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

Daniel J Wieczynski[1], Kristin M Yoshimura[2], Elizabeth R Denison[2], Stefan Geisen[3], Jennifer M DeBruyn[2], A Jonathan Shaw[1], David J Weston[4], Dale A Pelletier[4], Steven W Wilhelm[2], and Jean P Gibert[1]

[1]Duke University
[2]University of Tennessee
[3]Wageningen University
[4]Oak Ridge National Laboratory

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**Abstract**

Climate change is affecting how energy and matter flow within ecosystems, 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, 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 severely understudied. In this perspective, we 1) synthesize existing knowledge about virus-microbe-temperature interactions and 2) 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.

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**Authors:**
Daniel J. Wieczynski[1,a,*], Kristin M. Yoshimura[2,a], Elizabeth R. Denison[2], Stefan Geisen[3], Jennifer M. DeBruyn[5], A. Jonathan Shaw[1], David J. Weston[4], Dale A. Pelletier[4], Steven W. Wilhelm[2], Jean P. Gibert[1]

**Affiliations:**
[1]Department of Biology, Duke University; [2]Department of Microbiology, The University of Tennessee, Knoxville; [3]Netherlands Institute of Ecology; [4]Biosciences Division, Oak Ridge National Laboratory; [5]Department of Biosystems Engineering and Soil Science, The University of Tennessee, Knoxville
*Corresponding author—email: daniel.wieczynski@duke.edu
[a]Equal contributions

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**ABSTRACT**

Climate change is affecting how energy and matter flow within ecosystems, 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, 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 severely understudied. In this perspective, we 1) synthesize existing knowledge about virus-microbe-temperature interactions and 2) 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.

## INTRODUCTION

Climate change is warming terrestrial carbon (C) reserves, making them increasingly vulnerable to microbial respiration (Dorrepaal *et al.* 2009; Jassey *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, López and Montoya 2012; Barbour and Gibert 2021). Additionally, 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). 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 ($N_2$)-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

87 ($CO_2$ and $CH_4$) into the atmosphere (Falkowski *et al.* 2000; Canadell *et al.* 2021). The matter
88 recycled by decomposers reaches higher trophic levels through microbial predation—a process
89 known as the “the microbial loop” (Azam *et al.* 1983; Fenchel 2008). Predation by protists is a
90 major source of mortality among microbial primary producers (Geisen *et al.* 2020) and
91 decomposers (Sherr and Sherr 1988; Gao *et al.* 2019) (Fig. 1), that can drastically impact carbon
92 and nutrient cycling by reducing microbial biomass, increasing nutrient turnover, and altering
93 microbial respiration rates (Trap *et al.* 2016; Geisen *et al.* 2018, 2021; Gao *et al.* 2019; Rocca *et*
94 *al.* 2021). Because of these effects, protists have been called the “puppet masters" of the
95 microbiome (Gao *et al.* 2019). Due to changes in underlying physiological processes, protist
96 predation rates are expected to change with warming (DeLong and Lyon 2020), altering species
97 interactions within microbial food webs (DeLong and Lyon 2020; Thakur *et al.* 2021) and
98 influencing microbial biomass and respiration rates (O’Connor *et al.* 2009; Yvon-Durocher and
99 Allen 2012; Geisen *et al.* 2021). This complexity emphasizes the need for a food web
100 perspective to understand microbial responses to changing environmental conditions (Thakur and
101 Geisen 2019).
102
103 Perhaps our biggest oversight in understanding microbial food web responses to global change is
104 the neglected role of viruses, who have also recently been described as “puppet masters” in the
105 microbiome (Breitbart *et al.* 2018). All microbes are potential hosts for viruses, which may affect
106 microbial food web composition and functioning by increasing microbial mortality and, in turn,
107 nutrient cycling (*via* the Viral Shunt) (Fuhrman 1999; Wilhelm and Suttle 1999; Weinbauer
108 2004; Suttle 2005). Viruses are the most abundant biological entities on Earth (Weinbauer 2004;
109 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). Several 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), 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), 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 current state of understanding 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 kno0wledge regarding the effects of temperature on viruses and viral infections. Next, we 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 by exploring how virus-microbe responses to warming may alter ecosystem processes in *Sphagnum* moss-dominated peatlands, which are particularly vulnerable to future climate change (Page and Baird 2016) 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).

## 1. 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 1) host cell encounter, 2) adsorption, 3) introduction of virus or genetic material into the cell, 4) synthesis of viral particles, and 5) 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 infection and viral

156 production in systems in which current *in situ* temperatures are below $T_{opt}$, while systems already
157 near or at $T_{opt}$ may produce fewer viruses or undergo complete shutdown of viral propagation.
158
159 Encounter rates between viruses and hosts depend on virus and host densities (Murray and
160 Jackson 1992), host cell size, and host motility (Wilhelm *et al.* 1998). Host cell sizes (Atkinson,
161 Ciotti and Montagnes 2003; Daufresne, Lengfellner and Sommer 2009; Martin *et al.* 2020) and
162 population densities (Savage *et al.* 2004; Bernhardt, Sunday and O'Connor 2018) often decrease
163 while motility increases (Crozier and Federighi 1924; Maeda *et al.* 1976; Dell, Pawar and Savage
164 2011, 2014; Gibert *et al.* 2016) with temperature. Consequently, warming could have positive or
165 negative effects on virus-host encounter rates, although more studies are needed (Table 1, Fig.
166 2). Evidence suggests that the effect of temperature on adsorption are dependent on the host-
167 virus pair, in some cases increasing (Seeley and Primrose 1980; Hadas *et al.* 1997), decreasing
168 (Kendrick *et al.* 2014), or remaining unchanged (Seeley and Primrose 1980) with increases in
169 temperature (Table 1, Fig. 2). While cell membranes are more fluid and permeable at higher
170 temperatures (Marr and Ingraham 1962; Sinensky 1974), it is unknown whether this alters viral
171 infection. We are also unaware of studies that directly link temperature and virus synthesis rates
172 (Fig. 2). Seasonal changes in viral abundances (Nakayama *et al.* 2007; Payet and Suttle 2007;
173 Colombet *et al.* 2009) and community composition (Lymer *et al.* 2008), as well as climatic
174 differences in viral lysis rates (Mojica *et al.* 2016), have been observed, but confounding factors
175 such as nutrient availability and predation obscure the direct effects of temperature on viral
176 infection cycles. Variation in viral life strategies (*i.e.,* lysis vs. lysogeny in prokaryotes and/or
177 latency in multicellular eukaryotes (Correa *et al.* 2021)) is ecologically important (Stough *et al.*
178 2017) and these strategies likely exhibit unique trends with 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, Kimura and Yamaguchi 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, Hallam and Sullivan 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, Kimura and Yamaguchi 2014). Additionally, multiple viruses that infect the same host can have different temperature optima (Tomaru, Kimura and Yamaguchi 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 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), 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.

## 2. INTEGRATING VIRAL INFECTIONS WITHIN MICROBIAL FOOD WEBS UNDER WARMING

Although viruses are known to impact carbon and nutrient cycling directly, namely *via* the viral shunt (Wilhelm and Suttle 1999; Sullivan, Weitz and Wilhelm 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, Phillips and Milo 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, Setälä and Zheng 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) (Box 1, Figs. 2, 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, Gillooly and Brown 2005) (although a great deal of variation exists in temperature sensitivities among different microbial groups (Smith *et al.* 2019)). This suggests that warming could tip 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 $CO_2$ 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 complex and 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). Based on 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 (Box 1, Fig. B2d). However, the generality of these effects is very difficult to judge given how much uncertainty remains about the effects of temperature on viral infection, virus-host dynamics, and the impacts of viruses on microbial food web structure.

## 3. PEATLANDS AS A MODEL SYSTEM TO STUDY HOW VIRAL INFECTIONS MEDIATE MICROBIAL FOOD WEB RESPONSES TO WARMING

We use peatland microbial food webs as a real-world case study to explore 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, Sullivan and Callaway 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 1) their net impact on the global carbon cycle (Gorham 1991; Dorrepaal *et al.* 2009; Yu *et al.* 2010; Bu *et al.* 2011), 2) the functional diversity of their constituent microbial taxa (Gilbert *et al.* 1998; Trap *et al.* 2016; Geisen *et al.* 2018; Thakur and Geisen 2019), 3) their vulnerability to changes in temperature (Richardson *et al.* 2018; Norby *et al.* 2019; Smith *et al.* 2019; Geisen *et al.* 2021), and 4) 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, Box 1). Microbes play diverse functional roles in peatlands (Gilbert *et al.* 1998; Gilbert and Mitchell 2006; Lara *et al.* 2011; Kostka *et al.* 2016; Carrell *et al.* 2022a) (Fig. 3). 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, Nilsson and Gundale 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. 3). 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, Setälä and Zheng 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, Poimala and Vainio 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 (Box 1, Fig. B2). 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. We propose the following list of 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 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.

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**Box 1.**

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. B1). 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. Here we develop a conceptual model describing a simplified, example microbial food web from the *Sphagnum*-dominated peatland system and examine potential impacts of warming on ecosystem functioning.

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 ($N_2$) 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 host biochemistry and population dynamics (C uptake or release)

Essential elements

- **Inorganic carbon** from the atmosphere ($CO_2$) 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.

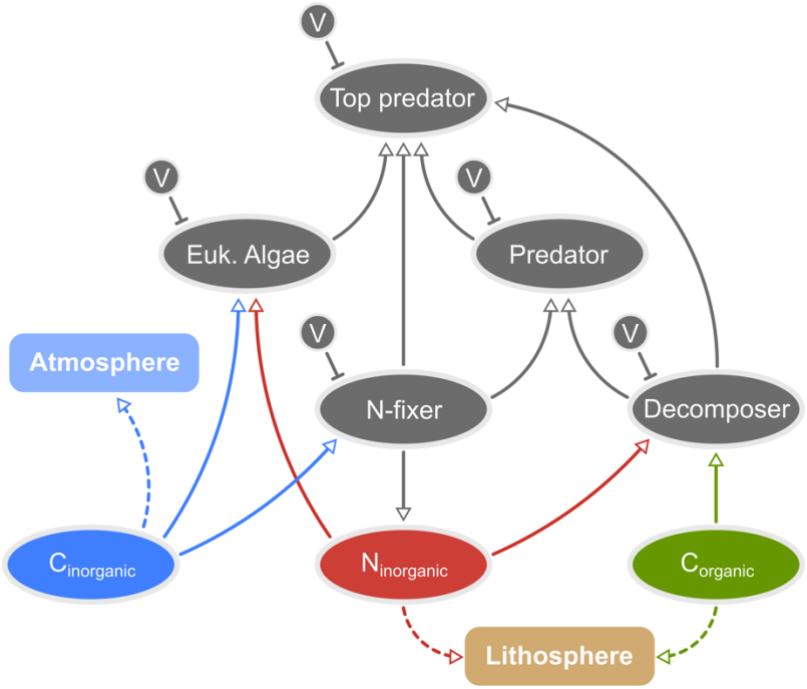


**Figure B1.** Hypothetical microbial food web in *Sphagnum* peatlands including organisms and nitrogen and carbon flow. Arrows represent flow between components. Each type of organism consumes elements or other organisms based on its unique stoichiometric requirements and is also subject to infection by viruses (V). Unused elements are released into the atmosphere or stored in the lithosphere.

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 (Fig. 1), many of which are poorly understood for most of these organisms (Figs. 1&4). However, photosynthesis is generally less sensitive to increases in temperature (activation energy of ~0.32eV (Allen, Gillooly and Brown 2005; López-Urrutia *et al.* 2006; O'Connor *et al.* 2009; Yvon-Durocher and Allen 2012)) than respiration and predation (~0.65eV (Brown *et al.* 2004; Dell, Pawar and Savage 2011, 2014)), while mortality lies somewhere in between (~0.45eV (Brown *et al.* 2004; Savage *et al.* 2004)).

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. B2 a&c). Protists significantly increase the amount of carbon stored but also reduce the amount of

bioavailable nitrogen ($N_{Inorganic}$) (Fig. B2c). 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. B2d), suggesting one possible way that viral infections may weaken the negative effects of warming on the global carbon cycle.

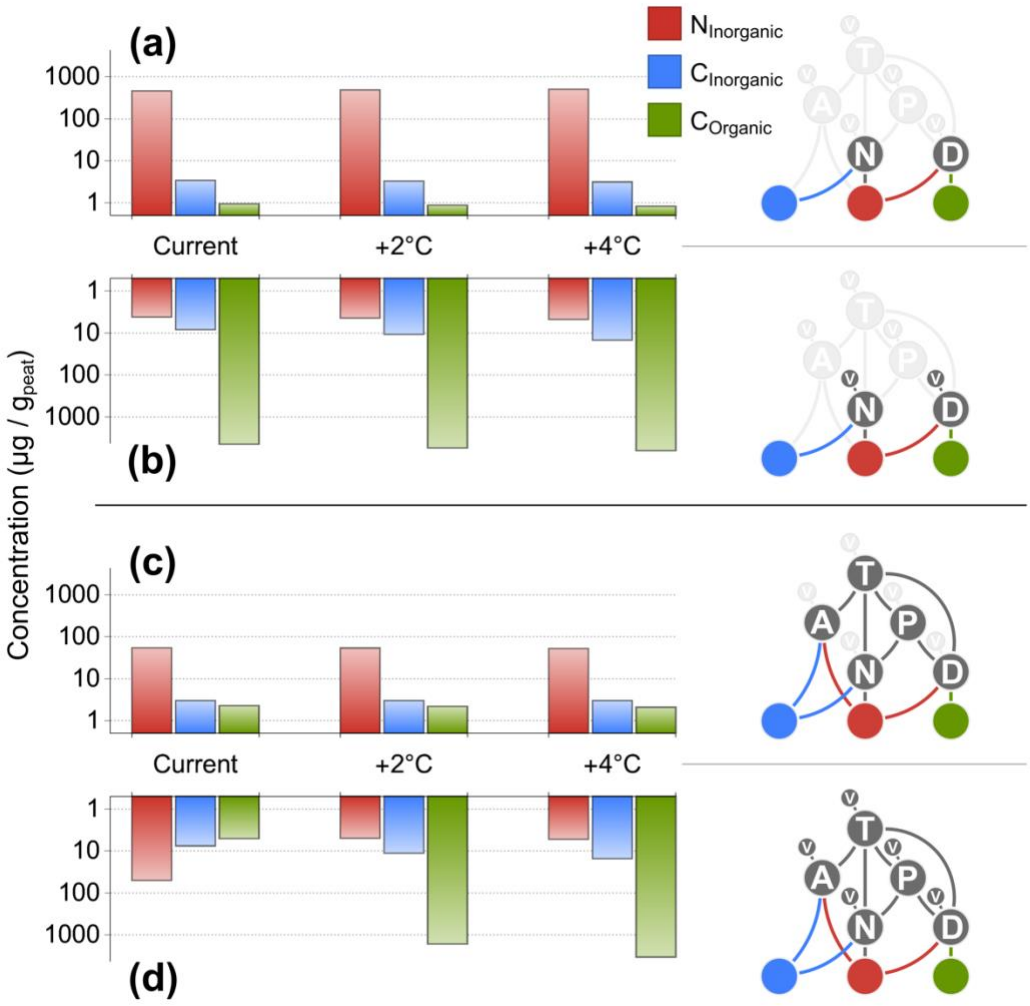


**Figure B2.** The effects of warming on equilibrium concentrations of nitrogen and carbon in the model microbial food web from Fig. B1. Four scenarios are shown to assess the influences of different food web components: (a) non-protists only (N + D), (b) non-protists + viruses (N + D + V), (c) non-protists + protists (N + D + A + P + T), and (d) all organisms and viruses.

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&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. Hence, 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. We advocate that investigating these unknowns is a critical step towards more accurately predicting ecosystem responses to climate change.

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## TABLES

**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]<br>- *Heterosigma akashiwo* (H93616, NM96) / Hav (HaV01, HaV08) (Lab) (Nagasaki and Yamaguchi 1998)[2]<br>- Bacteriophage 9A isolated from Arctic seawater (Lab) (Wells and Deming 2006)[3]<br>- Samples from Western Pacific Ocean (Lab) (Wei *et al.* 2018)[4] |
| Adsorption | Increases with temperature | - *Escherichia coli* / coliphage isolates from the River Swift (Lab) (Seeley and Primrose 1980)[5]<br>- *Escherichia coli* / T4 (Lab) (Hadas *et al.* 1997)[6]<br>- *Chaetoceros tenuissimus* / Cten DNAV and Cten RNAV (Lab) (Tomaru, Kimura and Yamaguchi 2014)[7] |
| | Decreases with temperature | - *Chaetoceros tenuissimus* / Cten DNAV and Cten RNAV (Lab) (Tomaru, Kimura and Yamaguchi 2014)[7]<br>- *Emiliana huyxleyi* CCMP374 / EhV86 (Lab) (Kendrick *et al.* 2014)[8] |
| | No effect of temperature | - *Escherichia coli* / coliphage isolates from the River Swift (Lab) (Seeley and Primrose 1980)[5] |
| Burst size | Increases with temperature | - Backwater system of Danube River (Field) (Mathias, Kirschner and Velimirov 1995)[1]<br>- *Escherichia coli* / T4 (Lab) (Hadas *et al.* 1997)[6]<br>- *Micromonas* sp. MicA, MicB, MicC / MicVA, MicVB, MicVC (Lab) (Demory *et al.* 2017)[9]<br>- *Micromonas polaris* / MpoV (Lab) (Maat *et al.* 2017)[10]<br>- *Micromonas polaris* strain RCC2257, strain RCC2258 / Mpov-45T (Lab) (Piedade *et al.* 2018)[11] |
| | Decreases with temperature | - Backwater system of Danube River (Field) (Mathias, Kirschner and Velimirov 1995)[1]<br>- *Micromonas* sp. MicA, MicB, MicC / MicVA, MicVB, MicVC (Lab) (Demory *et al.* 2017)[9] |
| Latency period | Increases with temperature | - *Micromonas* sp. MicA, MicB, MicC / MicVA, MicVB, MicVC (Lab) (Demory *et al.* 2017)[9]<br>- *Escherichia coli* / coliphage (Lab) (Ellis and Delbrück 1939)[12] |
| | Decreases with temperature | - *Heterosigma akashiwo* (H93616, NM96) / Hav (HaV01, HaV08) (Lab) (Nagasaki and Yamaguchi 1998)[2]<br>- *Escherichia coli* / T4 (Lab) (Hadas *et al.* 1997)[6]<br>- *Micromonas* sp. MicA, MicB, MicC / MicVA, MicVB, MicVC (Lab) (Demory *et al.* 2017)[9]<br>- *Micromonas polaris* / MpoV (Lab) (Maat *et al.* |

| | | |
|---|---|---|
| | | 2017)[10]<br>- *Micromonas polaris* strain RCC2257, strain RCC2258 / Mpov-45T (Lab) (Piedade *et al.* 2018)[11]<br>- *Escherichia coli* / coliphage (Lab) (Ellis and Delbrück 1939)[12]<br>- *Staphylococcus aureus* / S. aureus phage (Lab) (Krueger and Fong 1937)[13] |
| Virus abundance | Temperature effects unclear | - Backwater system of Danube River (Field) (Mathias, Kirschner and Velimirov 1995)[1]<br>- Southern Beaufort Sea and Amundsen Gulf (Field) (Payet and Suttle 2007)[14]<br>- Lake Pavin (Field) (Colombet *et al.* 2009)[15]<br>- Japanese paddy field (Field) (Nakayama *et al.* 2006)[16]<br>- Michigan agricultural soils (Field) (Roy *et al.* 2020)[17]<br>- Metadata (Danovaro *et al.* 2011[18]; Williamson *et al.* 2017[19]) |
| Lysis thermal range | Temperature effects are host-dependent | - *Heterosigma akashiwo* (H93616, NM96) / Hav (HaV01, HaV08) (Lab) (Nagasaki and Yamaguchi 1998)[2]<br>- Bacteriophage 9A isolated from Arctic seawater (Lab) (Wells and Deming 2006)[3]<br>- *Escherichia coli* / coliphage isolates from the River Swift (Lab) (Seeley and Primrose 1980)[5]<br>- Metadata (Mojica and Brussaard 2014) |
| Virus-induced host mortality | Increases with temperature | - North Atlantic Ocean (Field) (Mojica *et al.* 2016) |

## FIGURES

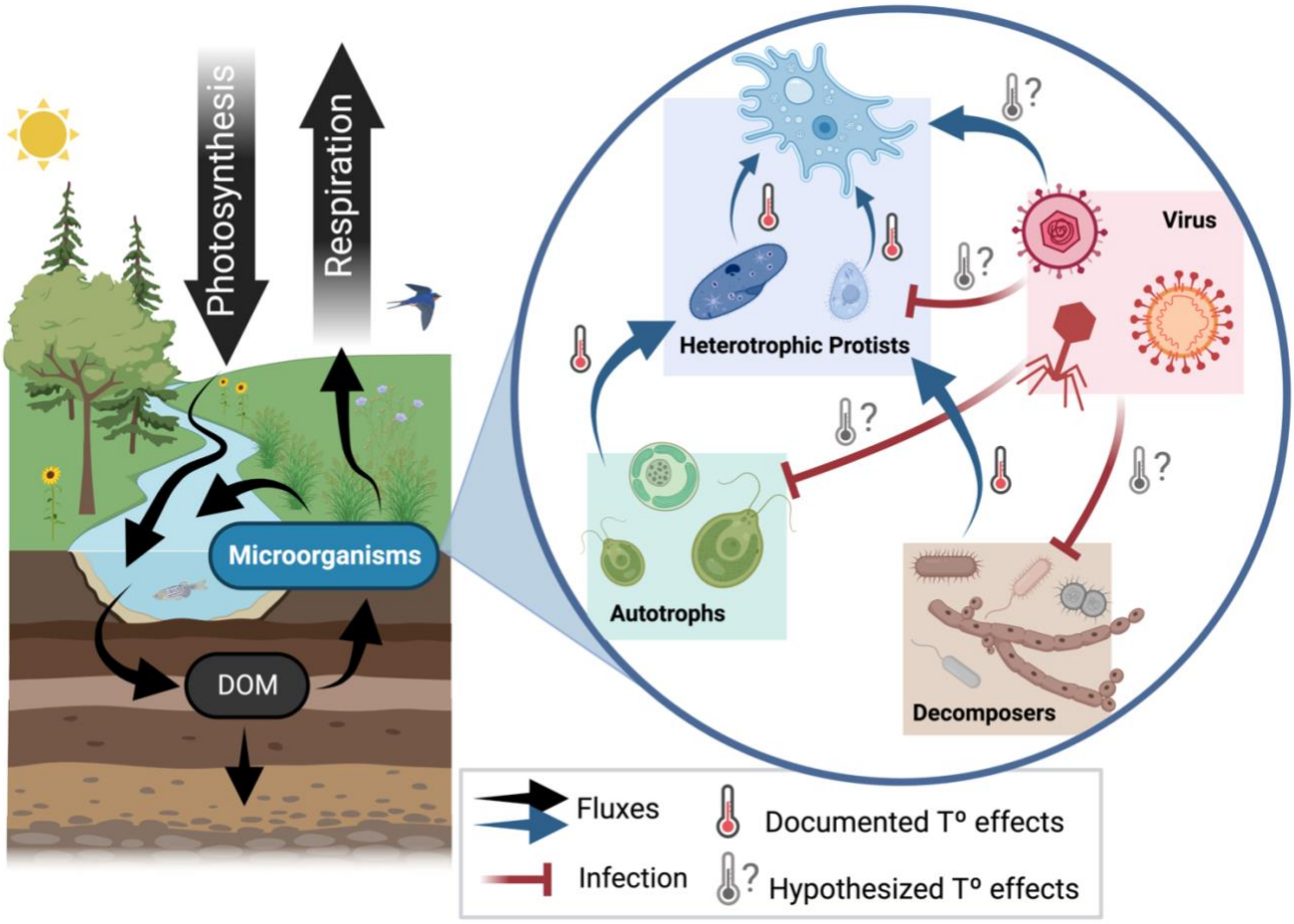


**Figure 1.** Conceptual diagram outlining the documented and hypothesized temperature effects on processes influencing global carbon cycling, including the impacts of decomposers (heterotrophic bacteria, archaea, and fungi), autotrophs (cyanobacteria and eukaryotic algae), heterotrophic protists that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

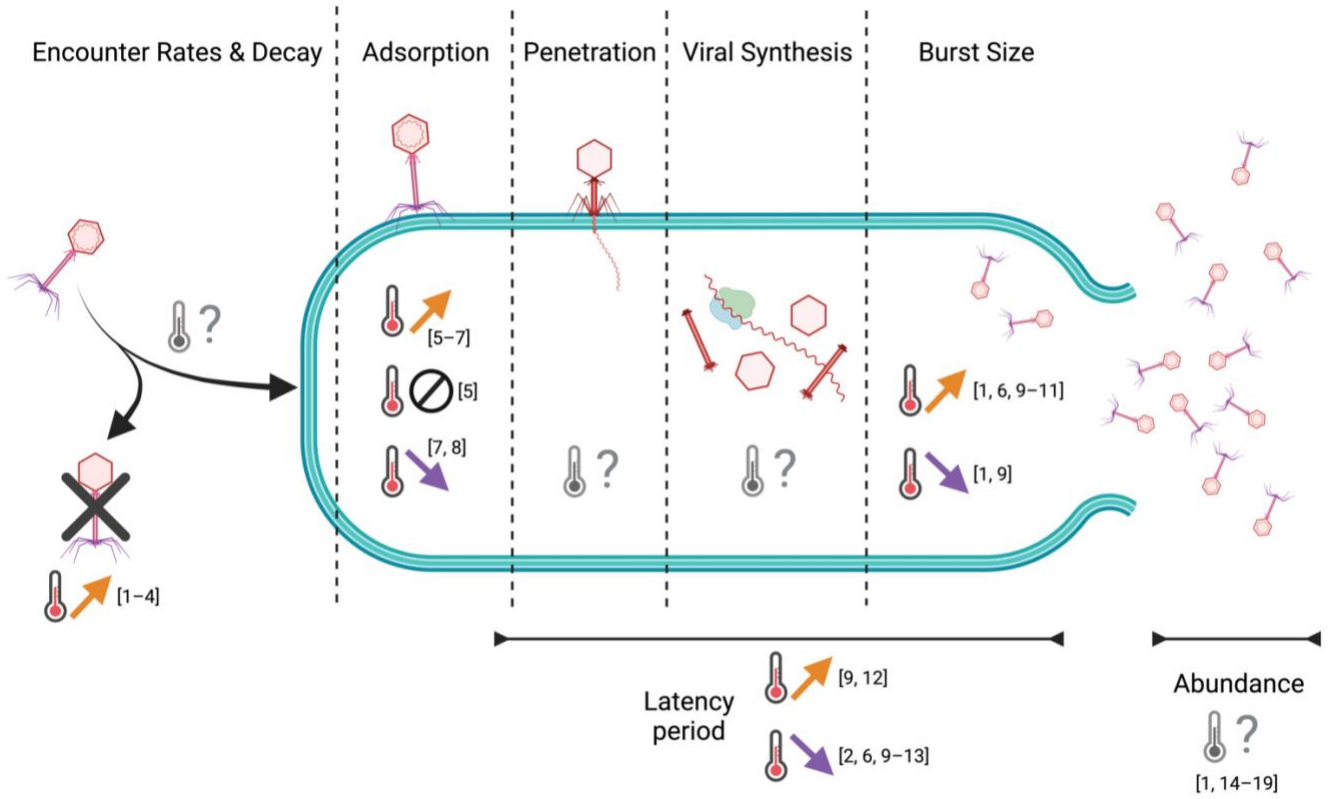


**Figure 2.** Stages of the viral lytic infection cycle and published temperature effects. Orange arrows indicate a positive effect, purple arrows indicate a negative effect, and interdictory symbols indicate no effect with warming. Gray thermometers indicate stages of the viral infection cycle that 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.

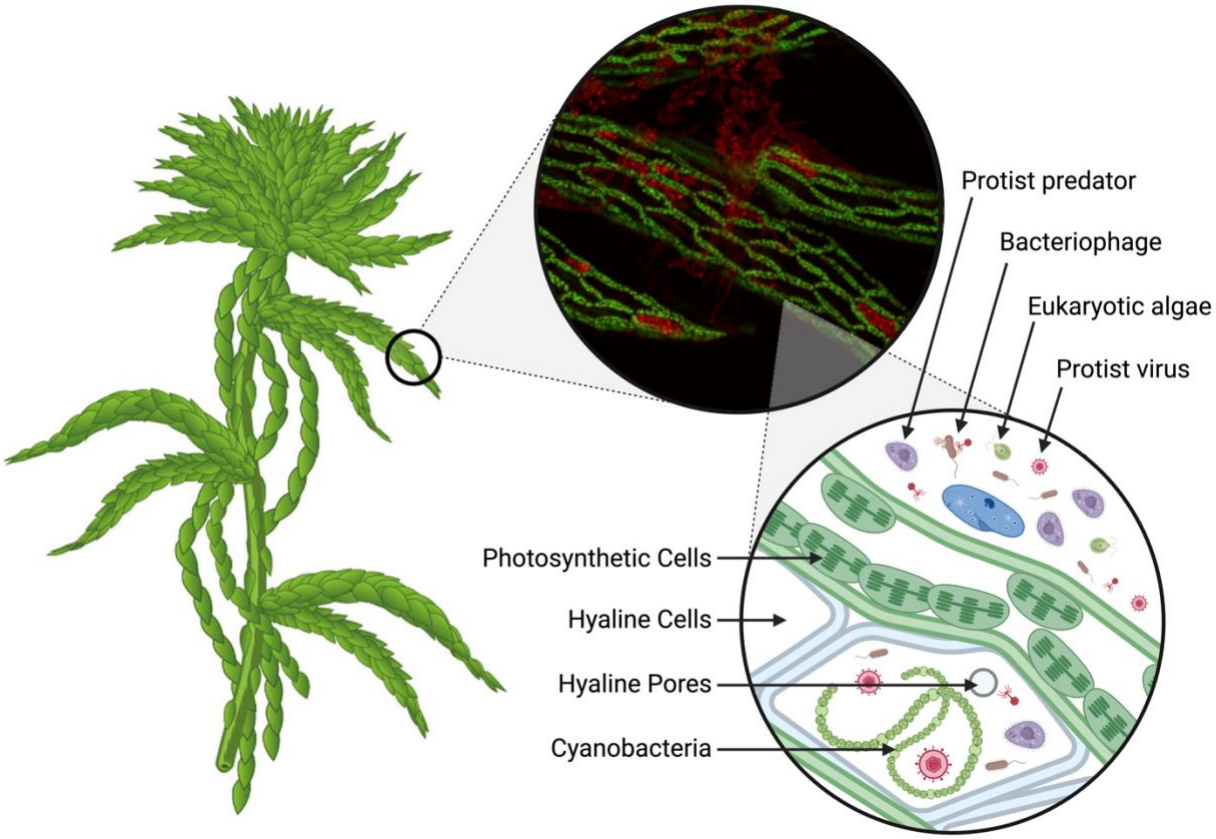


**Figure 3.** *Sphagnum* moss and associated microbial food web. Microbial species inhabit both water-filled hyaline cells of *Sphagnum* tissue and the external aquatic habitat. First inset shows cyanobacteria (in red) living inside *Sphagnum* tissue (in green, image taken using a Zeiss LSM 710 laser scanning confocal microscope, image credit: Andrea Timm and Collin Timm).

## REFERENCES


Allen AP, Gillooly JF, Brown JH. Linking the global carbon cycle to individual metabolism. *Functional Ecology* 2005;**19**:202–13.

Altermatt F, Fronhofer EA, Garnier A *et al.* Big answers from small worlds: a user's guide for protist microcosms as a model system in ecology and evolution. *Methods in Ecology and Evolution* 2015;**6**:218–31.

Atkinson D, Ciotti BJ, Montagnes DJS. Protists Decrease in Size Linearly with Temperature: ca. $2.5% \textdegree C^{-1}$. *Proceedings: Biological Sciences* 2003;**270**:2605–11.

Azam F, Fenchel T, Field JG *et al.* The Ecological Role of Water-Column Microbes in the Sea. *Marine Ecology Progress Series* 1983;**10**:257–63.

Ballaud F, Dufresne A, Francez A-J *et al.* Dynamics of Viral Abundance and Diversity in a Sphagnum-Dominated Peatland: Temporal Fluctuations Prevail Over Habitat. *Front Microbiol* 2016;**6**, DOI: 10.3389/fmicb.2015.01494.

Barbour MA, Gibert JP. Genetic and plastic rewiring of food webs under climate change. *J Anim Ecol* 2021, DOI: 10.1111/1365-2656.13541.

Bar-On YM, Phillips R, Milo R. The biomass distribution on Earth. *Proc Natl Acad Sci U S A* 2018;**115**:6506–11.

Basińska AM, Reczuga MK, Gąbka M *et al.* Experimental warming and precipitation reduction affect the biomass of microbial communities in a Sphagnum peatland. *Ecological Indicators* 2020;**112**:106059.

Bengtsson J, Setälä H, Zheng DW. Food Webs and Nutrient Cycling in Soils: Interactions and Positive Feedbacks. In: Polis GA, Winemiller KO (eds.). *Food Webs: Integration of Patterns & Dynamics*. Boston, MA: Springer US, 1996, 30–8.

Bernhardt JR, Sunday JM, O'Connor MI. Metabolic Theory and the Temperature-Size Rule Explain the Temperature Dependence of Population Carrying Capacity. *The American Naturalist* 2018;**192**:687–97.

Blodau C. Carbon cycling in peatlands — A review of processes and controls. *Environmental Reviews* 2002;**10**:111–34.

Bradford MA, McCulley RL, Crowther TW *et al.* Cross-biome patterns in soil microbial respiration predictable from evolutionary theory on thermal adaptation. *Nat Ecol Evol* 2019;**3**:223–31.

Breitbart M, Bonnain C, Malki K *et al.* Phage puppet masters of the marine microbial realm. *Nature Microbiology* 2018;**3**:754–66.

Brose U, Dunne JA, Montoya JM *et al.* Climate change in size-structured ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences* 2012;**367**:2903–12.

475 Brown JH, Gillooly JF, Allen AP *et al.* Toward a Metabolic Theory of Ecology. *Ecology*
476 2004;**85**:1771–89.

477 Bu Z, Hans J, Li H *et al.* The response of peatlands to climate warming: A review. *Acta*
478 *Ecologica Sinica* 2011;**31**:157–62.

479 Camill P, Clark JS. Climate Change Disequilibrium of Boreal Permafrost Peatlands Caused by
480 Local Processes. *The American Naturalist* 1998;**151**:207–22.

481 Canadell JG, Monteiro PMS, Costa MH *et al.* Global Carbon and other Biogeochemical Cycles
482 and Feedbacks. *IPCC AR6 WGI, Final Government Distribution*. 2021, chapter 5.

483 Carrell AA, Kolton M, Glass JB *et al.* Experimental warming alters the community composition,
484 diversity, and N2 fixation activity of peat moss (Sphagnum fallax) microbiomes. *Global*
485 *Change Biology* 2019;**25**:2993–3004.

486 Carrell AA, Lawrence TJ, Cabugao KGM *et al.* Habitat-adapted microbial communities mediate
487 Sphagnum peatmoss resilience to warming. *New Phytologist* 2022a;**234**:2111–25.

488 Carrell AA, Veličković D, Lawrence TJ *et al.* Novel metabolic interactions and environmental
489 conditions mediate the boreal peatmoss-cyanobacteria mutualism. *ISME J*
490 2022b;**16**:1074–85.

491 Cavicchioli R, Ripple WJ, Timmis KN *et al.* Scientists' warning to humanity: microorganisms and
492 climate change. *Nat Rev Microbiol* 2019;**17**:569–86.

493 Clymo RS, Hayward PM. The Ecology of Sphagnum. In: Smith AJE (ed.). *Bryophyte Ecology*.
494 Dordrecht: Springer Netherlands, 1982, 229–89.

495 Colombet J, Charpin M, Robin A *et al.* Seasonal Depth-Related Gradients in Virioplankton:
496 Standing Stock and Relationships with Microbial Communities in Lake Pavin (France).
497 *Microb Ecol* 2009;**58**:728–36.

498 Correa AMS, Howard-Varona C, Coy SR *et al.* Revisiting the rules of life for viruses of
499 microorganisms. *Nature Reviews Microbiology* 2021:1–13.

500 Crozier WJ, Federighi H. CRITICAL THERMAL INCREMENT FOR THE MOVEMENT OF
501 OSCILLATORIA. *Journal of General Physiology* 1924;**7**:137–50.

502 Danovaro R, Corinaldesi C, Dell'Anno A *et al.* Marine viruses and global climate change. *FEMS*
503 *Microbiology Reviews* 2011;**35**:993–1034.

504 Daufresne M, Lengfellner K, Sommer U. Global warming benefits the small in aquatic
505 ecosystems. *PNAS* 2009;**106**:12788–93.

506 Dell AI, Pawar S, Savage VM. Systematic variation in the temperature dependence of
507 physiological and ecological traits. *PNAS* 2011;**108**:10591–6.

508 Dell AI, Pawar S, Savage VM. Temperature dependence of trophic interactions are driven by
509 asymmetry of species responses and foraging strategy. *Journal of Animal Ecology*
510 2014;**83**:70–84.

511 DeLong JP, Lyon S. Temperature alters the shape of predator–prey cycles through effects on
512 underlying mechanisms. *PeerJ* 2020;**8**:e9377.

513 Demory D, Arsenieff L, Simon N *et al.* Temperature is a key factor in Micromonas-virus
514 interactions. *ISME J* 2017;**11**:601–12.

515 Dorrepaal E, Toet S, van Logtestijn RSP *et al.* Carbon respiration from subsurface peat
516 accelerated by climate warming in the subarctic. *Nature* 2009;**460**:616–9.

517 Ellis EL, Delbrück M. THE GROWTH OF BACTERIOPHAGE. *J Gen Physiol* 1939;**22**:365–84.

518 Emerson JB, Roux S, Brum JR *et al.* Host-linked soil viral ecology along a permafrost thaw
519 gradient. *Nat Microbiol* 2018;**3**:870–80.

520 Falkowski P, Scholes RJ, Boyle E *et al.* The Global Carbon Cycle: A Test of Our Knowledge of
521 Earth as a System. *Science* 2000;**290**:291–6.

522 Fenchel T. The microbial loop – 25 years later. *Journal of Experimental Marine Biology and*
523 *Ecology* 2008;**366**:99–103.

524 Field CB, Behrenfeld MJ, Randerson JT *et al.* Primary Production of the Biosphere: Integrating
525 Terrestrial and Oceanic Components. *Science* 1998;**281**:237–40.

526 Fischhoff IR, Huang T, Hamilton SK *et al.* Parasite and pathogen effects on ecosystem
527 processes: A quantitative review. *Ecosphere* 2020;**11**:e03057.

528 Frenken T, Brussaard CPD, Velthuis M *et al.* Warming advances virus population dynamics in a
529 temperate freshwater plankton community. *Limnology and Oceanography Letters*
530 2020;**5**:295–304.

531 Fuhrman JA. Marine viruses and their biogeochemical and ecological effects. *Nature*
532 1999;**399**:541–8.

533 Gao Z, Karlsson I, Geisen S *et al.* Protists: Puppet Masters of the Rhizosphere Microbiome.
534 *Trends in Plant Science* 2019;**24**:165–76.

535 Geisen S, Hu S, dela Cruz TEE *et al.* Protists as catalyzers of microbial litter breakdown and
536 carbon cycling at different temperature regimes. *The ISME Journal* 2021;**15**:618–21.

537 Geisen S, Lara E, Mitchell EAD *et al.* Soil protist life matters! *SOIL ORGANISMS* 2020;**92**:189–
538 96.

539 Geisen S, Mitchell EAD, Adl S *et al.* Soil protists: a fertile frontier in soil biology research. *FEMS*
540 *Microbiology Reviews* 2018;**42**:293–323.

541 Geisen S, Mitchell EAD, Wilkinson DM *et al.* Soil protistology rebooted: 30 fundamental
542 questions to start with. *Soil Biology and Biochemistry* 2017;**111**:94–103.

543 Gibert JP, Chelini M-C, Rosenthal MF *et al.* Crossing regimes of temperature dependence in
544 animal movement. *Global Change Biology* 2016;**22**:1722–36.

Gilbert D, Amblard C, Bourdier G *et al.* The Microbial Loop at the Surface of a Peatland:Structure, Function, and Impact of Nutrient Input. *Microb Ecol* 1998;**35**:83–93.

Gilbert D, Mitchell EAD. Chapter 13 Microbial diversity in Sphagnum peatlands. In: Martini IP, Martínez Cortizas A, Chesworth W (eds.). *Developments in Earth Surface Processes*. Vol 9. Elsevier, 2006, 287–318.

Gorham E. Northern Peatlands: Role in the Carbon Cycle and Probable Responses to Climatic Warming. *Ecological Applications* 1991;**1**:182–95.

Hadas H, Einav M, Fishov I *et al.* Bacteriophage T4 development depends on the physiology of its host Escherichia coli. *Microbiology (Reading)* 1997;**143 ( Pt 1)**:179–85.

ter Horst AM, Santos-Medellín C, Sorensen JW *et al.* Minnesota peat viromes reveal terrestrial and aquatic niche partitioning for local and global viral populations. *Microbiome* 2021;**9**:233.

Hurwitz BL, Hallam SJ, Sullivan MB. Metabolic reprogramming by viruses in the sunlit and dark ocean. *Genome Biology* 2013;**14**, DOI: 10.1186/gb-2013-14-11-r123.

Jassey VEJ, Signarbieux C, Hättenschwiler S *et al.* An unexpected role for mixotrophs in the response of peatland carbon cycling to climate warming. *Scientific Reports* 2015;**5**:16931.

Kayranli B, Scholz M, Mustafa A *et al.* Carbon Storage and Fluxes within Freshwater Wetlands: a Critical Review. *Wetlands* 2010;**30**:111–24.

Kendrick BJ, DiTullio GR, Cyronak TJ *et al.* Temperature-Induced Viral Resistance in Emiliania huxleyi (Prymnesiophyceae). *PLOS ONE* 2014;**9**:e112134.

Kimura M, Jia Z-J, Nakayama N *et al.* Ecology of viruses in soils: Past, present and future perspectives. *Soil Science and Plant Nutrition* 2008;**54**:1–32.

Kirschbaum MUF. Will changes in soil organic carbon act as a positive or negative feedback on global warming? *Biogeochemistry* 2000;**48**:21–51.

Kostka JE, Weston DJ, Glass JB *et al.* The Sphagnum microbiome: new insights from an ancient plant lineage. *New Phytologist* 2016;**211**:57–64.

Krueger AP, Fong J. THE RELATIONSHIP BETWEEN BACTERIAL GROWTH AND PHAGE PRODUCTION. *J Gen Physiol* 1937;**21**:137–50.

Kuppardt-Kirmse A, Chatzinotas A. Intraguild Predation: Predatory Networks at the Microbial Scale. In: Jurkevitch E, Mitchell RJ (eds.). *The Ecology of Predation at the Microscale*. Cham: Springer International Publishing, 2020, 65–87.

Lafferty KD, Allesina S, Arim M *et al.* Parasites in food webs: the ultimate missing links. *Ecology Letters* 2008;**11**:533–46.

Lara E, Mitchell EAD, Moreira D *et al.* Highly Diverse and Seasonally Dynamic Protist Community in a Pristine Peat Bog. *Protist* 2011;**162**:14–32.

Larmola T, Leppänen SM, Tuittila E-S *et al.* Methanotrophy induces nitrogen fixation during peatland development. *PNAS* 2014;**111**:734–9.

Liebner S, Svenning MM. Environmental Transcription of mmoX by Methane-Oxidizing Proteobacteria in a Subarctic Palsa Peatland. *Applied and Environmental Microbiology* 2013;**79**:701–6.

Lindo Z, Nilsson M-C, Gundale MJ. Bryophyte-cyanobacteria associations as regulators of the northern latitude carbon balance in response to global change. *Global Change Biology* 2013;**19**:2022–35.

Litchman E, de Tezanos Pinto P, Edwards KF *et al.* Global biogeochemical impacts of phytoplankton: a trait-based perspective. *Journal of Ecology* 2015;**103**:1384–96.

López-Urrutia Á, San Martin E, Harris RP *et al.* Scaling the metabolic balance of the oceans. *PNAS* 2006;**103**:8739–44.

Lurgi M, López BC, Montoya JM. Novel communities from climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* 2012;**367**:2913–22.

Lymer D, Logue JB, Brussaard CPD *et al.* Temporal variation in freshwater viral and bacterial community composition. *Freshwater Biology* 2008;**53**:1163–75.

Maat DS, Biggs T, Evans C *et al.* Characterization and Temperature Dependence of Arctic Micromonas polaris Viruses. *Viruses* 2017;**9**:134.

Maeda K, Imae Y, Shioi JI *et al.* Effect of temperature on motility and chemotaxis of Escherichia coli. *Journal of Bacteriology* 1976;**127**:1039–46.

Marr AG, Ingraham JL. Effect of temperature on the composition of fatty acids in escherichia coli. *Journal of Bacteriology* 1962;**84**:1260–7.

Martin RM, Moniruzzaman M, Stark GF *et al.* Episodic Decrease in Temperature Increases mcy Gene Transcription and Cellular Microcystin in Continuous Cultures of Microcystis aeruginosa PCC 7806. *Front Microbiol* 2020;**11**:601864.

Masson-Delmotte V, Zhai P, Pirani A *et al.* IPCC, 2021: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. In Press.

Mathias CB, Kirschner A, Velimirov B. Seasonal variations of virus abundance and viral control of the bacterial production in a backwater system of the danube river. *Appl Environ Microbiol* 1995;**61**:3734–40.

Mojica KDA, Brussaard CPD. Factors affecting virus dynamics and microbial host-virus interactions in marine environments. *FEMS Microbiol Ecol* 2014;**89**:495–515.

Mojica KDA, Huisman J, Wilhelm SW *et al.* Latitudinal variation in virus-induced mortality of phytoplankton across the North Atlantic Ocean. *ISME J* 2016;**10**:500–13.

Murray AG, Jackson GA. Viral dynamics: a model of the effects of size, shape, motion and abundance of single-celled planktonic organisms and other particles. *Marine Ecology Progress Series* 1992;**89**:103–16.

Nagasaki K, Yamaguchi M. Effect of temperature on the algicidal activity and the stability of HaV (Heterosigma akashiwo virus). *Aquatic Microbial Ecology* 1998;**15**:211–6.

Nakayama N, Okabe A, Toyota K *et al.* Phylogenetic distribution of bacteria isolated from the floodwater of a Japanese paddy field. *Soil Science and Plant Nutrition* 2006;**52**:305–12.

Nakayama N, Okumura M, Inoue K *et al.* Seasonal variations in the abundance of virus-like particles and bacteria in the floodwater of a Japanese paddy field. *Soil Science and Plant Nutrition* 2007;**53**:420–9.

Norby RJ, Childs J, Hanson PJ *et al.* Rapid loss of an ecosystem engineer: Sphagnum decline in an experimentally warmed bog. *Ecology and Evolution* 2019;**9**:12571–85.

O'Connor MI, Piehler MF, Leech DM *et al.* Warming and Resource Availability Shift Food Web Structure and Metabolism. *PLOS Biology* 2009;**7**:e1000178.

Page SE, Baird AJ. Peatlands and Global Change: Response and Resilience. *Annual Review of Environment and Resources* 2016;**41**:35–57.

Payet J, Suttle C. Physical and biological correlates of virus dynamics in the southern Beaufort Sea and Amundsen Gulf. *J Mar Syst* 2007;**74**, DOI: 10.1016/j.jmarsys.2007.11.002.

Petchey OL, McPhearson PT, Casey TM *et al.* Environmental warming alters food-web structure and ecosystem function. *Nature* 1999;**402**:69–72.

Piedade GJ, Wesdorp EM, Montenegro-Borbolla E *et al.* Influence of Irradiance and Temperature on the Virus MpoV-45T Infecting the Arctic Picophytoplankter Micromonas polaris. *Viruses* 2018;**10**:676.

Quaiser A, Dufresne A, Ballaud F *et al.* Diversity and comparative genomics of Microviridae in Sphagnum- dominated peatlands. *Frontiers in Microbiology* 2015;**6**:375.

Richardson AD, Hufkens K, Milliman T *et al.* Ecosystem warming extends vegetation activity but heightens vulnerability to cold temperatures. *Nature* 2018;**560**:368–71.

Rocca JD, Yammine A, Simonin M *et al.* Predation by protists influences the temperature response of microbial communities. *bioRxiv* 2021:2021.04.08.439073.

Rocca JD, Yammine A, Simonin M *et al.* Protist Predation Influences the Temperature Response of Bacterial Communities. *Frontiers in Microbiology* 2022;**13**.

Roy K, Ghosh D, DeBruyn JM *et al.* Temporal Dynamics of Soil Virus and Bacterial Populations in Agricultural and Early Plant Successional Soils. *Frontiers in Microbiology* 2020;**11**:1494.

650 Sarmento H, Montoya JM, Vázquez-Domínguez E *et al.* Warming effects on marine microbial
651 food web processes: how far can we go when it comes to predictions? *Philosophical*
652 *Transactions of the Royal Society B: Biological Sciences* 2010;**365**:2137–49.

653 Savage VM, Gilloly JF, Brown JH *et al.* Effects of body size and temperature on population
654 growth. *Am Nat* 2004;**163**:429–41.

655 Schimel J, Schaeffer S. Microbial control over carbon cycling in soil. *Frontiers in Microbiology*
656 2012;**3**.

657 Seeley ND, Primrose SBY 1980. The Effect of Temperature on the Ecology of Aquatic
658 Bacteriophages. *Journal of General Virology* 1980;**46**:87–95.

659 Shan J, Korbsrisate S, Withatanung P *et al.* Temperature dependent bacteriophages of a
660 tropical bacterial pathogen. *Frontiers in Microbiology* 2014;**5**:599.

661 Sherr E, Sherr B. Role of microbes in pelagic food webs: A revised concept. *Limnology and*
662 *Oceanography* 1988;**33**:1225–7.

663 Sinensky M. Homeoviscous Adaptation—A Homeostatic Process that Regulates the Viscosity of
664 Membrane Lipids in Escherichia coli. *PNAS* 1974;**71**:522–5.

665 Singer D, Metz S, Unrein F *et al.* Contrasted Micro-Eukaryotic Diversity Associated with
666 Sphagnum Mosses in Tropical, Subtropical and Temperate Climatic Zones. *Microb Ecol*
667 2019;**78**:714–24.

668 Singh BK, Bardgett RD, Smith P *et al.* Microorganisms and climate change: terrestrial
669 feedbacks and mitigation options. *Nature Reviews Microbiology* 2010;**8**:779–90.

670 Slate ML, Sullivan BW, Callaway RM. Desiccation and rehydration of mosses greatly increases
671 resource fluxes that alter soil carbon and nitrogen cycling. *Journal of Ecology*
672 2019;**107**:1767–78.

673 Smith TP, Thomas TJH, García-Carreras B *et al.* Community-level respiration of prokaryotic
674 microbes may rise with global warming. *Nature Communications* 2019;**10**:5124.

675 Steinberg DK, Landry MR. Zooplankton and the Ocean Carbon Cycle. *Annual Review of Marine*
676 *Science* 2017;**9**:413–44.

677 Stough JMA, Kolton M, Kostka JE *et al.* Diversity of Active Viral Infections within the Sphagnum
678 Microbiome. *Appl Environ Microbiol* 2018;**84**, DOI: 10.1128/AEM.01124-18.

679 Stough JMA, Tang X, Krausfeldt LE *et al.* Molecular prediction of lytic vs lysogenic states for
680 Microcystis phage: Metatranscriptomic evidence of lysogeny during large bloom events.
681 *PLOS ONE* 2017;**12**:e0184146.

682 Sullivan MB, Weitz JS, Wilhelm S. Viral ecology comes of age. *Environmental Microbiology*
683 *Reports* 2017;**9**:33–5.

684 Sutela S, Poimala A, Vainio EJ. Viruses of fungi and oomycetes in the soil environment. *FEMS*
685 *Microbiology Ecology* 2019;**95**, DOI: 10.1093/femsec/fiz119.

686 Suttle CA. Viruses in the sea. *Nature* 2005;**437**:356–61.

687 Thakur MP, Geisen S. Trophic Regulations of the Soil Microbiome. *Trends in Microbiology*
688 2019;**27**:771–80.

689 Thakur MP, Putten WH van der, Apon F *et al.* Resilience of rhizosphere microbial predators and
690 their prey communities after an extreme heat event. *Functional Ecology* 2021;**35**:216–
691 25.

692 Tomaru Y, Kimura K, Yamaguchi H. Temperature alters algicidal activity of DNA and RNA
693 viruses infecting Chaetoceros tenuissimus. *Aquatic Microbial Ecology* 2014;**73**:171–83.

694 Trap J, Bonkowski M, Plassard C *et al.* Ecological importance of soil bacterivores for ecosystem
695 functions. *Plant Soil* 2016;**398**:1–24.

696 Vaqué D, Lara E, Arrieta JM *et al.* Warming and CO2 Enhance Arctic Heterotrophic Microbial
697 Activity. *Frontiers in Microbiology* 2019;**10**:494.

698 Vile MA, Kelman Wieder R, Živković T *et al.* N2-fixation by methanotrophs sustains carbon and
699 nitrogen accumulation in pristine peatlands. *Biogeochemistry* 2014;**121**:317–28.

700 Wei W, Zhang R, Peng L *et al.* Effects of temperature and photosynthetically active radiation on
701 virioplankton decay in the western Pacific Ocean. *Sci Rep* 2018;**8**:1525.

702 Weinbauer MG. Ecology of prokaryotic viruses. *FEMS Microbiology Reviews* 2004;**28**:127–81.

703 Weitz JS, Stock CA, Wilhelm SW *et al.* A multitrophic model to quantify the effects of marine
704 viruses on microbial food webs and ecosystem processes. *The ISME Journal*
705 2015;**9**:1352–64.

706 Wells LE, Deming JW. Effects of temperature, salinity and clay particles on inactivation and
707 decay of cold-active marine Bacteriophage 9A. *Aquatic Microbial Ecology* 2006;**45**:31–9.

708 Wieczynski DJ, Singla P, Doan A *et al.* Linking species traits and demography to explain
709 complex temperature responses across levels of organization. *PNAS* 2021;**118**, DOI:
710 10.1073/pnas.2104863118.

711 Wilhelm SW, Suttle CA. Viruses and Nutrient Cycles in the Sea: Viruses play critical roles in the
712 structure and function of aquatic food webs. *BioScience* 1999;**49**:781–8.

713 Wilhelm SW, Weinbauer MG, Suttle CA *et al.* The role of sunlight in the removal and repair of
714 viruses in the sea. *Limnology and Oceanography* 1998;**43**:586–92.

715 Williamson KE, Fuhrmann JJ, Wommack KE *et al.* Viruses in Soil Ecosystems: An Unknown
716 Quantity Within an Unexplored Territory. *Annual Review of Virology* 2017;**4**:201–19.

717 Wyatt KH, McCann KS, Rober AR *et al.* Letter: Trophic interactions regulate peatland carbon
718 cycling. *Ecology Letters* 2021;**24**:781–90.

719 Yu Z, Loisel J, Brosseau DP *et al.* Global peatland dynamics since the Last Glacial Maximum.
720 *Geophysical Research Letters* 2010;**37**, DOI: 10.1029/2010GL043584.

721 Yvon-Durocher G, Allen AP. Linking community size structure and ecosystem functioning using
722 metabolic theory. *Philosophical Transactions of the Royal Society B: Biological Sciences*
723 2012;**367**:2998–3007.

724 Zhang C, Dang H, Azam F *et al.* Evolving paradigms in biological carbon cycling in the ocean.
725 *National Science Review* 2018;**5**:481–99.

726 Zhou J, Xue K, Xie J *et al.* Microbial mediation of carbon-cycle feedbacks to climate warming.
727 *Nature Climate Change* 2012;**2**:106–10.

728

## SUPPORTING INFORMATION

### Supplementary methods

*Microbial food web model*

To illustrate the potential impacts of temperature, microbial food web structure, and viral infection on the carbon and nutrient cycling, we developed a mathematical model to study the dynamics of an assortment of organisms that exist at different trophic levels and play distinct functional roles within microbial food webs—including N-fixers (*NF*), decomposers (*D*), eukaryotic algae (*A*), protist grazers (*G*), protist top predators (*P*), and viruses ($V_i$) that exclusively infect each organism (Box 1, Figure B1). The model also includes pools (external to organisms) of relevant essential elements—including, inorganic nitrogen ($N_I$; converted from $N_2$ by N-fixers), inorganic carbon ($C_I$; i.e., carbon fraction of $CO_2$), and organic carbon ($C_O$; carbon fraction of dead organic matter). These pools of essential elements are available for use by organisms and their concentrations are influenced by biological processes (e.g., photosynthesis, respiration, and mortality). Biological populations and elemental pools are referred to in terms of mass concentrations standardized by units of peat mass (units of μg / g of peat). The dynamics of all components are governed by a system of ordinary differential equations (Eqns. S1-S13). Variable and parameter definitions, units, and values used for analysis are given in Table S2. Parameter values were chosen such that all organisms exhibited non-zero equilibrium densities using the same parameter values across all biological scenarios shown in Figure B2, allowing for more direct comparison of biological scenarios.

In this model, all basal organisms (i.e., organisms that do not consume other organisms; *NF*, *D*, *A*) grow logistically and consume elements from external pools ($N_I$, $C_I$, $C_O$) according to their modes of energy acquisition: autotrophs (*NF* and *A*) use $C_I$, non-N-fixers (*D* and *A*) use $N_I$, and decomposers (*D*) use $C_O$. Element uptake rates follow Michaelis-Menten kinetics. Biomass production rates in all organisms is reduced by inefficient conversion of resources ($\varepsilon_i$). Conversion efficiency in consumers is also reduced according to the lowest stoichiometric ratio (carbon or nitrogen) between a given resource organism and its consumer ($q_{element,resource}$ / $q_{element,consumer}$; i.e., Leipig's law of the minimum). All organisms are infected by viruses that are specific to each host. All elemental pools operate as chemostats with an inflow rate ($\alpha_k$) and an outflow rate ($\delta_k$). Inorganic nitrogen ($N_I$) increases with respiration and decreases with growth of decomposers (*D*) and eukaryotic algae (*A*). Inorganic carbon ($C_I$) increases with respiration and decreases with growth of N-fixers (*NF*) and eukaryotic algae (*A*). Organic carbon increases with mortality (*m*, organisms and viruses) and viral lysis ($\phi$) and decreases with growth of decomposers (*D*). All temperature dependencies follow Sharpe-Schoolfield functional forms (Schoolfield *et al.* 1981) (Eqn. S14) with activation energies that are specific to each rate: respiration (0.65eV (Brown *et al.* 2004)), photosynthesis (0.32eV (Allen *et al.* 2005)), mortality (0.45eV (Savage *et al.* 2004)), and consumption (0.65eV (Brown *et al.* 2004; Dell *et al.* 2011a)). Viral lysis rates and burst sizes were assumed to follow established activation energies of consumption (0.65eV). Although we assume these temperature sensitivities here for simplicity, we note that a great deal of variation exists in the activation energies of various metabolic processes and across taxa (Dell *et al.* 2011b; Smith *et al.* 2019) and that this variation could

affect overall food web responses to warming. More specific temperature responses could easily be incorporated in future models by replaced those used here.

| | | |
|---|---|---|
| Nitrogen-fixer: | $\dot{NF} = NF\left(\varepsilon_N \mu_{NF}(T)\frac{C_I}{h_{C_I,NF}+C_I}\left(1-\frac{NF}{K_{NF}}\right) - a_{NF,G}(T)G - a_{NF,P}(T)P - \phi_{NF}(T)V_{NF} - r_{NF}(T) - m_{NF}(T)\right)$ | (S1) |
| Decomposer: | $\dot{D} = D\left(\varepsilon_D \mu_D(T)\frac{N_I}{h_{N_I,D}+N_I}\frac{C_O}{h_{C_O,D}+C_O}\left(1-\frac{D}{K_D}\right) - a_{D,G}(T)G - a_{D,P}(T)P - \phi_D(T)V_D - r_D(T) - m_D(T)\right)$ | (S2) |
| Eukaryotic Algae: | $\dot{A} = A\left(\varepsilon_A \mu_A(T)\frac{N_I}{h_{N_I,A}+N_I}\frac{C_I}{h_{C_I,A}+C_I}\left(1-\frac{A}{K_A}\right) - a_{A,P}(T)P - \phi_A(T)V_A - r_A(T) - m_A(T)\right)$ | (S3) |
| Grazer: | $\dot{G} = G\left(\varepsilon_G min\left(\frac{q_{N,NF}}{q_{N,G}},\frac{q_{C,NF}}{q_{C,G}}\right)a_{NF,G}(T)NF + \varepsilon_G min\left(\frac{q_{N,D}}{q_{N,G}},\frac{q_{C,D}}{q_{C,G}}\right)a_{D,G}(T)D - a_{G,P}(T)P - \phi_G(T)V_G - r_G(T) - m_G(T)\right)$ | (S4) |
| Predator: | $\dot{P} = P\left(\varepsilon_P min\left(\frac{q_{N,NF}}{q_{N,P}},\frac{q_{C,NF}}{q_{C,P}}\right)a_{NF,P}(T)NF + \varepsilon_P min\left(\frac{q_{N,D}}{q_{N,P}},\frac{q_{C,D}}{q_{C,P}}\right)a_{D,P}(T)D + \varepsilon_P min\left(\frac{q_{N,A}}{q_{N,P}},\frac{q_{C,A}}{q_{C,P}}\right)a_{A,P}(T)A + \varepsilon_P min\left(\frac{q_{N,G}}{q_{N,P}},\frac{q_{C,G}}{q_{C,P}}\right)a_{G,P}(T)G - \phi_P(T)V_P - r_P(T) - m_P(T)\right)$ | (S5) |
| Virus (N-fixer): | $\dot{V}_{NF} = V_{NF}\left(\beta_{NF}(T)\phi_{NF}(T)NF - m_V(T)\right)$ | (S6) |
| Virus (Decomposer): | $\dot{V}_D = V_D\left(\beta_D(T)\phi_D(T)D - m_V(T)\right)$ | (S7) |
| Virus (Algae): | $\dot{V}_A = V_A\left(\beta_A(T)\phi_A(T)A - m_V(T)\right)$ | (S8) |
| Virus (Grazer): | $\dot{V}_G = V_G\left(\beta_G(T)\phi_G(T)G - m_V(T)\right)$ | (S9) |
| Virus (Predator): | $\dot{V}_P = V_P\left(\beta_P(T)\phi_P(T)P - m_V(T)\right)$ | (S10) |
| Inorganic Nitrogen ($N_I$): | $\dot{N}_I = \alpha_{N_I} + r_{NF}(T)q_{N,NF}NF + r_D(T)q_{N,D}D + r_A(T)q_{N,A}A + r_G(T)q_{N,G}G + r_P(T)q_{N,P}P - q_{N,D}\mu_D(T)\frac{N_I}{h_{N_I,D}+N_I}\frac{C_O}{h_{C_O,D}+C_O}D - q_{N,A}\mu_A(T)\frac{N_I}{h_{N_I,A}+N_I}\frac{C_I}{h_{C_I,A}+C_I}A - \delta_{N_I}N_I$ | (S11) |
| Inorganic Carbon ($C_I$): | $\dot{C}_I = \alpha_{C_I} + r_{NF}(T)q_{C,NF}NF + r_D(T)q_{C,D}D + r_A(T)q_{C,A}A + r_G(T)q_{C,G}G + r_P(T)q_{C,P}P - q_{C,NF}\mu_{NF}(T)\frac{C_I}{h_{C_I,NF}+C_I}NF - q_{C,A}\mu_A(T)\frac{N_I}{h_{N_I,A}+N_I}\frac{C_I}{h_{C_I,A}+C_I}A - \delta_{C_I}C_I$ | (S12) |
| Organic Carbon ($C_O$): | $\dot{C}_O = \alpha_{C_O} + m_{NF}(T)q_{C,NF}NF + m_D(T)q_{C,D}D + m_A(T)q_{C,A}A + m_G(T)q_{C,G}G + m_P(T)q_{C,P}P + m_V(T)q_{C,V}(V_{NF}+V_D+V_A+V_G+V_P) + \phi_{NF}(T)V_{NF}q_{C,NF}NF + \phi_D(T)V_Dq_{C,D}D + \phi_A(T)V_Aq_{C,A}A + \phi_G(T)V_Gq_{C,G}G + \phi_P(T)V_Pq_{C,P}P - q_{C,D}\mu_D(T)\frac{N_I}{h_{N_I,D}+N_I}\frac{C_O}{h_{C_O,D}+C_O}D - \delta_{C_O}C_O$ | (S13) |

## Supplementary Tables

**Table S1.** Variables and parameters used in the microbial food web model. For parameters that are functions of temperature ($f(T)$), values are given at a reference temperature of 20°C.

| Variable/Parameter | Definition | Units | Value |
|---|---|---|---|
| $(NF, D, A, G, P)$ | Biomass conc. | µg $g_{peat}^{-1}$ | na |
| $(N_I, C_I, C_O)$ | Nutrient conc. | µg $g_{peat}^{-1}$ | na |
| $\varepsilon_i$ | Production efficiency | na | 0.8 |
| $\mu_i(T)$ | Max growth rate | $d^{-1}$ | 2.5 |
| $h_{k,i}$ | Half-saturation constant | g | 10 |
| $K_i$ | Carrying capacity | µg $g_{peat}^{-1}$ | $K_{NF}, K_A$ = 500<br>$K_D$ = 1000 |
| $a_{i,j}(T)$ | Consumption rate | $d^{-1}$ (µg $g_{peat}$)$^{-1}$ | $a_{NF,G}, a_{D,G}$ = 0.01<br>$a_{NF,P}, a_{D,P}$ = 0.0001<br>$a_{A,P}$ = 0.001<br>$a_{G,P}$ = 0.08 |
| $\phi_i(T)$ | Lysis rate | $d^{-1}$ (µg $g_{peat}$)$^{-1}$ | 0.01 |
| $r_i(T)$ | Respiration rate | $d^{-1}$ | $r_{NF}, r_A$ = 0.05<br>$r_D$ = 0.09<br>$r_G$ = 0.2<br>$r_P$ = 0.3 |
| $m_i(T)$ | Mortality rate | $d^{-1}$ | $m_{NF}$ = 0.05<br>$m_D$ = 0.01<br>$m_A, m_G, m_P$ = 0.1 |
| $q_{k,i}$ | Elemental content | g $g^{-1}$ | $q_{N,NF}, q_{N,D}$ = 0.05<br>$q_{N,A}, q_{N,G}$ = 0.03<br>$q_{N,P}$ = 0.08<br>$q_C$ = 0.5 |
| $\beta_i(T)$ | Burst size | $d^{-1}$ (µg $g_{peat}$)$^{-1}$ | $\beta_{NF}, \beta_D$ = 0.05<br>$\beta_A, \beta_G, \beta_P$ = 0.03 |
| $\alpha_k$ | Inflow rate | µg $g_{peat}^{-1}$ $d^{-1}$ | $\alpha_{N_I}$ = 6<br>$\alpha_{C_I}$ = 100<br>$\alpha_{C_O}$ = 30 |
| $\delta_k$ | Outflow rate | $d^{-1}$ | $\delta_{N_I}, \delta_{C_I}, \delta_{C_O}$ = 0.01 |

**Table S2.** Detailed description and summarized results for select published studies of temperature effects on viruses.

| Type of Study | Location or Host-Virus system | Observed Temperature Effects | Reference |
|---|---|---|---|
| Environmental | Backwater system of Danube River | · Higher temperature induced higher viral decay rates<br>· Viral abundance was tightly correlated with seasonal bacterial abundance one year, but not the next<br>· The lowest percentage of bacteria infected by phage were observed at 23-26°C, the highest at 6-22°C, and between at ≤ 5°C<br>· Burst size was temperature dependent | (Mathias *et al.* 1995) |
| Laboratory | *Heterosigma akashiwo* (H93616, NM96) / Hav (HaV01, HaV08) | · Decay rates increased with increasing temperature<br>· Latent phase decreased with increasing temperature<br>· Thermal ranges of lysis by virus were unique for different host-virus pairs | (Nagasaki & Yamaguchi 1998) |
| Laboratory | Bacteriophage 9A isolated from Arctic seawater | · The half-life of infective phages decreased with increasing temperature | (Wells & Deming 2006) |
| Laboratory | Samples from Western Pacific Ocean | · Increases in temperature and photosynthetic radiation resulted in higher virus decay rates<br>· Low fluorescence viruses were more sensitive to warming and increased PAR than high fluorescence viruses | (Wei *et al.* 2018) |
| Metadata | *N/A* | · Temperatures at which most marine viruses are inactivated fall outside of the host temperature range | (Mojica & Brussaard 2014) |
| Laboratory | *Escherichia coli* / coliphage isolates from the River Swift | · Temperature range of phages were independent of host growth temperature<br>· Temperature was seen to affect the adsorption of 2 phages and the multiplication of another 2 | (Seeley & Primrose 1980) |
| Laboratory | *Escherichia coli* / T4 | · Adsorptions rates increased with increasing growth rate and positively correlated with cell size<br>· The rate of phage release and burst size increased with growth rate, but the length of the eclipse and latent periods decreased with growth rate<br>· Burst size was dependent on both growth rate and time until lysis | (Hadas *et al.* 1997) |
| Laboratory | *Emiliana huyxleyi* CCMP374 / EhV86 | · 3°C increase in temperature induces a viral resistant host phenotype | (Kendrick *et al.* 2014) |
| Laboratory | *Chaetoceros tenuissimus* / Cten DNAV and Cten RNAV | · Susceptibility of all strains to Cten DNAV increased with temperature up to $T_{opt}$<br>· Temperature range and degree of susceptibility to Cten RNAV was strain dependent<br>· Maximum burst size of Cten DNAV and minimum burst size of Cten RNAV were both observed between 15-20°C | (Tomaru *et al.* 2014) |

| | | | |
|---|---|---|---|
| Laboratory | *Staphylococcus aureus* / *S. aureus* phage | · The rate of phage production is related to the growth rate of the host. Higher growth rates up to T(opt) result in shorter latency periods, though T > T(opt) result in longer latency periods | (Krueger & Fong 1937) |
| Laboratory | *Escherichia coli* / coliphage | · Latency period decreases with increasing temperature and is directly inversely proportional to the division rate of bacteria | (Ellis & Delbrück 1939) |
| Laboratory | *Micromonas* sp. MicA, MicB, MicC / MicVA, MicVB, MicVC | · At temperatures < $T_{opt}$, latent periods were increased, host cell lysis was delayed, and viral yield was reduced<br>· Cell lysis did not usually occur at temperatures > $T_{opt}$<br>· At temperatures slightly above $T_{opt}$, chronic infection (viral production with no cell lysis) was observed<br>· At temperatures much above $T_{opt}$, no viral progeny were produced | (Demory *et al.* 2017) |
| Laboratory | *Micromonas polaris* / MpoV | · Higher temperatures resulted in shorter latent periods and increased burst sizes | (Maat *et al.* 2017) |
| Laboratory | *Micromonas polaris* strain RCC2257, strain RCC2258 / Mpov-45T | · Higher temperature (7°C vs. 3°C) caused earlier cell lysis and increased burst size, except in low light conditions | (Piedade *et al.* 2018) |
| Environmental | Southern Beaufort Sea and Amundsen Gulf | · Seasonal and spatial variation in virus concentrations were correlated with Chl-a concentration, bacterial abundance and composition, temperature, salinity, and depth<br>· Percentage of variance explained by temperature was inconsistent between seasons | (Payet & Suttle 2007) |
| Environmental | Lake Pavin | · Virus abundances correlated most closely with host abundance<br>· Surface bacterial abundances were largely influenced by temperature while monimolimnion bacterial abundances likely influenced by organic matter export during surface blooms | (Colombet *et al.* 2009) |
| Metadata | N/A | · Positive relationships were observed between viral abundance and temperature within all distinct oceanic regions examined, however a global decreasing trend was seen across these regions when all data was assessed together<br>· Water column viral production increased with temperature in polar and cold temperate regions, but decreased with temperature in warm temperate systems | (Danovaro *et al.* 2011) |
| Environmental | Japanese paddy field flood waters | · Viral abundance changed seasonally, but was highly correlated with bacterial abundance | (Nakayama *et al.* 2007) |
| Environmental | North Atlantic Ocean | · Shift from virus-induced to grazing-induced phytoplankton mortality with increased latitude (decreased temperature) | (Mojica *et al.* 2016) |

| | | | |
|---|---|---|---|
| Environmental | Michigan agricultural soils | -Viral abundance changed seasonally; abundance was highly correlated to bacterial abundance, organic carbon content and total nitrogen | (Roy *et al.* 2020) |
| Metadata | Global | -Viral abundances are several orders of magnitude higher in cold deserts compared to hot deserts | (Williamson *et al.* 2017) |

**References**


Allen, A.P., Gillooly, J.F. & Brown, J.H. (2005). Linking the global carbon cycle to individual metabolism. *Funct. Ecol.*, 19, 202–213.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004). Toward a Metabolic Theory of Ecology. *Ecology*, 85, 1771–1789.

Colombet, J., Charpin, M., Robin, A., Portelli, C., Amblard, C., Cauchie, H.M., *et al.* (2009). Seasonal Depth-Related Gradients in Virioplankton: Standing Stock and Relationships with Microbial Communities in Lake Pavin (France). *Microb. Ecol.*, 58, 728–736.

Danovaro, R., Corinaldesi, C., Dell'Anno, A., Fuhrman, J.A., Middelburg, J.J., Noble, R.T., *et al.* (2011). Marine viruses and global climate change. *FEMS Microbiol. Rev.*, 35, 993–1034.

Dell, A.I., Pawar, S. & Savage, V.M. (2011a). Systematic variation in the temperature dependence of physiological and ecological traits. *Proc. Natl. Acad. Sci.*, 108, 10591–10596.

Dell, A.I., Pawar, S. & Savage, V.M. (2011b). Systematic variation in the temperature dependence of physiological and ecological traits. *Proc. Natl. Acad. Sci.*, 108, 10591–10596.

Demory, D., Arsenieff, L., Simon, N., Six, C., Rigaut-Jalabert, F., Marie, D., *et al.* (2017). Temperature is a key factor in Micromonas-virus interactions. *ISME J.*, 11, 601–612.

Ellis, E.L. & Delbrück, M. (1939). THE GROWTH OF BACTERIOPHAGE. *J. Gen. Physiol.*, 22, 365–384.

Hadas, H., Einav, M., Fishov, I. & Zaritsky, A. (1997). Bacteriophage T4 development depends on the physiology of its host Escherichia coli. *Microbiol. Read. Engl.*, 143 ( Pt 1), 179–185.

Kendrick, B.J., DiTullio, G.R., Cyronak, T.J., Fulton, J.M., Mooy, B.A.S.V. & Bidle, K.D. (2014). Temperature-Induced Viral Resistance in Emiliania huxleyi (Prymnesiophyceae). *PLOS ONE*, 9, e112134.

Krueger, A.P. & Fong, J. (1937). THE RELATIONSHIP BETWEEN BACTERIAL GROWTH AND PHAGE PRODUCTION. *J. Gen. Physiol.*, 21, 137–150.

Maat, D.S., Biggs, T., Evans, C., Van Bleijswijk, J.D.L., Van der Wel, N.N., Dutilh, B.E., *et al.* (2017). Characterization and Temperature Dependence of Arctic Micromonas polaris Viruses. *Viruses*, 9, 134.

Mathias, C.B., Kirschner, A. & Velimirov, B. (1995). Seasonal variations of virus abundance and viral control of the bacterial production in a backwater system of the danube river. *Appl. Environ. Microbiol.*, 61, 3734–3740.

Mojica, K.D.A. & Brussaard, C.P.D. (2014). Factors affecting virus dynamics and microbial host-virus interactions in marine environments. *FEMS Microbiol. Ecol.*, 89, 495–515.

Mojica, K.D.A., Huisman, J., Wilhelm, S.W. & Brussaard, C.P.D. (2016). Latitudinal variation in virus-induced mortality of phytoplankton across the North Atlantic Ocean. *ISME J.*, 10, 500–513.

Nagasaki, K. & Yamaguchi, M. (1998). Effect of temperature on the algicidal activity and the stability of HaV (Heterosigma akashiwo virus). *Aquat. Microb. Ecol.*, 15, 211–216.

Nakayama, N., Okumura, M., Inoue, K., Asakawa, S. & Kimura, M. (2007). Seasonal variations in the abundance of virus-like particles and bacteria in the floodwater of a Japanese paddy field. *Soil Sci. Plant Nutr.*, 53, 420–429.

Payet, J. & Suttle, C. (2007). Physical and biological correlates of virus dynamics in the southern Beaufort Sea and Amundsen Gulf. *J Mar Syst*, 74.

Piedade, G.J., Wesdorp, E.M., Montenegro-Borbolla, E., Maat, D.S. & Brussaard, C.P.D. (2018). Influence of Irradiance and Temperature on the Virus MpoV-45T Infecting the Arctic Picophytoplankter Micromonas polaris. *Viruses*, 10, 676.

Roy, K., Ghosh, D., DeBruyn, J.M., Dasgupta, T., Wommack, K.E., Liang, X., *et al.* (2020). Temporal Dynamics of Soil Virus and Bacterial Populations in Agricultural and Early Plant Successional Soils. *Front. Microbiol.*, 11, 1494.

Savage, V.M., Gilloly, J.F., Brown, J.H. & Charnov, E.L. (2004). Effects of body size and temperature on population growth. *Am. Nat.*, 163, 429–441.

Schoolfield, R.M., Sharpe, P.J.H. & Magnuson, C.E. (1981). Non-linear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. *J. Theor. Biol.*, 88, 719–731.

Seeley, N.D. & Primrose, S.B.Y. 1980. (1980). The Effect of Temperature on the Ecology of Aquatic Bacteriophages. *J. Gen. Virol.*, 46, 87–95.

Smith, T.P., Thomas, T.J.H., García-Carreras, B., Sal, S., Yvon-Durocher, G., Bell, T., *et al.* (2019). Community-level respiration of prokaryotic microbes may rise with global warming. *Nat. Commun.*, 10, 5124.

Tomaru, Y., Kimura, K. & Yamaguchi, H. (2014). Temperature alters algicidal activity of DNA and RNA viruses infecting Chaetoceros tenuissimus. *Aquat. Microb. Ecol.*, 73, 171–183.

Wei, W., Zhang, R., Peng, L., Liang, Y. & Jiao, N. (2018). Effects of temperature and photosynthetically active radiation on virioplankton decay in the western Pacific Ocean. *Sci. Rep.*, 8, 1525.

Wells, L.E. & Deming, J.W. (2006). Effects of temperature, salinity and clay particles on inactivation and decay of cold-active marine Bacteriophage 9A. *Aquat. Microb. Ecol.*, 45, 31–39.

Williamson, K.E., Fuhrmann, J.J., Wommack, K.E. & Radosevich, M. (2017). Viruses in Soil Ecosystems: An Unknown Quantity Within an Unexplored Territory. *Annu. Rev. Virol.*, 4, 201–219.