include methods for enrichment of virus-sized particles prior to metagenome sequencing (Göller et al. 2020; Santos-Medellin et al. 2021); advances in sequencing approaches to link viruses with hosts (Wu et al. 2023); improvements in sequencing throughput, long-read sequencing, and assembly approaches for higher recovery of viral genomes from soils (Mageeney, Trubl, and Williams 2022; Roux and Emerson 2022; Trubl et al. 2020); and implementation of concentration techniques like tangential flow filtration

that enable manipulative experiments of soil viruses (Braga et al. 2020; Tong et al. 2023). These approaches are generating novel insights into the potential mechanisms in which viruses impact soil biogeochemistry and carbon cycling. To support the interpretation of these emerging data in the context of global processes, there is a pressing need for a revised soil carbon cycling conceptual model that addresses the myriad relationships between viruses and their microbial hosts under various environmental conditions.

Here we propose an updated and virus-explicit conceptualization of soil carbon cycling by integrating knowledge from marine virology and soil ecology. We derive the first known estimates of viral impacts on global soil carbon pools and fluxes, culminating in a quantitative and virus-explicit soil carbon budget. Our proposed budget highlights the potential magnitude and substantial uncertainty of soil viral impacts, and it can guide empirical investigations to refine virus-mediated processes. We then discuss the mechanisms by which viral infection may enhance carbon storage and/or release from soil ecosystems. Finally, we incorporate evolving views on the complexity of viral infection modes into our framework. Throughout, we identify key knowledge gaps and opportunities to validate and quantify the impact viruses may have on global biogeochemistry and climate change via land-atmosphere carbon exchange.

2 | Viral Carbon Pools and Fluxes in Terrestrial Systems

Since viruses can redirect substantial amounts of carbon among various pools and augment their chemical nature (Ankrah et al. 2014; Kuhlisch et al. 2021), we posit that accounting for these mechanisms may dramatically improve our ability to predict and manage soil carbon stocks globally. We expect that incorporating viral influences in soil biogeochemical models will have a transformative impact similar to including microbial physiology in an Earth system model to accurately represent climate feedbacks and improve carbon projections (Wieder, Bonan, and Allison 2013; Wieder et al. 2015). However, the paucity of quantitative estimates limits soil biogeochemical models from representing viral biomass as a carbon pool or viral activity as a mediator of carbon flux, even those that include multiple soil organic carbon (SOC) pools or an explicit microbial component (e.g., Waring et al. 2020; Zhang et al. 2021). To address this gap, we synthesized the first quantitative soil carbon budget from published literature that includes estimates of viral contributions (Figure 1; see Supporting Information for details and Zimmerman and Hofmockel 2024) as a hypothesis for empirical evaluation and a starting point for model integration.

Methods and measurements of soil carbon pools and fluxes vary considerably; therefore, in the Supporting Information, we outline the selection and/or calculation of all values in Figure 1 (Zimmerman and Hofmockel 2024), which represent the current understanding of the global terrestrial carbon budget in our estimation. Briefly, all belowground carbon pools and fluxes shown are estimated to 1 m soil depth and ecosystem-specific estimates were extrapolated in instances where global estimates were unavailable. Viral estimates are based on published data from *bacteriophages* (*or phages*). We acknowledge that other viral types, such as eukaryotic viruses, giant viruses, and RNA viruses, can be highly abundant in soils (e.g., Fischer 2023; Roux and Emerson 2022; Schulz et al. 2018; Swanson et al. 2009; Williamson, Radosevich, and Wommack 2005; Williamson et al. 2017; Wu, Zimmerman, and Hofmockel 2024). Additionally, since lysis is the best understood mechanism for viral influence on microbial carbon cycling, our estimated virus-mediated carbon fluxes assume *lytic* cycles of infection with relatively rapid host mortality. We offer an extension to non-lytic infection cycles below (section "Incorporating complexities of virus–host interactions into soil carbon cycling"), where we identify key knowledge gaps that must be resolved to extend soil carbon budgets that accommodate distinct viral infection modes.

2.1 | Viral Biomass Carbon Pool

Viral biomass carbon is a logical first target for a virus-explicit soil carbon budget because viruses are abundant in terrestrial ecosystems (reviewed in Jansson 2023) and are comprised of *bioavailable* carbon (i.e., most viruses are composed of nucleic acids protected by a protein coat). Published estimates of the abundance of soil bacteriophages globally range from 6×10^{28} (Bar-On, Phillips, and Milo 2018) to 3.8×10^{30} (Cobián Güemes et al. 2016), when adjusted to 1 m soil depth. The carbon in a single bacteriophage varies with genome length and capsid size as well as morphotype (e.g., tailed or non-tailed) (Jover et al. 2014). Here we use 0.06 fg carbon per virus, which has been derived from indirect calculations to approximate a "typical" bacteriophage (Cobián Güemes et al. 2016; Jover et al. 2014), and is within the range of other published conversion factors (0.02 fg carbon (Bar-On, Phillips, and Milo 2018) to 0.2 fg carbon per virus (Suttle 2005; Wilhelm and Suttle 1999)). Together, using the mean of available global estimates, these values lead to a global estimate of ~0.116 petagrams (Pg; 116 billion kg) carbon in soil bacteriophage biomass, with a range from 0.0036–0.228 Pg (using each individual global abundance to establish a range). Our estimate for the carbon in terrestrial bacteriophages is within (Bar-On, Phillips, and Milo 2018) estimate that all bacteriophages, regardless of ecosystem, globally represent 0.6 Pg carbon when applying the same carbon-per-virus conversion factor. While soil viral biomass represents just a fraction of the carbon in bacterial/archaeal biomass, its biogeochemical importance lies primarily in its impact on the distribution of microbial biomass carbon, which requires a better understanding of encounter and infection rates in soil, which are dependent on accurate abundance estimates.

The large range in our estimate of the terrestrial bacteriophage carbon pool reflects variation in the reported estimates of global soil virus abundances (Bar-On, Phillips, and Milo 2018; Cobián Güemes et al. 2016). Since biomes influence the biogeography of soil viruses (Ma et al. 2024), a biome/habitat-specific approach will improve the accuracy of global numbers, similar to the approach used by previous studies to estimate global microbial biomass and growth rates (Gao et al. 2022, 2024; Xu, Thornton, and Post 2013). In addition, the orders-of-magnitude range in this carbon pool increases depending on the conversion factor used to translate viral abundances into carbon mass. A

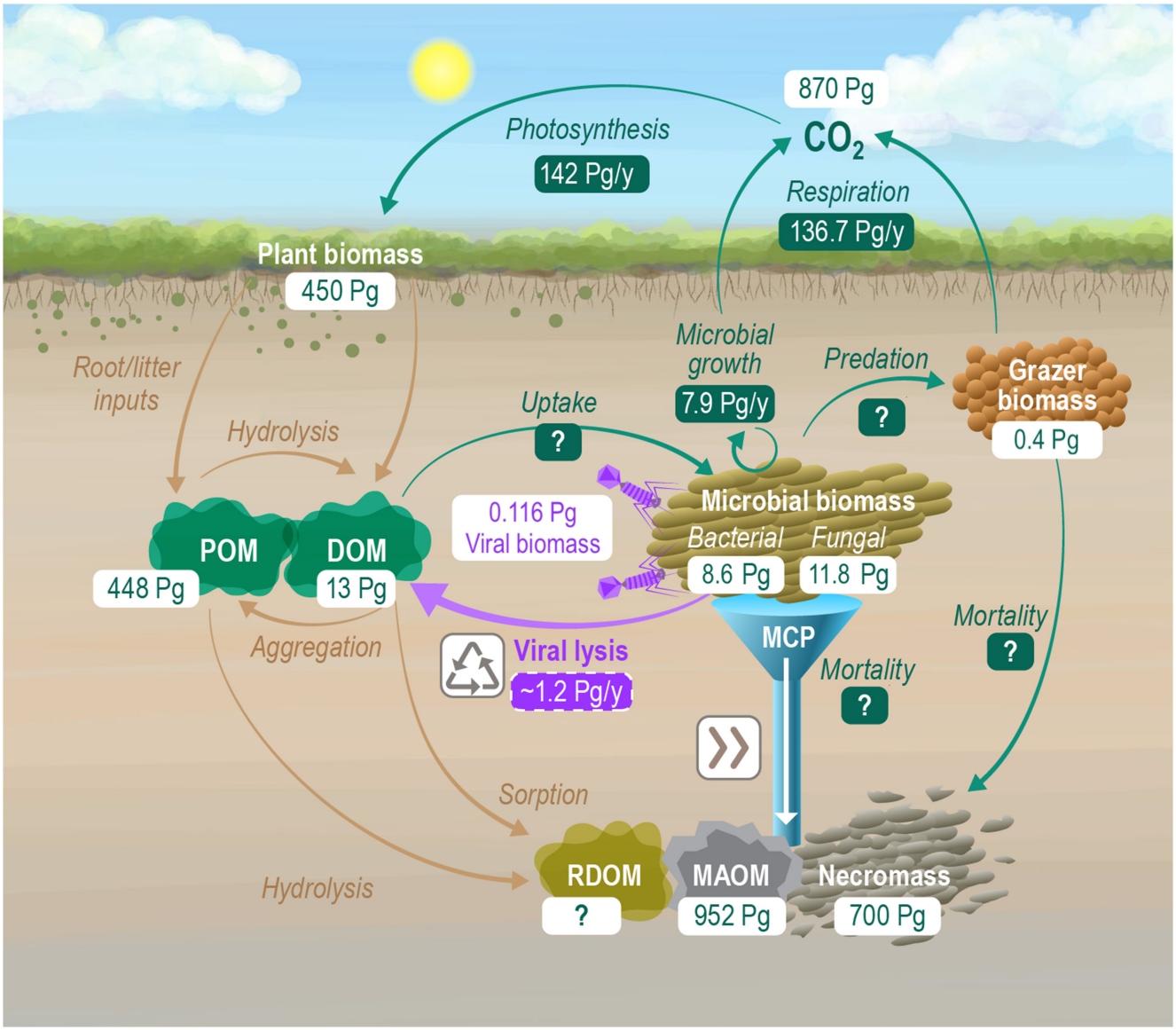

FIGURE 1 | Representing viral pools and fluxes in the terrestrial carbon cycle budget. Current soil biogeochemical models do not explicitly include viral biomass as a carbon pool or viral infection as a mediator of carbon flux, though viral infection and mortality is expected to be a hidden, universal factor (Kuzyakov and Mason-Jones 2018). We estimate that the carbon pool represented by soil viruses globally is on the order of 0.116 Pg carbon (0.0036–0.228 Pg). In addition, approximately 7.9 Pg of bacterial carbon (based on previous estimates of bacterial production, see text for details) could be vulnerable to viral infection and lysis annually on a global scale. Microbial mortality attributable to viral infection is poorly constrained. Here we apply a bacterial mortality rate of 15% due to viral lysis, estimating that viruses could mediate redistribution of 1.185 Pg of bacterial carbon per year to organic matter in soils globally. Since this hypothesis remains to be tested, the associated flux is indicated with a dashed outline. Note that the vertical position within the diagram is not intended to reflect depth distribution. Carbon stocks are shown in white boxes (in units of petagrams, Pg) while fluxes are shown in green boxes (in units of Pg per year).

standard conversion factor inadequately represents the diversity of soil virus types and sizes (e.g., Fischer 2023; Jansson and Wu 2022; Roux and Emerson 2022; Schulz et al. 2018; Swanson et al. 2009; Williamson, Radosevich, and Wommack 2005; Williamson et al. 2017). Broader profiling of the distribution of various viral morphotypes with corresponding carbon contents would enable extension beyond bacteriophage-centric estimates and possibly challenge the assumption that bacteriophage dominate soil viral communities by refining when and where larger viruses may be more important carbon contributors (Schulz et al. 2018; Wu, Zimmerman, and Hofmockel 2024). For example, larger viruses contain more carbon, but are assumed to be so low in abundance that their contribution relative to the bacteriophage pool would be small. Furthermore, most abundance estimates capture only extracellular DNA viruses, excluding viruses with RNA genomes and the non-trivial proportion of viruses that reside inside cells during *pseudo/lysogenic infection* cycles (Liang et al. 2020; Williamson et al. 2007), which would not directly contribute to the viral carbon pool but indirectly influence microbial carbon cycling. Advances in imaging of viruses, surveys of virus types across different biomes, and improved techniques to estimate the carbon in a single bacteriophage are needed to constrain these estimates but are labor intensive.

2.2 | Potential Virus-Mediated Carbon Flux

Viral infection and lysis contribute to soil carbon fluxes through the turnover of microbial biomass. Thus, contributions of lytic viral infections to soil carbon cycling are directly related to the size and productivity of the microbial biomass pool that is vulnerable to infection. Soil microbial biomass represents one of the largest carbon pools on Earth, with estimates ranging from 14.6 to 23.5 Pg carbon at 0–1 m depth (He et al. 2020; Serna-Chavez, Fierer, and Van Bodegom 2013; Wang et al. 2017; Whitman, Coleman, and Wiebe 1998; Xu, Thornton, and Post 2013) (mean = 20.4 Pg, sd = 3.6 Pg, $n = 5$ studies). Turnover of this microbial carbon pool into *necromass* (Buckeridge, Creamer, and Whitaker 2022) represents an important component of stabilized SOC (e.g., 33%–62% in temperate soils; Liang et al. 2019), highlighting a substantial putative pathway for viral impacts on soil carbon cycling.

Although fungal biomass dominates the soil microbial carbon pool (He et al. 2020; Joergensen and Wichern 2008), with an estimated contribution of ~60% in topsoil globally (Bar-On, Phillips, and Milo 2018), and fungal viruses are abundant in soil (Starr et al. 2019; Wu, Bottos, et al. 2022; Wu, Zimmerman, and Hofmockel 2024), there is no evidence of lytic viral infections in fungi (and often no detectable changes in host phenotype; Ghabrial et al. 2015; Sutela, Poimala, and Vainio 2019). Therefore, we estimated potential virus-mediated carbon fluxes in soils from bacterial/archaeal biomass only (~42% of living soil microbial biomass is non-fungal; Bar-On, Phillips, and Milo 2018). We recognize that virus-mediated shifts in fungal communities may have unquantified indirect influences on SOC accumulation, and the sparse literature on this subject points to a knowledge gap for future research.

Whitman, Coleman, and Wiebe (1998) estimated a global prokaryotic (bacterial/archaeal only) biomass production rate of 7.9×10^{28} cells per year in soils (adjusted to 1 m depth, see Supporting Information for details) using a conservative average generation time of 2.5 years in soil. Although microbial growth is generally expected to be slower in soils than seawater, this generation time estimate is even longer than the days-to-weeks turnover times compiled by (Rousk and Bååth 2011) or community-level rates determined by lipid-SIP (Caro et al. 2023). Assuming an average mass of 100 fg carbon per cell (Bolter et al. 2002; Whitman, Coleman, and Wiebe 1998), the generation time from (Whitman, Coleman, and Wiebe 1998) translates to at least 7.9 Pg of soil bacterial/archaeal carbon per year that is vulnerable to viral infection. This aligns with the standing stock estimate of ~8.6 Pg carbon in non-fungal microbial biomass shown in Figure 1. Fluxes like this are critical parameters that govern biogeochemical cycling and yet are notoriously challenging to quantify, thus motivating a collective focus on improved quantification of flux parameters.

The proportion of bacterial, archaeal, and fungal mortality in soil attributable to viral infection is virtually unknown (Camenzind et al. 2023), and therefore, the amount of carbon released through viral lysis of microbial cells is a key unknown for virus-explicit models. The few pioneering studies that have attempted to empirically quantify virus-mediated mortality in soils suggest that the frequency of visibly infected bacteria (i.e., cells in the final, irreversible stages before lysis), may be higher in terrestrial than aquatic systems (Binder 1999; Bowatte et al. 2010; Proctor and Fuhrman 1990; Takahashi et al. 2011, 2013). However, modeling mortality from visible infection frequency critically depends on assumptions about infection *latent periods* (Binder 1999), which remain uncharacterized for soil viruses. To our knowledge, the only published estimate of virus-mediated mortality in soil based on changes in virus and (potential) host abundances relied on qPCR of 16S rRNA genes for bacterial/archaeal mortality and viral metagenomics for estimates of viral abundances (with several stated assumptions), to infer virus-mediated prokaryotic mortality of 0.25%–46.6% following a "wet-up" event (Nicolas et al. 2023). Although this mortality estimate carries massive uncertainty, it overlaps with reports that on average 10%–20% of marine bacteria are lysed daily (Suttle 1994), within a background of large spatial and temporal variation (Cram, Parada, and Fuhrman 2016; Pasulka, Samo, and Landry 2015; Vincent and Vardi 2023; Wilhelm, Brigden, and Suttle 2002). The orders-of-magnitude range of the Nicolas et al. (2023) estimate reflects uncertainty in the *burst sizes* of soil viruses (Williamson et al. 2008) and underscores a pressing need for more empirical studies into basic infection parameters of soil viruses.

These published estimates provide a basis for incorporating virus-mediated carbon fluxes into terrestrial ecosystem models. As a starting point for model incorporation, we applied a virus-mediated mortality rate of 15%, chosen to represent the center of reported soil and marine values. We recognize that the true mortality rate will fluctuate with the time scale considered (Nicolas et al. 2023) and several environmental factors that may facilitate or hinder virus–host interactions within the soil matrix (e.g., drought; Wu et al. 2023), as well as microbial community composition (e.g., variation in infection efficiency across virus–host pairs; Howard-Varona et al. 2018) and metabolic activity (e.g., release from dormancy; Van Goethem et al. 2019). Using the global annual soil bacterial/archaeal biomass production rate detailed above that captures the overall slow community-level growth of soil microorganisms (7.9 Pg of soil bacterial/archaeal carbon per year) and assuming steady state (Blazewicz, Schwartz, and Firestone 2014), 15% mortality yields an estimate of ~1.2 Pg terrestrial prokaryotic carbon per year transformed by viral lysis into organic detritus across all global soils. This estimate constitutes approximately ~0.85% of all terrestrial photosynthetically fixed carbon annually (based on an estimated 142 Pg carbon per year incorporated into plant biomass; Canadell et al. 2021). For comparison, lytic viruses in deep-sea sediments are estimated to redistribute 0.37–0.63 Pg carbon per year globally (Danovaro et al. 2008) and 6%–26% of marine photosynthetically fixed carbon is released by viruses on an annual basis (Fuhrman 1999; Weinbauer 2004; Wilhelm and Suttle 1999), with the important distinction that primary producers are susceptible to viral lysis in oceans but not in soils. Unicellular algae are the dominant microbial eukaryotes in oceans and viral infections of algal blooms can cause cell lysis on a scale that can be observed from space (Lehahn et al. 2014). Thus, a key point of contrast between aquatic and terrestrial systems in terms of viral contributions to carbon cycling is the degree to which viral infection impacts the eukaryotic community. The ecological impacts of fungal viruses in soil are not well understood and represent a key research opportunity.

Efforts to empirically test our estimates of terrestrial virus-mediated carbon flux are bound to find that the in situ mortality attributed to viral lysis and associated consequences for carbon cycling are highly variable across conditions that constrain or enable encounters within the soil matrix (discussed in Chevallereau et al. 2022; Kuzyakov and Mason-Jones 2018; Williamson et al. 2017) and influence viral infection strategies (discussed below). A key research priority is to refine basic infection parameters, such as burst size and latent period, for soil viruses under field-relevant conditions to make progress toward reducing the orders-of-magnitude uncertainty in the first estimates provided here. Additional progress can be made towards incorporating explicit viral pools and fluxes into ecosystem-scale carbon models by working to adjust our estimates for specific biomes. Eventually, establishing which environmental factors are most predictive of viral infection and lysis (vs. other sources of mortality) across terrestrial ecosystems will help identify which biomes may be more susceptible to higher viral impacts under current and future climates.

3 | Viral Mechanisms of Soil Carbon Storage and Release

Beyond constraining the large uncertainty of viral carbon pools and fluxes in soils, it is important to understand the mechanisms by which these processes occur and their vulnerabilities to future changes in the global climate. Perceptions about the roles that viral ecology might play in soil carbon cycling stem from decades of aquatic research that have established viruses as key contributors to ecosystem dynamics and biogeochemical cycles (Locke et al. 2022; Vincent and Vardi 2023; Zimmerman et al. 2020). The marine viral ecology field has observed, tested, and refined several mechanisms by which viral infection impacts long-term carbon storage in the oceans, which are frequently invoked to motivate parallel studies in terrestrial habitats. Here, we assess the facets of these mechanisms that may translate to soil habitats and review evidence for the conditions that influence their contributions to soil carbon dynamics.

3.1 | Mechanisms of Viral Carbon Cycling in Oceans

Viruses interact with marine carbon cycling through the *viral shunt* and *viral shuttle* that affect the vertical flux of carbon in microbial biomass (Figure 2 inset). The viral shunt (Fuhrman 1999; Wilhelm and Suttle 1999) holds that infection and lysis of microbial hosts by viruses shifts (or "shunts") carbon in microbial biomass from particulate organic matter to primarily dissolved lysates (Fuhrman 1992; Weinbauer, Chen, and Wilhelm 2011). By lysing a portion of the microbial community, the viral shunt reduces resource competition and simultaneously regenerates bioavailable carbon and nutrients in surface waters to stimulate carbon recycling by the remaining community, delaying the downward export of carbon to the deep ocean (Gobler et al. 1997; Middelboe, Jørgensen, and Kroer 1996; Motegi et al. 2009; Riemann and Middelboe 2002; Weinbauer, Chen, and Wilhelm 2011). The viral shuttle posits that viral infection accelerates carbon storage through the release of "sticky" organic polymers upon lysis, such as *transparent exopolymer particles* (*TEP*), that act as biological binding agents to enhance aggregation (Vincent et al. 2023; Yamada et al. 2018) and sinking (or "shuttling") to the deep ocean for sequestration (Proctor and Fuhrman 1991; Sullivan, Weitz, and Wilhelm 2017; Weinbauer 2004; Weinbauer et al. 2009).

In addition to shunting carbon away from sinking/storage or shuttling carbon toward sequestration in the deep ocean, viruses also impact marine carbon dynamics via the *microbial carbon pump* (*MCP*). While many cytosolic compounds released during lysis appear to be rapidly degraded (Gobler et al. 1997; Middelboe, Jørgensen, and Kroer 1996; Middelboe and Jørgensen 2006; Riemann and Middelboe 2002), a small, although unquantified, proportion of cellular lysates are not rapidly reused and contributes directly to the MCP (Jiao et al. 2010; Weinbauer, Chen, and Wilhelm 2011) – a "horizontal" mechanism of carbon stabilization where a portion of primary production is metabolized into microbial biomass components (e.g., muramic acid, LPS) that persist (Jiao et al. 2010, 2011; Jiao and Zheng 2011; Polimene et al. 2016). Viral infection may accelerate the MCP through enhanced carbon recycling (i.e., released lysates support growth of the surviving community), per the viral shunt (Figure 2 inset), potentially leading to a net increase in stabilized carbon by increasing the ratio of slowly (persistent) vs. rapidly (bioavailable) degradable carbon over time (Weinbauer, Chen, and Wilhelm 2011). The marine MCP framework has recently been adapted for soils (Kästner and Miltner 2018; Liang 2020; Liang, Schimel, and Jastrow 2017) to describe the roles microbial growth and metabolism have in shaping the persistent soil carbon pool through necromass production (Kästner et al. 2021; Liang et al. 2019; Miltner et al. 2012; Rempfert et al. 2024).

3.2 | Translation of Virus-Mediated Marine Carbon Cycling to Terrestrial Environments

Although virus-mediated cycling of carbon in soils has been previously proposed (Kuzyakov and Mason-Jones 2018; Liang et al. 2023; Williamson et al. 2017), empirical evidence is just now emerging. The first empirical evidence of active viral replication in soils tracked ^{13}C from labeled rice cells into the major capsid protein genes of T4-like phages (Li et al. 2013). More recently, SIP-metagenomics demonstrated incorporation of $^{13}CO_2$ into circularized soil phage genomes within the context of a native soil community, indicating active lytic infections during the experiment (Starr et al. 2021). A similar approach took this a step further by linking the proliferation of phage genomes to a decline in putative host abundances in soils amended with ^{13}C-labeled organic carbon substrates, implicating not just viral replication but associated host mortality (Barnett and Buckley 2023). Recent microcosm experiments have generated empirical support for the viral shunt and associated acceleration of the MCP in soils, which is the first direct evidence for viral augmentation of soil carbon cycling. Addition of phage suspension to soil microcosms increased signals of slowly degradable organic matter (Tong et al. 2023) or microbial necromass residues (Liang et al. 2024) and shifted CO_2 production (Albright et al. 2022; Osburn et al. 2024; Tong et al. 2023). These studies are notable for quantifying viral contributions to carbon cycling in sand and/or processed soil to

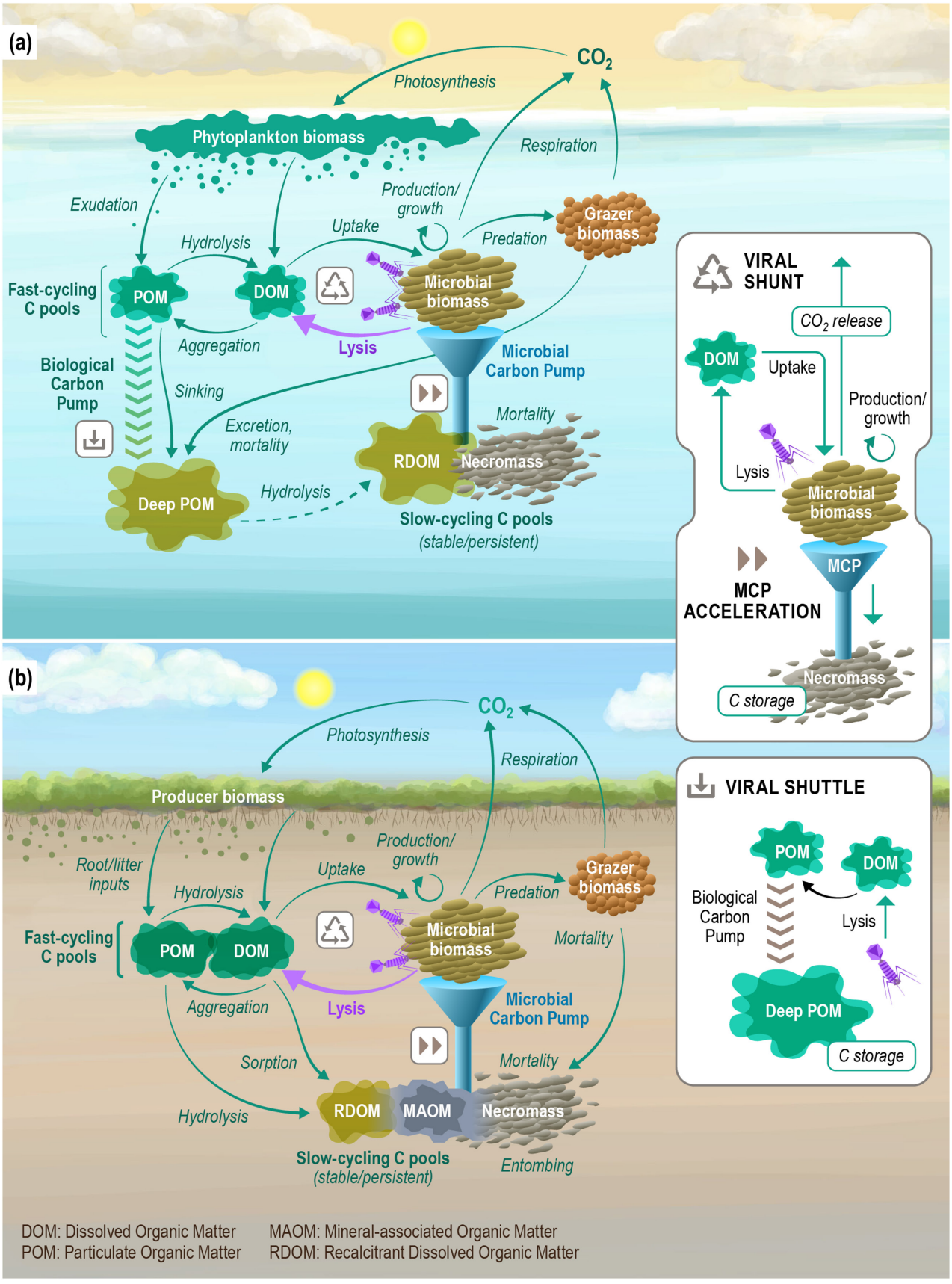

FIGURE 2 | Legend on next page

FIGURE 2 | Translation of virus-mediated marine carbon cycling (a) to terrestrial environments (b). (Inset) Microbial carbon cycling can be augmented by viral infection through the viral shunt, viral shuttle, and/or acceleration of the Microbial Carbon Pump (MCP). When viruses infect and lyse microbial cells, carbon in microbial biomass is redistributed to the dissolved phase, generating bioavailable carbon and nutrients while reducing resource competition within the surviving community. Viral shunting of carbon that would otherwise contribute to slow-cycling pools through vertical transport and sequestration (Biological Carbon Pump, BCP), death and necromass formation (MCP), or other forms of physical/chemical protection (e.g., mineral association), instead enhances microbial growth and CO_2 production, if it is accessible. Enhanced recycling of carbon, catalyzed by the viral shunt, is likely to accelerate turnover of microbial biomass and increase the rate of necromass formation through the MCP. In other cases, viral lysis may release sticky organic compounds (e.g., extracellular polymeric substances, EPS) that can increase the rate of aggregation and sinking or occlusion, "shuttling" carbon toward long-term storage. Numerous factors, including microbial growth efficiency, will determine the net effect of these mechanisms on the balance of carbon storage vs. release. Note that the vertical position within (b) is not intended to reflect depth distribution.

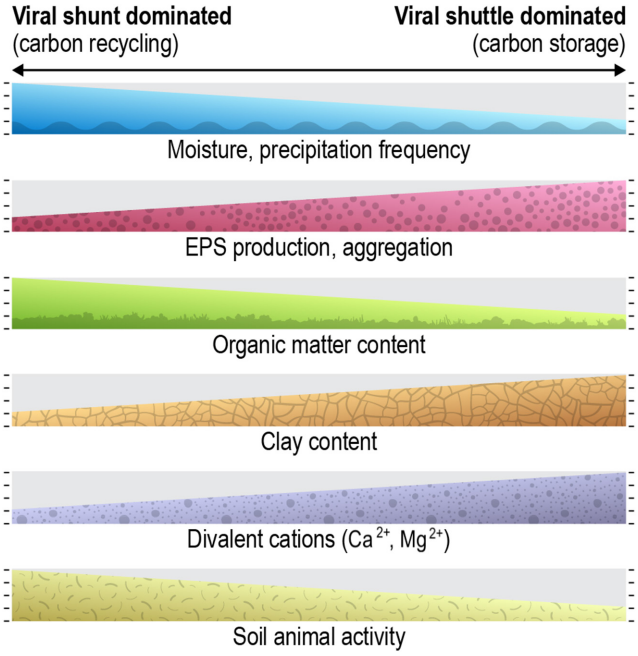

FIGURE 3 | Examples of environmental factors that may influence mechanisms of virus-mediated soil carbon cycling. The relative importance of carbon recycling by the viral shunt and storage mediated by the viral shuttle, depends on multiple features of soil habitats that interactively influence mobility/accessibility of organic matter released from viral lysis. For simplicity, we show each factor independently. Evidence to support depicted trends is reviewed in Kimura et al. 2008; Kuzyakov and Mason-Jones 2018; Marschner and Kalbitz 2003; Sollins, Homann, and Caldwell (1996). This figure was inspired by Figure 3 from Locke et al. (2022).

retain some of the key features that distinguish terrestrial and aquatic habitats and that affect predictions for the relative importance of each viral mechanism across systems. Since specific soil properties and their impacts on viral distribution and infections in soils have been reviewed extensively elsewhere (Kimura et al. 2008; Kuzyakov and Mason-Jones 2018), here we highlight the soil structure and mineralogy for their potential impact on viral shunt and shuttle dynamics.

We hypothesize that constrained diffusion and enhanced mineral sorption in soil ecosystems may dampen the recycling of cellular lysates generated by virus-mediated shunting of carbon from microbial biomass into the bioactive pool. Compared to relatively well-mixed aqueous environments, translocation of carbon is greatly reduced in soils where access to organic matter exerts a strong control over biodegradation (Marschner and Kalbitz 2003; Sollins, Homann, and Caldwell 1996). We expect viral shunt contributions to soil carbon cycling to be highly localized in "hotspots" of microbial activity such as soil pores (Kuzyakov and Blagodatskaya 2015), but that these signals may be diluted at broader spatial (e.g., soil profile, ecosystem) and temporal (e.g., seasonal, annual) scales (Smercina, Bailey, and Hofmockel 2021). Pairing approaches that could profile viral transformation of carbon at the nano- or micro-scales (e.g., nanoSIMS) (Mueller et al. 2012) with advanced characterization of soil structural properties (e.g., porosity and pore size distribution by X-ray CT) (Ghosh et al. 2023), could advance efforts to scale estimates of virus-mediated carbon turnover to soil profile and eventually ecosystem levels.

Additionally, we hypothesize that viral shuttling of microbial biomass carbon away from active circulation may be enhanced in soil relative to marine ecosystems because the large surface area of soil particles may elevate rates of sorption (reviewed in Kimura et al. 2008), aggregation, and carbon storage. Importantly, the ecologically relevant impact of the viral shuttle—enhancing carbon sequestration—is similar between marine and terrestrial systems even though the underlying processes differ (i.e., translocation in marine systems vs. physical/chemical inaccessibility in soils). Association with minerals and aggregate occlusion protect a portion of the soil carbon pool from further mineralization, leading to long-term storage (Jastrow 1996; Lajtha et al. 2018; Liang, Schimel, and Jastrow 2017; Schimel and Schaeffer 2012). *Extracellular polymeric substances* (*EPS*) produced in soils, which form the basis of biofilms (Cai et al. 2019), are resistant to degradation and have a gel-like consistency with strong links to aggregate formation and soil structural integrity (Costa, Raaijmakers, and Kuramae 2018; Redmile-Gordon et al. 2020; Sher et al. 2020). Unlike TEP in marine systems, which has an established association with viral infection and enhanced aggregation and sinking for specific marine organisms (Laber et al. 2018; Lønborg, Middelboe, and Brussaard 2013; Vincent et al. 2023; Yamada et al. 2018), links between viral infection and EPS production in soils are variable (reviewed in Fernández, Rodríguez, and García 2018). Further work to untangle the factors driving variability in virus-EPS linkages could help determine the circumstances under which EPS could be used as an indicator of the viral shuttle in soils.

The relative importance of different viral mechanisms to soil carbon cycling is likely to fluctuate with seasonal factors like precipitation—where a "wet-up" can stimulate substantial lysis (Nicolas

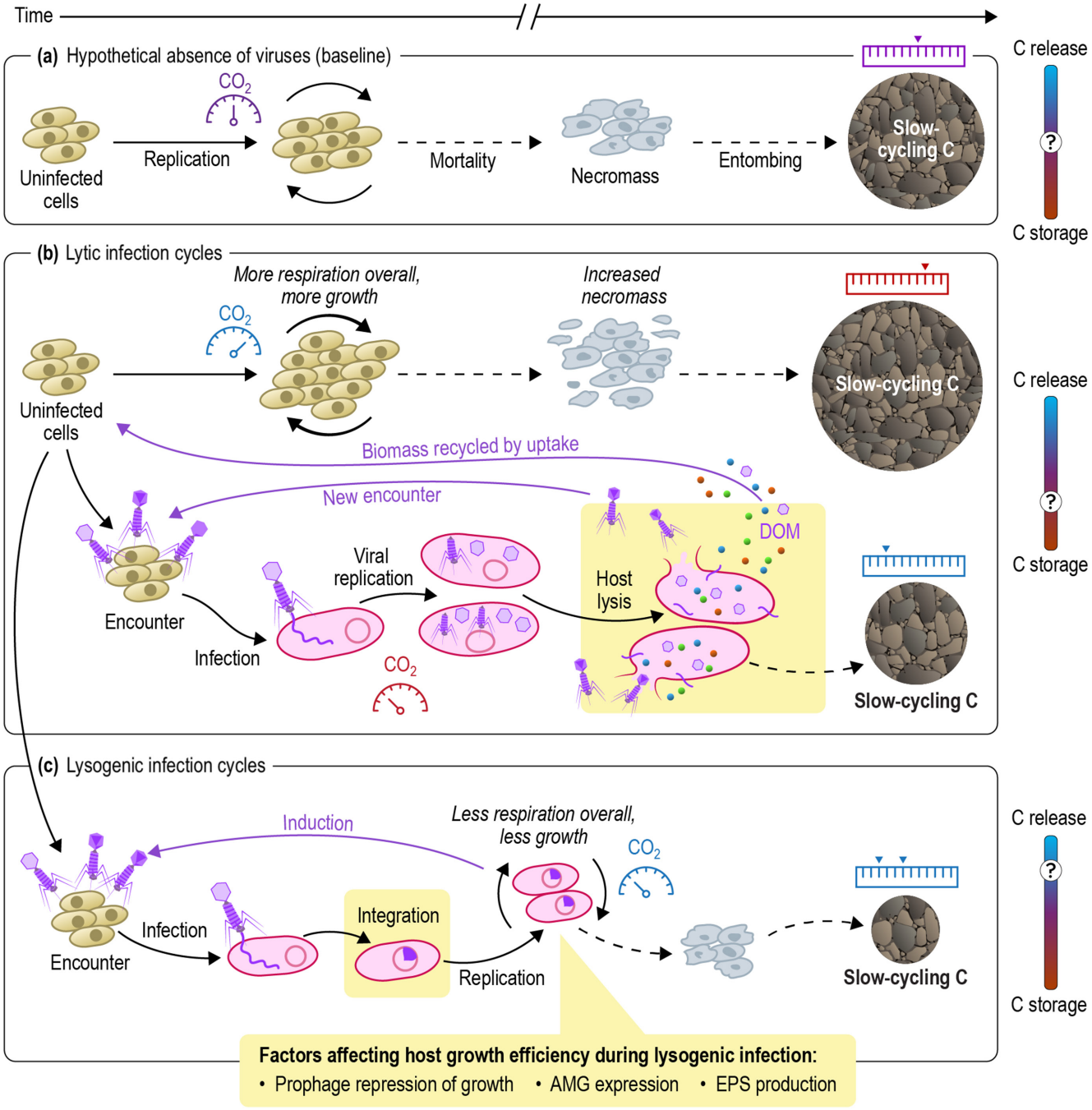

FIGURE 4 | Legend on next page

et al. 2023; Van Goethem et al. 2019)—and vary across ecosystems (Albright et al. 2022; Osburn et al. 2024) resulting from differences in soil parent material and climate, potentially reflecting observed patterns in soil virus diversity and composition (Ma et al. 2024). Figure 3 provides select examples of specific environmental factors that may influence the dominant mechanism of virus-mediated soil carbon cycling by changing the mobility/accessibility of organic matter released from viral lysis. For example, alleviating drought can increase diffusive transport while clay and cations enhance adsorption of virus particles and released organic matter (reviewed in Kimura et al. 2008; Kuzyakov and Mason-Jones 2018; Marschner and Kalbitz 2003; Sollins, Homann, and Caldwell 1996). Temperature (reviewed recently in Jansson and Wu 2022) and pH (Bi et al. 2021; Lee et al. 2022; Liang et al. 2021; Liao et al. 2022; Narr et al. 2017; Williamson et al. 2017) are other environmental factors that have significant direct (i.e., by affecting extracellular survival, infection mode, infection latent period and/or burst size) and indirect (i.e., by influencing microbial host metabolism and/or community composition) effects on soil virus communities. The effects of pH on sorption are likely to be virus- and site-specific depending on soil mineralogy since pH influences the charges on virus and soil particles (Kimura et al. 2008; Williamson et al. 2017). Higher temperatures may accelerate the timescale of virus-mediated carbon cycling (Wang et al. 2022) by shortening lytic cycles (as observed for aquatic cyanophages; Yadav and Ahn 2021), though there is a known tradeoff with viral persistence in soil (reviewed in Jansson and Wu 2022; Kimura et al. 2008; Williamson et al. 2017).

FIGURE 4 | Conceptual model for the potential impact of viral infection mode on soil carbon fate. (a) Microbial cells produce both CO_2 and biomass during replication/growth, and eventually contribute to soil carbon storage following death (necromass formation) and mineral association (entombing). The CO_2 dial and slow-cycling carbon ruler are intended to represent "baseline" production in the hypothetical absence of viral infection as a point of comparison. The carbon balance thermometers on the right represent the hypothesized net impacts (uncertainty reflected by "?" on each thermometer) of each viral infection mode on overall flux of carbon in the system, relative to (a). Whether viral infection tips the balance toward net carbon release or storage depends on the time frame considered (here, we represent hypothesized long-term dynamics of multiple generations / infection cycles) and myriad ecosystem-specific factors. Ultimately, the net outcome will depend on bacterial growth efficiency during viral infection (the balance of respiration and biomass production). (b) Lytic infection cycles release new viruses upon host lysis along with a mixture of rapidly degradable cellular compounds, which can stimulate metabolism and CO_2 production in populations of uninfected cells (viral shunt), accelerate the rate of necromass production, and increase microbially-derived slow-cycling carbon (MCP), as long as the lysis products are accessible to other constituents of the microbial community. These virus-mediated shifts in fluxes may be partially offset by reduced necromass and slow-cycling carbon production from infected/lysed microbial cell populations, depending on relative population sizes and contributions to necromass. (c) During lysogenic infection cycles, viruses generally integrate into the host genome and replicate with the host for multiple generations. Cells harboring lysogenic viruses may express distinct phenotypes from uninfected cells and have been shown to exhibit virus-directed suppression of host growth rate or reduced growth efficiency, affecting overall CO_2, biomass, and necromass production. In all cases (lytic and lysogenic infection cycles), viral infection may alter soil microbiome composition, community interactions, and metabolism. While these impacts are not denoted in the figure, they represent additional indirect pathways of viral contributions to soil carbon cycling. AMG, auxiliary metabolic genes; DOM, dissolved organic matter; EPS, extracellular polymeric substances.

Additionally, viral activity can indirectly influence the efficiency of carbon storage in soils through modulation of microbial community composition (i.e., bacterial vs. fungal abundances and/or interactions; Albright et al. 2022; Braga et al. 2020; Liang et al. 2024; Liu et al. 2023), which affects the persistence of the resultant necromass pool (Domeignoz-Horta et al. 2021). Such effects could be further augmented by a range of community ecology dynamics that impact microbial trait distributions but vary across soil ecosystems, including virus–host specificity, density-dependent virus–host interactions (Silveira, Luque, and Rohwer 2021), the degree of community functional redundancy, and community assembly processes. Determining when enhanced respiration stimulated by the viral shunt compensates for the accelerated production of microbial biomass and slow-cycling organic carbon through the MCP remains an open question. The efforts toward evaluating the net movement of carbon could help establish biological and environmental conditions that promote carbon sequestration.

4 | Incorporating Complexities of Virus–Host Interactions Into Soil Carbon Cycling

4.1 | Continuum of Viral Infection Modes

Beyond the multiple generalized mechanisms by which viruses contribute to soil carbon cycling (Figure 2), various possible viral infection modes (reviewed in Correa et al. 2021; Hobbs and Abedon 2016) further complicates efforts to model and predict viral impacts. Both the viral shunt and shuttle concepts are largely derived from observations of lytic infection, which is the most well-understood infection mode (Figure 4b). However, viral infection modes vary in the duration of an infection cycle, the number of progeny released, and the fate of the host cell (Correa et al. 2021). Lytic infections, for example, are classified as efficient (i.e., rapid infection and host lysis) or *inefficient* (i.e., stalled viral release and host lysis), and variation across this continuum is likely to impact the amount and rates of carbon fluxes. By contrast, lysogenic infections are multi-generational associations of integrated virus–host genomes without fatal release of new viruses, which contrasts with the direct release of microbial carbon from lysis in that lysogeny indirectly impacts carbon cycling through augmented host metabolism (see Box 2 for specific examples). *Chronic infections* are in between lytic and lysogenic infection cycles (i.e., slow viral release without host lysis) and may result in more moderate impacts on soil carbon cycles. Increasing recognition of the prevalence (e.g., Brum et al. 2016; Ghosh et al. 2008; Howard-Varona et al. 2017; Liang et al. 2020; Silveira, Luque, and Rohwer 2021; Srinivasiah et al. 2008; Williamson et al. 2007, 2008) and potential fitness advantages of lysogeny (Weitz et al. 2019) suggest that non-fatal infection strategies carry distinct consequences for carbon cycling and are equally if not more ecologically relevant to soil ecosystems than lytic infections.

We hypothesize that by foregoing cell lysis, alternative infection strategies may dampen remineralization of carbon via the viral shunt. Beyond this broad hypothesis, the net consequences for carbon flux from alternative infection modes are difficult to predict due to a complex suite of factors operating simultaneously at the population and community scales. At the population level, the allocation of cellular carbon to continually release low levels of viral biomass may decrease host growth efficiency, leading to a relative increase in respiration per unit cellular biomass within the infected host population (Figure 4c). At the community level, cells harboring lysogenic viruses (*lysogens*) may express distinct phenotypes from uninfected cells, including suppressed host growth rates (Chen et al. 2005; Paul 2008) and/or novel functions (Box 2) that could impact competition and community dynamics.

In addition to considering the fate of the host cell (i.e., lysed or intact), the duration of infection is critical to predicting the potential impacts of different infection modes on soil carbon cycling. Each of the different infection strategies operates on distinct time scales (Correa et al. 2021) that directly relate to rates of carbon flux. How infection duration impacts carbon pool sizes, for example through suppressing microbial decomposition of SOC or enhancing necromass formation, remains an open question. It may be best addressed through modeling approaches that can capture the complex system dynamics

BOX 2 | Viral Alterations of Host Phenotype Relevant to Carbon Cycling.

All infection strategies fundamentally alter the host cell (Forterre 2013; Rosenwasser et al. 2016). In the case of lytic infections, host metabolism is rapidly redirected toward the production of viral building blocks (nucleic acids, proteins, and lipids), and microbial biomass is converted into more bioavailable organic matter (including new viruses). Lytic marine viruses have been shown to carry AMGs that overcome metabolic bottlenecks during infection; for example, to support the energy (photosynthetic electron flow; Thompson et al. 2011), reducing power (Hurwitz, Hallam, and Sullivan 2013), or nitrogen demands (Monier et al. 2017; Waldbauer et al. 2019) of viral genome replication and protein synthesis. Such changes in host phenotype (specifically, elevated metabolic activity) during lytic infection, although ephemeral, would aggregate to decrease host growth efficiency during the brief time that assimilated carbon is redirected from biomass to virus production. AMGs harbor substantial potential to impact microbial metabolism and cycling of organic matter, yet it remains unclear whether the vast majority of AMGs encode functionally active proteins (with a few exceptions: Emerson et al. 2018; Monier et al. 2017; Wu, Smith, et al. 2022). Furthermore, the magnitude of AMG contributions to in vivo metabolic rates as well as during lysogenic infection cycles is extremely challenging to quantify and has only been well documented for marine cyanophage photosynthetic proteins to date (e.g., Puxty et al. 2018). With those caveats in mind, we highlight a few examples of AMGs that are particularly relevant to soil carbon dynamics and have the potential to influence the balance of carbon storage or release in terrestrial systems.

AMGs encoding carbon-degrading enzymes are commonly found in the genomes of soil viruses (Bi et al. 2022; Emerson et al. 2018; Jin et al. 2019; Trubl et al. 2018; Wu et al. 2021) and have the potential to enable the decomposition of carbon sources that are otherwise inaccessible to the host organism. For example, virus-encoded glycoside hydrolases in permafrost may contribute to the degradation of plant litter and release of bioavailable substrates that stimulate microbial growth (Emerson et al. 2018). The recent discovery of a functional viral chitosanase from soil (Wu, Smith, et al. 2022) lends support to the hypothesis that carbon-degrading enzymes carried by soil viruses may improve host fitness by expanding access to resources, particularly during longer-term lysogenic infections (Wu et al. 2021). This provides a direct mechanism for viral influence over carbon storage through mobilization of genes with the potential to increase carbon turnover from SOC. Despite substantial methodological challenges, the realized impact of viral AMGs on carbon cycling is an active area of research that may have significant impacts on soil biogeochemistry.

The expression of virus-encoded sporulation genes likewise has the capacity to augment the nature of the microbial biomass carbon pool and associated fluxes. In soils, sporulation and dormancy are common mechanisms for surviving drought and desiccation by ramping down microbial metabolism (Lebre, De Maayer, and Cowan 2017), pausing the dynamic churn of active carbon cycling through microbial biomass until favorable conditions return. Genes involved in sporulation have been found in viral sequences from permafrost (Trubl et al. 2018), hyperarid deserts (Hwang et al. 2021), and grassland soils (Wu et al. 2021). In hyperarid deserts, virally encoded sporulation genes are hypothesized to enhance viral fitness by aiding host survival through extreme desiccation (Hwang et al. 2021). Whether this functions similarly to a viral shuttle mechanism for carbon storage depends on the duration of dormancy, which can last for years or decades (Van Vliet 2015). In comparison to the refuge that sporulation can provide for lysogenic viruses in extreme conditions, evidence from viruses infecting *Bacillus*, a ubiquitous soil bacterium, indicates that some viruses have the capacity to keep microbial carbon in the active pool by expressing virus-encoded sigma factors that reduce spore yield (Schuch and Fischetti 2009; Schwartz, Lehmkuhl, and Lennon 2022). Additional work is needed to disentangle the specific contexts that favor viral regulation of host metabolism through sporulation and other dormancy-related strategies that may impact soil carbon cycling.

Finally, virus-conferred changes in host phenotype during lysogenic cycles, termed *lysogenic conversion*, are presumed to promote survival of the infected host, thereby ensuring survival of the virus. The production of EPS during biofilm formation is an intriguing example of lysogenic conversion that has a direct correlation to carbon storage. Viruses employ multiple mechanisms to influence host biofilm phenotype (Fernández, Rodríguez, and García 2018) and factors driving observed variation in EPS production and biofilm formation across virus–host pairs are not fully understood. *Prophages* have been shown to enhance biofilm formation in *Bacillus anthracis* (Schuch and Fischetti 2009) and *E. coli* (Wang et al. 2010), which could function like the viral shuttle and lead to enhanced carbon storage, but through occlusion rather than sinking. By contrast, prophage appears to downregulate EPS production and virulence in the bacterial plant pathogen *Ralstonia solanacearum*, but improve survival of the lysogen by outcompeting other strains (Ahmad, Stulberg, and Huang 2017). Given the prevalence of biofilms as a microbial survival strategy in soil and strong links between EPS production, aggregate formation, and soil structural integrity (Costa, Raaijmakers, and Kuramae 2018; Redmile-Gordon et al. 2020), continuing to address this knowledge gap is a critical step towards incorporating viral mechanism of carbon transformations into current representations of soil carbon cycling.

that could alter net carbon movement. In line with this, early experimental evidence for lytic infection strategies points to the importance of considering timescale when extrapolating virus–host interactions to soil carbon mineralization. In the near term (days), addition of viruses to soils or soil bacteria can reduce CO_2 production, presumably by directly effecting microbial metabolism, but elevate CO_2 production over longer timescales (>month), with site-specific responses (Albright et al. 2022; Osburn et al. 2024; Tong et al. 2023; Wang et al. 2022). CO_2 emissions may be augmented for weeks to months from the extracellular release of enzymes during viral lysis (Blankinship and Schimel 2018; Kéraval et al. 2018; Kuzyakov and Mason-Jones 2018).

4.2 | Conceptual Model for Relating Distinct Viral Infection Modes to Soil Carbon Cycling

Based on the literature synthesized above, we present a conceptual model describing potential viral contributions to soil carbon dynamics with explicit consideration of the breadth of infection modes and associated modifications of host phenotype

(Figure 4). We propose that in the hypothetical absence of infection (Figure 4a), microbial cells replicate freely and rapidly, producing both CO_2 and biomass. In this scenario, subsequent microbial mortality produces necromass, which can associate with minerals to form stable SOC. During lytic infection cycles (Figure 4b), new viruses are released upon lysis along with bioavailable cytosolic compounds that support the metabolism of the surviving microbial community through the viral shunt. This new microbial growth augments the rate of necromass production which accelerates the formation of persistent carbon compounds via the MCP. A smaller proportion of more chemically recalcitrant cell components are also released by lytic infections, which may persist as part of the stable carbon pool. Therefore, when lytic viral life cycles are dominant (Figure 4b), we propose that overall virus-mediated recycling of organic matter may accelerate both respiration via the viral shunt and carbon storage through the MCP. Whether this lysis-driven carbon cycling will tip the balance toward net carbon release or storage depends on the time frame considered and myriad ecosystem scale factors (e.g., soil moisture, mineralogy, microbial community composition, fungal: bacterial ratios, etc.). Work that quantitates the flux of microbial carbon redistributed by viral lysis to mineralized CO_2 or stabilized SOC under field-relevant conditions is promising for understanding the net impact of lytic viral contributions to soil carbon dynamics.

In contrast, the primary way in which lysogenic viruses may impact soil carbon cycling is through alterations to microbial growth and/or metabolism. During lysogenic infection cycles (Figure 4c), viruses generally integrate into the host genome and replicate with the host. As discussed in Box 2, cells harboring lysogenic viruses may express distinct phenotypes from uninfected populations. The limited evidence available suggests that lysogeny may curtail soil carbon storage via the MCP either through virus-directed suppression of host growth rate (Chen et al. 2005; Paul 2008) or growth efficiency (Bragg and Chisholm 2008), both of which lead to slowed microbial necromass production and carbon stabilization. However, the nature of the phenotypic modification may also directly influence soil carbon storage and release, if, for example, an expressed viral *auxiliary metabolic gene* (*AMG*) is a carbon degrading enzyme (e.g., Emerson et al. 2018; Wu, Smith, et al. 2022) or enhances soil aggregation by EPS production (Fernández, Rodríguez, and García 2018; Redmile-Gordon et al. 2020). To accurately quantify lysogenic viral effects on soil carbon, additional progress needs to be made toward understanding the fundamental biology regulating switches between viral infection modes, resulting microbial phenotypes, and their effects on soil carbon pathways and persistence.

5 | Conclusions and Outlook

The potential of viruses to contribute to soil carbon cycling is substantial. Here, we argue that accounting for virus-mediated carbon cycling in soils, which directly impacts microbial metabolism and community composition, can enhance our ability to predict and manage carbon flux and storage. To that end, we synthesized the first quantitative estimates of global soil viral carbon pools and fluxes (Figure 1) within a soil-explicit framework detailing the mechanisms by which viruses may enhance carbon storage and/or release from soil ecosystems (Figure 2). We explored one aspect in greater detail—the diversity of virus–host interactions during infection—that complicates how we think about viral impacts on biogeochemical cycles (Figure 4, Box 2). By doing so, we are providing hypotheses for the scientific community to build upon.

The conceptualization of viral contributions to soil biogeochemistry that we present here can be expanded by exploring several additional factors. To further build upon this framework, we suggest empirical assessments of diverse viral infection modes on carbon transformation rates as well as theoretical and empirical work on other potential drivers of virus-mediated carbon cycling in terrestrial environments, including aspects of the soil habitat (structure, hydrology, physiochemistry), abiotic environmental factors such as moisture and temperature, and biotic factors such as host specificity and microbiome community composition/function. At this time, insufficient data is available to explicitly account for fungi and mycoviruses in this framework, although their interactions in soil merit further exploration since fungi are key players in soil carbon cycling and storage (Emilia Hannula and Morriën 2022 and references therein). While we focused solely on carbon dynamics, the ultimate impact of viral infection on soil carbon storage and release is likely constrained by nitrogen and phosphorous availability which are also impacted by viral activity (Kuzyakov and Mason-Jones 2018; Tong et al. 2023). Viruses themselves are enriched in nitrogen and phosphorus relative to microbial biomass (Jover et al. 2014), providing a critical link among terrestrial biogeochemical cycles. Emerging empirical data (Braga et al. 2020; Tong et al. 2023; Wu, Wan, et al. 2022) are providing new information about when viral lysis may alleviate or exacerbate (Kuzyakov and Mason-Jones 2018) nitrogen and phosphorus limitation in soil. As understanding about the impacts of viral infections on microbial nutrient limitation develops, we envision integrating nutrient interactions into the framework detailed here.

The importance of identifying major driving forces behind soil carbon dynamics becomes more pressing with climate change. To evaluate the climate feedbacks and mitigation strategies, we need to constrain the flux of soil carbon among different pools and processes, including this elusive mechanism of carbon transformation in soils.

Author Contributions

Amy E. Zimmerman: conceptualization, visualization, writing – original draft, writing – review and editing. **Emily B. Graham:** conceptualization, visualization, writing – original draft, writing – review and editing. **Jason McDermott:** conceptualization, visualization, writing – original draft, writing – review and editing. **Kirsten S. Hofmockel:** conceptualization, funding acquisition, visualization, writing – original draft, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available in Zenodo at https://zenodo.org/records/13839485.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.