

Viral infections likely mediate microbial controls on ecosystem responses to global warming

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Abstract

Climate change is affecting how energy and matter flow through ecosystems, thereby altering global carbon and nutrient cycles. Microorganisms play a fundamental role in carbon and nutrient cycling and are thus an integral link between ecosystems and climate. Here, we highlight a major black box hindering our ability to anticipate ecosystem climate responses: viral infections within complex microbial food webs. We show how understanding and predicting ecosystem responses to warming could be challenging—if not impossible—without accounting for the direct and indirect effects of viral infections on different microbes (bacteria, archaea, fungi, protists) that together perform diverse ecosystem functions. Importantly, understanding how rising temperatures associated with climate change influence viruses and virus-host dynamics is crucial to this task, yet is severely understudied. In this perspective, we (i) synthesize existing knowledge about virus-microbe-temperature interactions and (ii) identify important gaps to guide future investigations regarding how climate change might alter microbial food web effects on ecosystem functioning. To provide real-world context, we consider how these processes may operate in peatlands—globally significant carbon sinks that are threatened by climate change. We stress that understanding how warming affects biogeochemical cycles in any ecosystem hinges on disentangling complex interactions and temperature responses within microbial food webs.

Keywords: virus, food webs, climate change, microbiome, carbon cycle, ecosystem functioning

Introduction

Climate change is warming terrestrial carbon (C) reserves, making them increasingly vulnerable to microbial respiration (Dorrepaal et al. 2009, Jasse et al. 2015, Page and Baird 2016, Masson-Delmotte et al. In Press). Because microbial respiration increases with temperature (Zhou et al. 2012, Bradford et al. 2019, Smith et al. 2019, Wieczynski et al. 2021), microbes will likely accelerate carbon release at ever increasing rates as Earth warms, creating a positive atmospheric feedback loop not currently represented in predictive models of future climate (Cavicchioli et al. 2019). However, warming is expected to restructure microbial food webs through changes in species composition (Petchey et al. 1999) (but see (Thakur et al. 2021)) and species interactions (Lurgi et al. 2012, Barbour and Gibert 2021). Additionally, evidence from marine systems indicate that microbial impacts on carbon cycling are likely mediated by viral infections of both microbes and their predators (Wilhelm and Suttle 1999, Weitz et al. 2015, Fischhoff et al. 2020). It has been assumed that viruses have similar impacts in terrestrial systems (Williamson et al. 2017, Emerson et al. 2018), but evidence is lacking due to the difficulty of recovering viruses from these systems. Soil viruses thus remain understudied and more research is clearly needed to determine whether viral infections influence microbial effects on terrestrial carbon

cycling as seems to be the case in marine ecosystems (Kuzayakov and Mason-Jones 2018, Trubl et al. 2018). Despite the increasing recognition that infectious agents like viruses are integral components of food webs (Lafferty et al. 2008), the role they play in microbial food webs and their associated temperature dependencies remain poorly understood. Identifying and understanding the temperature-dependence of these biotic controls on microbial respiration is paramount to properly forecast current and future ecosystem-climate feedbacks.

Autotrophic and heterotrophic bacteria, archaea, fungi, and micro-eukaryotes play functionally unique roles in microbial communities as primary producers, nitrogen (N₂)-fixers (diazotrophs), and organic biomass decomposers. For example, microbial autotrophs provide about half of global primary production (Field et al. 1998, Litchman et al. 2015). Decomposers recycle carbon and nutrients from dead organic matter and act as major carbon emitters by respiring carbon (CO₂ and CH₄) into the atmosphere (Falkowski et al. 2000, Canadell et al. 2021). The matter recycled by decomposers reaches higher trophic levels through microbial predation—a process known as the “the microbial loop” (Azam et al. 1983, Fenchel 2008). Predation by protists is a major source of mortality among microbial primary producers (Geisen et al. 2020) and decomposers (Sherr and Sherr 1988, Gao et al.

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2019) (Fig. 1), that can drastically impact carbon and nutrient cycling by reducing microbial biomass, increasing nutrient turnover, and altering microbial respiration rates (Trap et al. 2016, Geisen et al. 2018, 2021, Gao et al. 2019, Rocca et al. 2021). Because of these effects, protists have been called the “puppet masters” of the microbiome (Gao et al. 2019). Due to changes in underlying physiological processes, protist predation rates are expected to change with warming (DeLong and Lyon 2020), altering species interactions within microbial food webs (DeLong and Lyon 2020, Thakur et al. 2021, Han et al. 2022) and influencing microbial biomass and respiration rates (O'Connor et al. 2009, Yvon-Durocher and Allen 2012, Geisen et al. 2021). This complexity emphasizes the need for a food web perspective to understand microbial responses to changing environmental conditions (Thakur and Geisen 2019).

Perhaps our biggest oversight in understanding microbial food web responses to global change is the neglected role of viruses, who have also recently been described as “puppet masters” of the microbiome (Breitbart et al. 2018). All microbes are potential hosts for viruses, which may affect microbial food web composition and functioning by increasing microbial mortality and, in turn, nutrient cycling (via the viral shunt) (Fuhrman 1999, Wilhelm and Suttle 1999, Weinbauer 2004, Suttle 2005). Viruses are likely the most abundant biological entities on Earth (Weinbauer 2004, Suttle 2005); therefore, viral mediation of carbon and nutrient flux within microbial food webs is likely widespread, having important consequences for ecosystem functioning at both local and global scales (Fuhrman 1999, Wilhelm and Suttle 1999, Weinbauer 2004, Suttle 2005, Weitz et al. 2015). Many aspects of the viral infection cycle and virus-host dynamics could potentially be affected by warming (Table 1), yet the effects of temperature on these processes is unclear and severely understudied (Fig. 2). Additionally, there is a lack of understanding about how the effects of temperature may be different in distinct environments and across biomes, undermining our ability to predict how microbial food webs will respond to global change.

Although the individual effects of microbes and viruses on ecosystem functioning have been discussed (Azam et al. 1983, Fenchel 2008, Quaiser et al. 2015, Ballaud et al. 2016, Stough et al. 2017, Gao et al. 2019, Geisen et al. 2021, DeLong et al. 2022), we lack a baseline understanding about how these top-down controls jointly influence ecosystem processes within broader microbial food webs and in response to novel climates. Here, we outline the state-of-the-art regarding temperature effects on infections within microbial food webs and propose ways to conceptualize and address existing knowledge gaps, with a focus on potential effects of warming on carbon and nutrient cycling. First, we present the current state of knowledge about the effects of temperature on viruses and viral infections. Next, we conceptually and mathematically integrate viruses into microbial food webs to discuss how viruses might mediate the effects of warming on food web dynamics and functioning. Finally, to provide real-world context for the potential effects of warming on viral infections within microbial food webs, we conclude with a short case study exploring how virus-microbe responses to warming may alter ecosystem processes in *Sphagnum* moss-dominated peatlands. These peatlands are particularly vulnerable to future climate change (Dorrepaal et al. 2009, Bu et al. 2011, Jassej et al. 2013, Schuur et al. 2015, Page and Baird 2016, Hugelius et al. 2020) and, despite occupying less than 3% of the Earth's surface, store ~25%–30% of the world's soil carbon (Yu et al. 2010) and produce 5%–10% of global atmospheric methane (Blodau 2002).

Temperature effects on viruses and viral infections

All components of microbial food webs can be infected by viruses. While it is recognized that rising temperatures influence the ecology and physiology of microorganisms across environments (Labbate et al. 2016), it is still unclear how the direct and indirect effects of warming will influence viruses, their infection cycles, and how that will ultimately cascade to influence microbial food web functioning. Viral infection occurs in a sequence of steps (Cann 2008) (Fig. 2) including (i) host cell encounter, (ii) adsorption, (iii) introduction of virus or genetic material into the cell, (iv) synthesis of viral particles, and (v) assembly and release of viral progeny. Any one, and likely all, of these steps could be temperature dependent (Fig. 2, Table 1; Table S2), but much research is still needed to evaluate the extent and nature of these temperature dependencies. Furthermore, temperature may affect viral production directly by affecting the particle itself (Nagasaki and Yamaguchi 1998) or indirectly by altering host physiology (Kendrick et al. 2014). Understanding each of these temperature effects is paramount to determine how warming might impact carbon and nutrient cycling within microbial food webs.

Increasing temperature can cause a decrease in latent period (time from infection until release of viral progeny) and an increase in burst size (number of viral progeny released) (Hadas et al. 1997, Nagasaki and Yamaguchi 1998, Demory et al. 2017, Maat et al. 2017, Piedade et al. 2018) (Fig. 2), followed by a reversal of these trends past a virus-specific thermal optimum (T_{opt}) (Kimura et al. 2008, Demory et al. 2017). Temperature effects on burst size and latent period are likely the result of host metabolism and virus synthesis kinetics, but direct evidence is lacking. Based on these findings, we hypothesize that future warming may increase viral production in systems in which current *in situ* temperatures are below T_{opt} , while systems already near or at T_{opt} may produce fewer viruses or undergo complete shutdown of viral propagation.

Encounter rates between viruses and hosts depend on virus and host densities (Murray and Jackson 1992), host cell size, and host motility (Wilhelm et al. 1998). Host cell sizes (Atkinson et al. 2003, Daufresne et al. 2009, Martin et al. 2020) and population densities (Savage et al. 2004; Bernhardt et al. 2018) often decrease while motility increases (Crozier and Federighi 1924, Maeda et al. 1976, Dell et al. 2011, 2014, Gibert et al. 2016) with temperature. Consequently, warming could have positive or negative effects on virus-host encounter rates, although more studies are needed (Table 1, Fig. 2). Evidence suggests that the effect of temperature on adsorption are dependent on the host-virus pair, in some cases increasing (Seeley and Primrose 1980, Hadas et al. 1997), decreasing (Kendrick et al. 2014), or remaining unchanged (Seeley and Primrose 1980) with increases in temperature (Table 1, Fig. 2). While cell membranes are more fluid and permeable at higher temperatures (Marr and Ingraham 1962, Sinensky 1974), it is unknown whether this alters viral infection. We are also unaware of studies that directly link temperature and virus synthesis rates (Fig. 2). Seasonal changes in viral abundances (Nakayama et al. 2007, Payet and Suttle 2007, Colombet et al. 2009) and community composition (Lymer et al. 2008), as well as climatic differences in viral lysis rates (Mojica et al. 2016), have been observed in freshwater, soils, and marine environments, but confounding factors such as nutrient availability and predation obscure the direct effects of temperature on viral infection cycles. Variation in viral life strategies (i.e., lysis vs. lysogeny in prokaryotes and/or latency in multicellular eukaryotes (Correa et al. 2021)) is ecologically important (Stough et al. 2017) and these strategies likely exhibit unique trends with

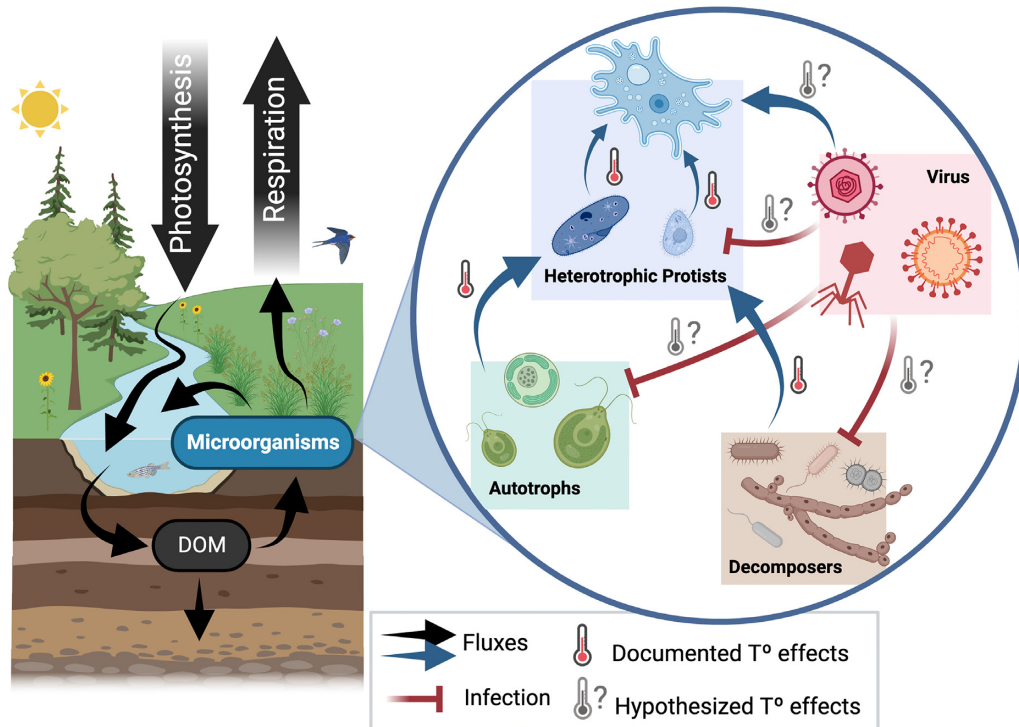


Figure 1. Conceptual diagram outlining the documented and hypothesized temperature effects on processes influencing global carbon cycling, including the impacts of decomposers (heterotrophic bacteria, archaea, and fungi), autotrophs (cyanobacteria and eukaryotic algae), heterotrophic protists that consume all organisms, and viruses that infect all organisms. Note that some organisms (prokaryotes and eukaryotes) can occupy both autotrophic and heterotrophic compartments (mixotrophs).

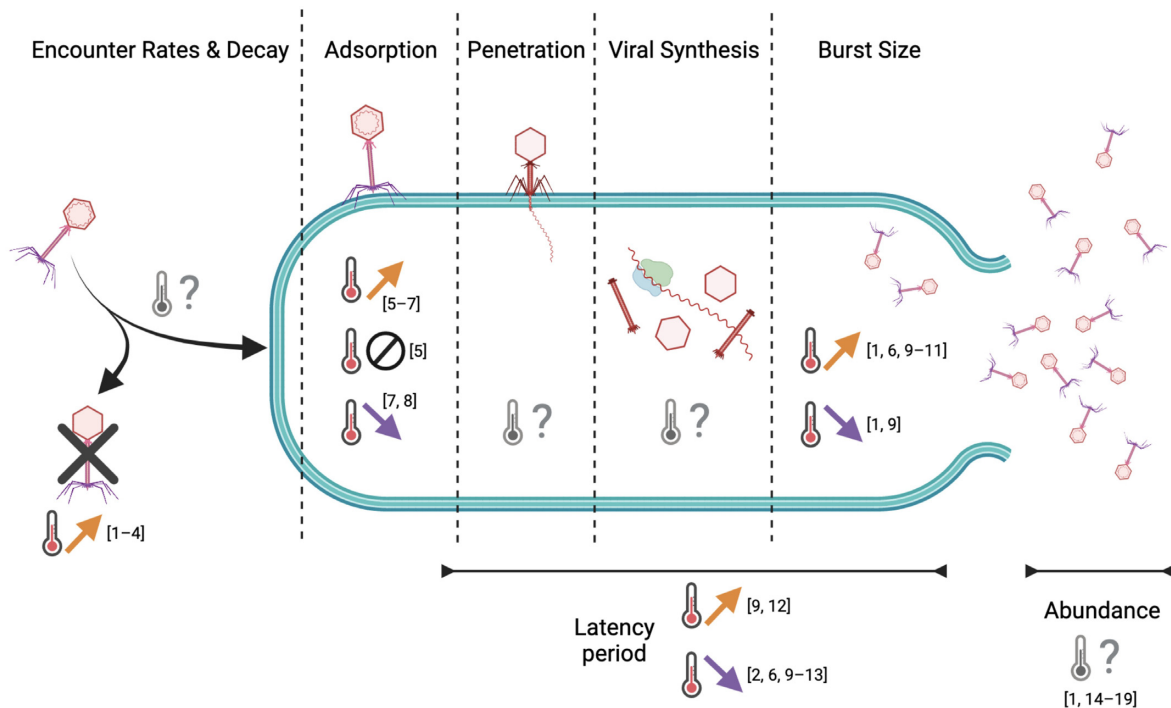


Figure 2. Stages of the viral lytic infection cycle and published temperature effects. Orange arrows indicate a positive effect, purple arrows indicate a negative effect, and interdictory symbols indicate no effect with warming. Gray thermometers indicate stages of the viral infection cycle that either have no published experimental data or published effects are confounded by other environmental/biological factors (e.g. abundances from field studies). Numbers correspond to references in Table 1. More details from these studies can be found in Table S2.

Table 1. Select published studies of temperature effects on viruses. A more detailed description of each study, including summarized results, can be found in Table S2.

Process	Temperature Effects	Location or Host-Virus System
Viral decay	Increases with temperature	- Backwater system of Danube River (Field) (Mathias, Kirschner and Velimirov 1995) ¹ - <i>Heterosigma akashiwo</i> (H93616, NM96) / Hav (HaV01, HaV08) (Lab) (Nagasaki and Yamaguchi 1998) ² - Bacteriophage 9A isolated from Arctic seawater (Lab) (Wells and Deming 2016) ³ - Samples from Western Pacific Ocean (Lab) (Wei et al. 2018) ⁴
Adsorption	Increases with temperature	- <i>Escherichia coli</i> / coliphage isolates from the River Swift (Lab) (Seeley and Primrose 1980) ⁵ - <i>Escherichia coli</i> / T4 (Lab) (Hadas et al. 1997) ⁶ - <i>Chaetoceros tenuissimus</i> / Cten DNAV and Cten RNAV (Lab) (Tomaru et al. 2014) ⁷ - <i>Chaetoceros tenuissimus</i> / Cten DNAV and Cten RNAV (Lab) (Tomaru et al. 2014) ⁷
	Decreases with temperature	- <i>Emiliana huxleyi</i> CCMP374 / EhV86 (Lab) (Kendrick et al. 2014) ⁸
Burst size	No effect of temperature	- <i>Escherichia coli</i> / coliphage isolates from the River Swift (Lab) (Seeley and Primrose 1980) ⁵
	Increases with temperature	- Backwater system of Danube River (Field) (Mathias, Kirschner and Velimirov 1995) ¹ - <i>Escherichia coli</i> / T4 (Lab) (Hadas et al. 1997) ⁶ - <i>Micromonas</i> sp. MicA, MicB, MicC / MicVA, MicVB, MicVC (Lab) (Demory et al. 2017) ⁹ - <i>Micromonas polaris</i> / MpoV (Lab) (Maat et al. 2017) ¹⁰ - <i>Micromonas polaris</i> strain RCC2257, strain RCC2258 / MpoV-45T (Lab) (Piedade et al. 2018) ¹¹
Latency period	Decreases with temperature	- Backwater system of Danube River (Field) (Mathias, Kirschner and Velimirov 1995) ¹ - <i>Micromonas</i> sp. MicA, MicB, MicC / MicVA, MicVB, MicVC (Lab) (Demory et al. 2017) ⁹
	Increases with temperature	- <i>Micromonas</i> sp. MicA, MicB, MicC / MicVA, MicVB, MicVC (Lab) (Demory et al. 2017) ⁹ - <i>Escherichia coli</i> / coliphage (Lab) (Ellis and Delbrück 1939) ¹²
Virus abundance	Decreases with temperature	- <i>Heterosigma akashiwo</i> (H93616, NM96) / Hav (HaV01, HaV08) (Lab) (Nagasaki and Yamaguchi 1998) ² - <i>Escherichia coli</i> / T4 (Lab) (Hadas et al. 1997) ⁶ - <i>Micromonas</i> sp. MicA, MicB, MicC / MicVA, MicVB, MicVC (Lab) (Demory et al. 2017) ⁹ - <i>Micromonas polaris</i> / MpoV (Lab) (Maat et al. 2017) ¹⁰ - <i>Micromonas polaris</i> strain RCC2257, strain RCC2258 / MpoV-45T (Lab) (Piedade et al. 2018) ¹¹ - <i>Escherichia coli</i> / coliphage (Lab) (Ellis and Delbrück 1939) ¹² - <i>Staphylococcus aureus</i> / S. aureus phage (Lab) (Krueger and Fong 1937) ¹³
	Increases with temperature	- Backwater system of Danube River (Field) (Mathias, Kirschner and Velimirov 1995) ¹ - Southern Beaufort Sea and Amundsen Gulf (Field) (Payet and Suttle 2007) ¹⁴ - Lake Pavin (Field) (Colombet et al. 2009) ¹⁵ - Japanese paddy field (Field) (Nakayama et al. 2007) ¹⁶ - Michigan agricultural soils (Field) (Roy et al. 2020) ¹⁷ - Metadata (Danovaro et al. 2011) ¹⁸ ; Williamson et al. 2017 ¹⁹
Lysis thermal range	Temperature effects are host-dependent	- <i>Heterosigma akashiwo</i> (H93616, NM96) / Hav (HaV01, HaV08) (Lab) (Nagasaki and Yamaguchi 1998) ² - Bacteriophage 9A isolated from Arctic seawater (Lab) (Wells and Deming 2006) ³ - <i>Escherichia coli</i> / coliphage isolates from the River Swift (Lab) (Seeley and Primrose 1980) ⁵ - Metadata (Mojica and Brussaard 2014)
Virus-induced host mortality	Increases with temperature	- North Atlantic Ocean (Field) (Mojica et al. 2016)

temperature that are currently unresolved (e.g., increasing temperatures may or may not induce lysis (Shan et al. 2014)), exposing a crucial gap in our understanding of the temperature-dependencies of viral infection.

Viral production is linked to host cell physiology (Tomaru et al. 2014, Demory et al. 2017, Maat et al. 2017, Piedade et al. 2018) because viruses depend on and rewire the metabolism of host cells (Hurwitz et al. 2013). However, viral temperature ranges can be independent of, and often surpass, those of their hosts (Seeley and Primrose 1980, Mojica and Brussaard 2014, Tomaru et al. 2014). Additionally, multiple viruses that infect the same host can have different temperature optima (Tomaru et al. 2014), potentially promoting niche differentiation and a shift in dominant viral taxa with warming. This suggests that viruses could be less susceptible to extinction under warming than their hosts, but more research is needed to determine the extent of this phenomenon and the resulting impacts on nutrient and carbon cycling.

Finally, the potential consequences of viral temperature dependencies for microbial food web dynamics and functioning may be complex, context-dependent, and variable across systems. For example, Frenken et al. 2020 used aquatic mesocosm

experiments to show that, although warming advanced the seasonal timing of viral infection, it did not increase viral abundance or strengthen viral control over host populations. In addition, (Danovaro et al. 2011) predicted that the effects of warming on viral abundance in marine systems will vary by oceanic region and that a consistent response to rising temperatures across environments is unlikely. These examples illustrate that the temperature-dependent effects of viruses can manifest in different aspects of viral infection/virus-host interactions and may vary by region. We argue that controlled studies (e.g., mesocosms, synthetic communities) and *in situ* monitoring across diverse environments can aid in identifying and predicting complex viral responses to temperature in different environmental contexts. Moreover, the vast majority of data available for temperature effects on viral dynamics comes from marine environments or a select few model host-virus systems (Table 1). Much less is known about infection dynamics and viral-mediated biogeochemical cycling in terrestrial systems (Kuzakov and Mason-Jones 2018, Trubl et al. 2018, Jansson and Wu 2022), highlighting the need to expand studies to different environments and new systems to better comprehend the influences of virus-microbe interactions on ecosystem processes under warming conditions.

Integrating viral infections within microbial food webs under warming

Although viruses are known to impact carbon and nutrient cycling directly via the viral shunt (Wilhelm and Suttle 1999; Sullivan et al. 2017), how viruses might mediate microbial responses to warming is poorly understood. Microbes account for a substantial fraction of the biomass on Earth (Bar-On et al. 2018) and place major controls on carbon and nutrient cycling in terrestrial (Schimel and Schaeffer 2012), freshwater (Kayranli et al. 2010), and marine (Zhang et al. 2018) ecosystems worldwide. Microbial communities are complex, functionally-diverse, multi-trophic food webs (Bengtsson et al. 1996; Petchey et al. 1999; Gao et al. 2019; Thakur and Geisen 2019) in which energy and matter flow between organisms that occupy different trophic positions and play a variety of functional roles (Fenchel 2008; Steinberg and Landry 2017). Ecosystem responses to climate change are thus likely regulated by changes in overall microbial food web dynamics and organization (Thakur and Geisen 2019; Kuppardt-Kirmse and Chatzinotas 2020). Viruses could play important roles in these changes that depend on (i) the relative infection rates of hosts in different functional groups, (ii) the temperature dependencies of the viral infection cycle, (iii) thermal matching between virus-host pairs, and (iv) changes in host physiology, population dynamics, and species interactions associated with viral infection.

Broadly speaking, how viruses mediate microbial controls on ecosystem responses to warming hinges on how they impact the overall balance of carbon and nutrient uptake (via photosynthesis and decomposition), storage in biomass, sequestration in sediment, and release (via respiration) (Figs 2 and 3). Respiration and decomposition rates are expected to increase with warming (Petchey et al. 1999; Kirschbaum 2000; Smith et al. 2019) and may be more sensitive to temperature change than photosynthetic rates (Allen et al. 2005) (although temperature sensitivities vary significantly among different microbial groups (Smith et al. 2019)). This suggests that warming could tip some ecosystems from productivity-dominant carbon sinks (storing carbon in biomass and sediment) to respiration-dominant carbon sources (releasing carbon into the atmosphere) (Yvon-Durocher and Allen 2012). However, increases in microbial primary productivity should at least partially offset this uneven increase in carbon release (Zhou et al. 2012; Wyatt et al. 2021). Furthermore, warming is expected to alter the biomass and composition of microbial food webs, affecting ecosystem processes like CO₂ release via respiration (Geisen et al. 2021; Rocca et al. 2022). How viruses mediate this balance between carbon uptake and release under warming is poorly understood, but will likely involve differential impacts on the dynamics and mortality of hosts that perform different ecosystem functions (Sarmento et al. 2010; Danovaro et al. 2011; Vaqué et al. 2019).

Potential climate-driven shifts in nutrient and carbon cycling can be studied using mathematical models that track the collective responses of several essential organisms within microbial food webs (Fig. 3). Each organism plays a unique role in carbon and nutrient cycling depending on its metabolic requirements, trophic mode (autotroph, heterotroph), trophic position, stoichiometry, temperature sensitivity, etc. The fate of carbon—storage in biomass, storage in sediment, or respiration into the atmosphere—is therefore controlled by the composition and organization of microbial food webs. As a way to put forward testable hypotheses about the effects of viruses on nutrient and carbon cycling, we develop a conceptual model describing a simplified, hypothetical microbial food web and examine potential impacts of warming on ecosystem functioning. We describe the basic com-

ponents of our model below, but a detailed, technical explanation of the model and its formulation is provided in the Supporting Information.

Organisms

- **Decomposers** like heterotrophic bacteria and fungi recycle dead organic matter produced primarily by plants (C uptake) and are major contributors to microbial respiration (C release) and soil organic carbon via mortality (C sequestration).
- **Nitrogen-fixers** like cyanobacteria, methanogenic archaea, and some heterotrophic bacteria transform atmospheric nitrogen (N₂) into biologically usable forms that are metabolically required by all organisms and photosynthetic nitrogen-fixers also require carbon dioxide for photosynthesis (C uptake).
- **Predators** include protists such as heterotrophic flagellates, ciliates, and mixotrophs that consume both decomposers and nitrogen-fixers, altering elemental flows by reducing prey biomass and potentially increasing respiration (C release) and storing recycled carbon and nutrients in predator biomass (C uptake). We use the term “predators” here to differentiate these protists from those that also eat other protists (termed “top predators” below).
- **Eukaryotic algae** include protists that use carbon dioxide for photosynthesis (C uptake) and may represent a significant offset to microbial respiration.
- **Top predators** constitute a subnetwork within the overall food web and include larger protists (e.g., testate amoebae) that consume recycled carbon via predation on all trophic levels, altering biomass and elemental flows throughout (C uptake or release).
- **Viruses** impact elemental flows directly through lysis (C release) and indirectly by altering biochemistry and the population dynamics of host organisms in all of the categories above (C uptake or release).

Essential elements

- **Inorganic carbon** from the atmosphere (CO₂) is fixed and stored in biomass during photosynthesis and is released through respiration.
- **Organic carbon** is produced by mortality and viral lysis/decay and is transferred between organisms through decomposition and predation.
- **Essential nutrients** like nitrogen and phosphorus are required by all organisms and can affect competitive and trophic dynamics depending on the stoichiometric requirements of organisms. For example, inorganic nitrogen is required for growth by both nitrogen-fixing and heterotrophic bacteria and converted into organic forms that are then transferred to higher trophic levels through predation.

The impacts of global warming on the carbon cycle will ultimately depend on the temperature dependencies of several different processes within microbial food webs, including photosynthesis, respiration, predation, viral infection, and mortality, many of which are poorly understood for most of these organisms (Fig. 1). However, photosynthesis is generally less sensitive to increases in temperature (activation energy of ~0.32 eV (Allen et al. 2005, López-Urrutia et al. 2006, O'Connor et al. 2009, Yvon-Durocher and Allen 2012)) than respiration and predation (~0.65 eV (Brown et al. 2004, Dell et al. 2011, 2014)), while mortality lies somewhere in between (~0.45 eV (Brown et al. 2004, Savage et al. 2004)).

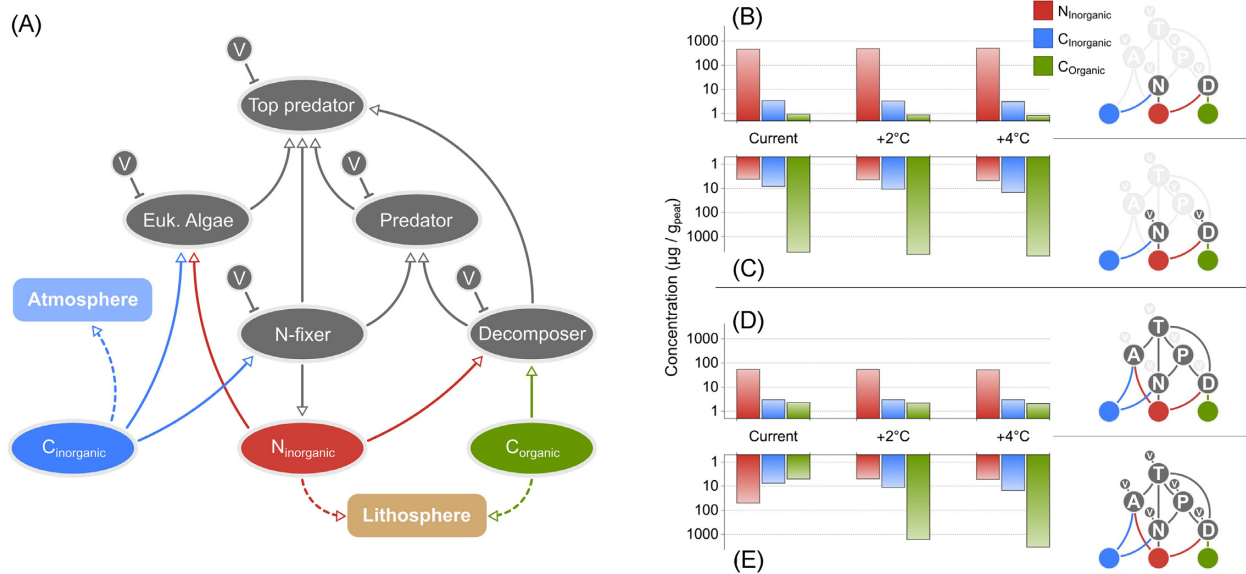


Figure 3. (A) Hypothetical microbial food web in *Sphagnum* peatlands including organisms and nitrogen and carbon flow. Arrows represent flow between components. Each type of organism consumes elements or other organisms based on its unique stoichiometric requirements and is also subject to infection by viruses (V). Unused elements are released into the atmosphere or stored in the lithosphere. (B–E) The effects of warming on equilibrium concentrations of nitrogen and carbon in the model microbial food web in (A). Four scenarios are shown to assess the influences of different food web components: (B) non-protists only (N + D), (C) non-protists + viruses (N + D + V), (D) non-protists + protists (N + D + A + P + T), and (E) all organisms and viruses.

Accounting for these temperature dependencies in our hypothetical food web suggests that warming will have little effect on the balance of carbon storage and release in systems composed of only decomposers, fungi, and protists—where carbon released into the atmosphere ($C_{inorganic}$) is expected to exceed carbon stored in the sediment ($C_{organic}$) (Fig. 3B and D). Protists significantly increase the amount of carbon stored but also reduce the amount of bioavailable nitrogen ($N_{inorganic}$) (Fig. 3D). However, in a system with prokaryotes, protists, and viruses, warming is expected to increase the amount of carbon both released and stored, but stored carbon is expected to surpass released carbon with a margin that increases with temperature (Fig. 3E), suggesting one possible way that viral infections may weaken the negative effects of warming on the global carbon cycle. Based on these preliminary model results, we hypothesize that warming could strengthen viral controls on decomposers, N-fixers, and protists, leading to reduced microbial biomass, increased nutrient cycling and respiration, shorter mean residence time of carbon in microbial food web compartments, and shifts in the balance of carbon sequestration and release into the atmosphere (Fig. 3E).

These results are merely suggestions based on limited knowledge of parameter space and many simplifying assumptions. True temperature responses will depend on changes in the composition and structure of specific microbial food webs, several temperature-dependencies that are poorly understood across organisms (Figs 1 and 4), possible changes in size across taxa that could change predation rates (Brose et al. 2012), and temperature-dependence at all stages of viral infection (Table 1). We stress that all of the parameters, interactions among organisms, and temperature dependencies outlined in this model are poorly understood and should be the subject of much-needed future investigation. The primary role of this model is to provide a roadmap that identifies the components of microbial food webs that could have important impacts on carbon flux. Hence, the generality of these effects is very difficult to judge given how much uncer-

tainty remains about the effects of temperature on viral infection, virus-host dynamics, and the impacts of viruses on microbial food web structure. We advocate that investigating these unknowns is a critical step towards more accurately predicting ecosystem responses to climate change.

Peatlands as a model system to study how viral infections mediate microbial food web responses to warming

Here, we highlight peatlands as a case study to provide real-world context for the ideas explored above. Peatlands include all of the essential components outlined in this perspective: a clearly-defined and functionally-diverse microbial food web, viruses that infect all organisms within that food web, a well-documented key role in global carbon and nutrient cycling, and high sensitivity to warming. Hence, peatlands provide an ideal model system to close some of the gaps in our current understanding about how viral infections may influence the effects of microbial activity on carbon and nutrient cycling in a warming world.

Peatlands are typically dominated by *Sphagnum* peat mosses, storing more carbon (in both living biomass and peat)—and therefore arguably having a greater influence on global carbon cycling and climate—than any other single genus of plants (Clymo and Hayward 1982, Gorham 1991). While *Sphagnum* plays a primary role in carbon dynamics (Slate et al. 2019), it serves a secondary role by insulating permafrost, thus dampening the impacts of rising temperatures on vast amounts of carbon stored in the arctic tundra (Camill and Clark 1998). Peatland microbial food webs are uniquely well-suited systems for studying ecosystem responses to global change due to (i) their net impact on the global carbon cycle (Gorham 1991, Dorrepaal et al. 2009, Yu et al. 2010, Bu et al. 2011), (ii) the functional diversity of their constituent microbial taxa (Gilbert et al. 1998, Trap et al. 2016, Geisen et al. 2018, Thakur and Geisen 2019), (iii) their vulnerability to changes in tempera-

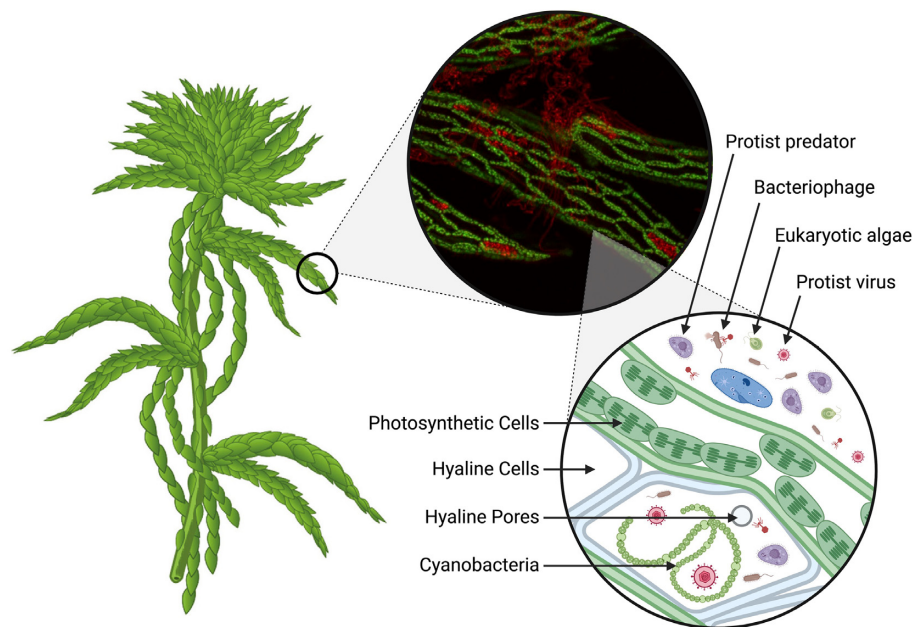


Figure 4. *Sphagnum* moss and associated microbial food web. Microbial species inhabit both water-filled hyaline cells of *Sphagnum* tissue and the external aquatic habitat. First inset shows cyanobacteria (in red) living inside *Sphagnum* tissue (in green, image taken using a Zeiss LSM 710 laser scanning confocal microscope, image credit: Andrea Timm and Collin Timm).

ture (Richardson et al. 2018, Norby et al. 2019, Smith et al. 2019, Turetsky et al. 2019, Geisen et al. 2021), and (iv) the ability to grow and study *Sphagnum* moss and associated microbial communities in the laboratory (Altermatt et al. 2015, Geisen et al. 2018, Carrell et al. 2019, 2022b). Doing so, however, will require a multifaceted approach—including characterization of microbial communities in the field, microbial experiments in the laboratory, -omics approaches, and mathematical modeling (Singh et al. 2010, Geisen et al. 2017), all of which can benefit from cross-scale integration.

We propose that the response of *Sphagnum*-dominated peatlands to warming is regulated by poorly understood controls on carbon and nutrient cycling from microbes and viral infections (Fig. 1). Microbes play diverse functional roles in peatlands both within the soil as well as in the aquatic environment above the soil (Gilbert et al. 1998, Gilbert and Mitchell 2006, Lara et al. 2011, Kostka et al. 2016, Carrell et al. 2022a). For example, bacterial and fungal decomposers are primarily responsible for breaking down dead organic material stored within peatlands (Gilbert et al. 1998, Gilbert and Mitchell 2006), a process being accelerated by warming (Dorrepaal et al. 2009). Additionally, *Sphagnum*'s ability to persist in harsh peatland habitats with extremely low mineral nitrogen availability depends on symbiotic interactions with microbial associates (Lindo et al. 2013, Kostka et al. 2016, Carrell et al. 2022a)—including diazotrophs that colonize the cell surface and water-filled hyaline cells in host plants (Kostka et al. 2016) (Fig. 4). Bacterial methanotrophs are also prevalent in boreal peat bogs (Liebner and Svenning 2013, Vile et al. 2014) and not only fix N_2 , but supply 5%–20% of CO_2 necessary for *Sphagnum* photosynthesis via methane oxidation (Larmola et al. 2014). *Sphagnum*'s microbial community composition varies widely with climate (Singer et al. 2019) and is expected to shift considerably under warming (Carrell et al. 2019, Basińska et al. 2020), likely altering associated microbial food webs (Bengtsson et al. 1996, Petchey et al. 1999, Geisen et al. 2018, Gao et al. 2019, Thakur and Geisen 2019).

Peatland ecosystems also harbor a diverse group of viruses that infect prokaryotes and eukaryotes (Ballaud et al. 2016, Emerson

et al. 2018, Stough et al. 2018) and are correlated with overall concentrations of both CO_2 and CH_4 (ter Horst et al. 2021). Surprisingly, the inferred frequency of protist infections in the *Sphagnum* microbiome was found to be higher than that of bacterial infection by phages (Stough et al. 2018), although the functional role of protist infection in this system remains unclear. Fungal viruses can have considerable downstream ecological consequences by lysing or altering the phenotypes of fungal decomposers, symbionts, or pathogens in *Sphagnum* (Sutela et al. 2019). In peatlands, viral community composition, abundance, and lifestyle strategies are influenced by environmental factors, including temperature (Ballaud et al. 2016, Emerson et al. 2018). However, how warming might modify the direct (lytic release of elements) and indirect (altered host phenotype/dynamics and food web processes) effects of viral infections on *Sphagnum*-associated microbial food webs—and carbon and nitrogen cycling in peatlands—is not well understood. Our simple model suggests that viral infections and microbial activity may jointly accelerate the positive effects of warming on C sequestration in peatlands (Fig. 3). However, this simple conceptual model is intended as a first attempt to generate hypotheses about the potential impacts of warming, rather than predict future scenarios. Indeed, the mechanisms and parameters governing such interactions between temperature, viruses, protists, and prokaryotes in this model—and the magnitude and direction of resulting changes in carbon cycling—have little empirical verification and will require much more experimental investigation to resolve, thus highlighting the importance of these missing data. A deeper understanding about how these ecological interactions occur in nature and how they are influenced by warming is direly needed, but peatland microbial food webs provide a promising system to begin to develop this understanding.

Conclusions

Microbial food webs play a central role in the global carbon cycle by processing and storing vast amounts of carbon. We suggest

that viral infections within microbial food web components that play distinct functional roles, and their associated temperature-dependencies, could control changes in carbon cycling and storage in response to global warming. We highlight the importance of studying the complex dynamics of microbial food webs to better understand and predict whether rising temperatures will lead to net carbon sequestration or release in globally important ecosystems like *Sphagnum*-dominated peatlands. But we also stress that these ecological interactions and their temperature-dependencies are poorly understood, highlighting several gaps for future research. Based on the information gathered in this perspective, we propose the following list of broad questions to serve as a guide moving forward:

- 1) How will warming influence different aspects of the viral infection cycle, including both host-dependent and host-independent processes? (Section 1)
- 2) How will virus-host interactions be affected by warming, including virus and host temperature sensitivities, niches, and matching? (Section 1)
- 3) How will warming affect virus life strategies? (Section 1)
- 4) How will viral infections mediate the rewiring of functionally- and trophically-diverse microbial food webs under warming? (Section 2)
- 5) How do viral infections alter host physiology, population dynamics and species interactions? (Section 2)
- 6) Will viral infections of functionally distinct microbial groups affect how warming shifts the balance of carbon uptake, storage, and release? (Section 2)
- 7) What are the relative viral abundances and infection rates across microbial hosts in real ecosystems like peatlands? (Section 3)
- 8) How can we leverage empirical data from systems like peatlands and models to study the coordinated impacts of warming and viral infection on microbial carbon and nutrient cycling? (Section 3)

Resolving these uncertainties will require a combination of empirical and theoretical analyses that specifically evaluate temperature-dependencies and virus-host interactions within microbial food webs. The effects of these important processes on microbial population dynamics and carbon flow may then shed light on the broader impacts of warming on carbon cycling and storage within and across whole ecosystems.

Statement of authorship

All authors conceived the study. DJW, KMY, and ERD reviewed the literature. DJW performed all mathematical modeling. DJW, KMY, SWW, and JPG wrote the first version of the manuscript and all authors contributed to subsequent versions.

Data accessibility statement

No new data were collected for this study.

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Supplementary data

Supplementary data is available at [FEMSEC](https://academic.oup.com/femsec/article/99/3/fiaad016/7057867) online.

Conflicts of interest statement. The authors claim no conflicts of interest.

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