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Viral infections mediate microbial controls on ecosystem responses to global warming

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Keywords: Virus, Food webs, Climate change, Microbiome, Carbon cycle, Ecosystem functioning

Article Type: Perspective

Word counts: Abstract (200), Main text (3575), Box (932)

References (129), Figures (5), Tables (1), Boxes (1)

Statement of authorship:

All authors conceived the study. DJW, KMY, and ERD reviewed literature. DJW performed all mathematical modeling. DJW, KMY, SWW, & 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

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 (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.* 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) 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” in 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 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). 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 knowledge 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

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, Ciotti and Montagnes 2003; Daufresne, Lengfellner and Sommer 2009; Martin *et al.* 2020) and population densities (Savage *et al.* 2004; Bernhardt, Sunday and O'Connor 2018) often decrease while motility increases (Crozier and Federighi 1924; Maeda *et al.* 1976; Dell, Pawar and Savage 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, 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 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 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 complex and differential impacts on the dynamics and mortality of hosts that perform different ecosystem functions (Sarmiento *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 N₂,
but supply 5%–20% of CO₂ 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 CO₂ and CH₄ (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.

ACKNOWLEDGMENTS

This work was supported by a U.S. Department of Energy, Office of Science, Office of Biological and Environmental Research, Genomic Science Program Grant to JPG, under Award Number DE-SC0020362. Oak Ridge National Laboratory is managed by UT-Battelle, LLC, for the US DOE under contract DE-AC05-00OR22725.

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 (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 host biochemistry and population dynamics (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.

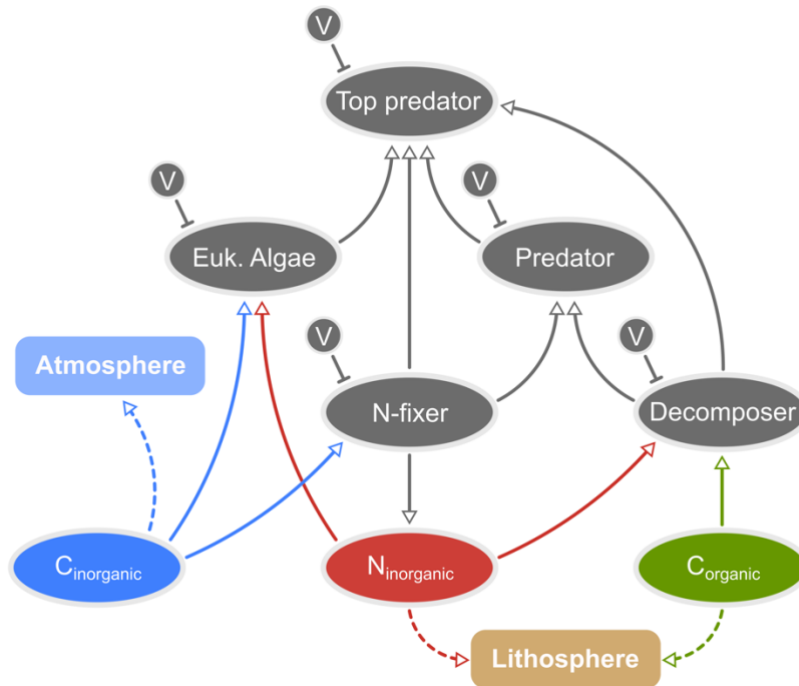


Figure B1. Hypothetical microbial food web in *Sphagnum* peatlands including organisms and nitrogen and carbon flow. Arrows represent flow between components. Each type of organism consumes elements or other organisms based on its unique stoichiometric requirements and is also subject to infection by 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.

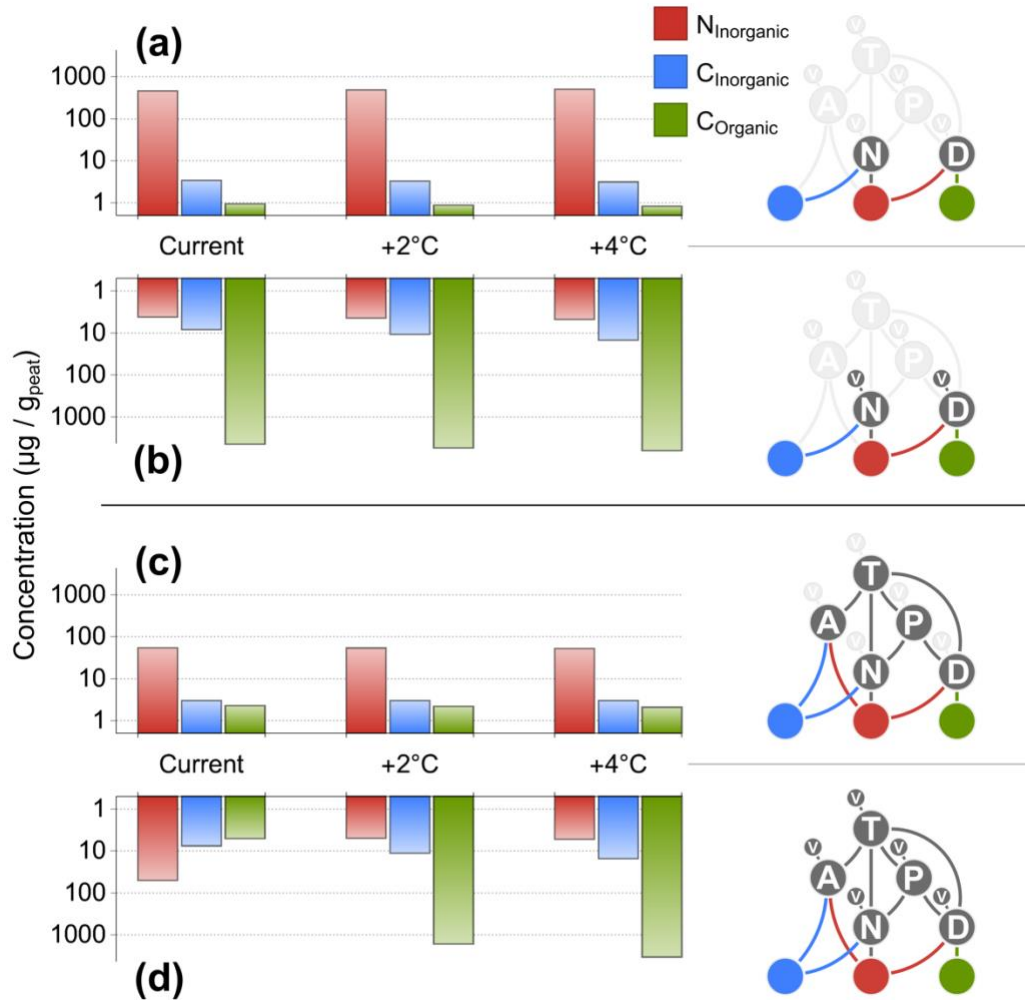


Figure B2. The effects of warming on equilibrium concentrations of nitrogen and carbon in the model microbial food web from Fig. B1. Four scenarios are shown to assess the influences of different food web components: (a) non-protists only (N + D), (b) non-protists + viruses (N + D + V), (c) non-protists + 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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386 TABLES

387 **Table 1.** Select published studies of temperature effects on viruses. A more detailed description
 388 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 2006) ³
		- Samples from Western Pacific Ocean (Lab) (Wei <i>et al.</i> 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 <i>et al.</i> 1997) ⁶
		- <i>Chaetoceros tenuissimus</i> / Cten DNAV and Cten RNAV (Lab) (Tomaru, Kimura and Yamaguchi 2014) ⁷
	Decreases with temperature	- <i>Chaetoceros tenuissimus</i> / Cten DNAV and Cten RNAV (Lab) (Tomaru, Kimura and Yamaguchi 2014) ⁷
		- <i>Emiliana huxleyi</i> CCMP374 / EhV86 (Lab) (Kendrick <i>et al.</i> 2014) ⁸
	No effect of temperature	- <i>Escherichia coli</i> / 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
		- <i>Escherichia coli</i> / T4 (Lab) (Hadas <i>et al.</i> 1997) ⁶
		- <i>Micromonas</i> sp. MicA, MicB, MicC / MicVA, MicVB, MicVC (Lab) (Demory <i>et al.</i> 2017) ⁹
		- <i>Micromonas polaris</i> / MpoV (Lab) (Maat <i>et al.</i> 2017) ¹⁰
	Decreases with temperature	- <i>Micromonas polaris</i> strain RCC2257, strain RCC2258 / Mpov-45T (Lab) (Piedade <i>et al.</i> 2018) ¹¹
		- Backwater system of Danube River (Field) (Mathias, Kirschner and Velimirov 1995) ¹
Latency period	Increases with temperature	- <i>Micromonas</i> sp. MicA, MicB, MicC / MicVA, MicVB, MicVC (Lab) (Demory <i>et al.</i> 2017) ⁹
		- <i>Escherichia coli</i> / coliphage (Lab) (Ellis and Delbrück 1939) ¹²
	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 <i>et al.</i> 1997) ⁶
		- <i>Micromonas</i> sp. MicA, MicB, MicC / MicVA, MicVB, MicVC (Lab) (Demory <i>et al.</i> 2017) ⁹
		- <i>Micromonas polaris</i> / MpoV (Lab) (Maat <i>et al.</i>

		2017) ¹⁰
		- <i>Micromonas polaris</i> strain RCC2257, strain RCC2258 / Mpov-45T (Lab) (Piedade <i>et al.</i> 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
Virus abundance	Temperature effects unclear	<ul style="list-style-type: none"> - 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 <i>et al.</i> 2009)¹⁵ - Japanese paddy field (Field) (Nakayama <i>et al.</i> 2006)¹⁶ - Michigan agricultural soils (Field) (Roy <i>et al.</i> 2020)¹⁷ - Metadata (Danovaro <i>et al.</i> 2011¹⁸; Williamson <i>et al.</i> 2017¹⁹)
Lysis thermal range	Temperature effects are host-dependent	<ul style="list-style-type: none"> - <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 <i>et al.</i> 2016)

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FIGURES

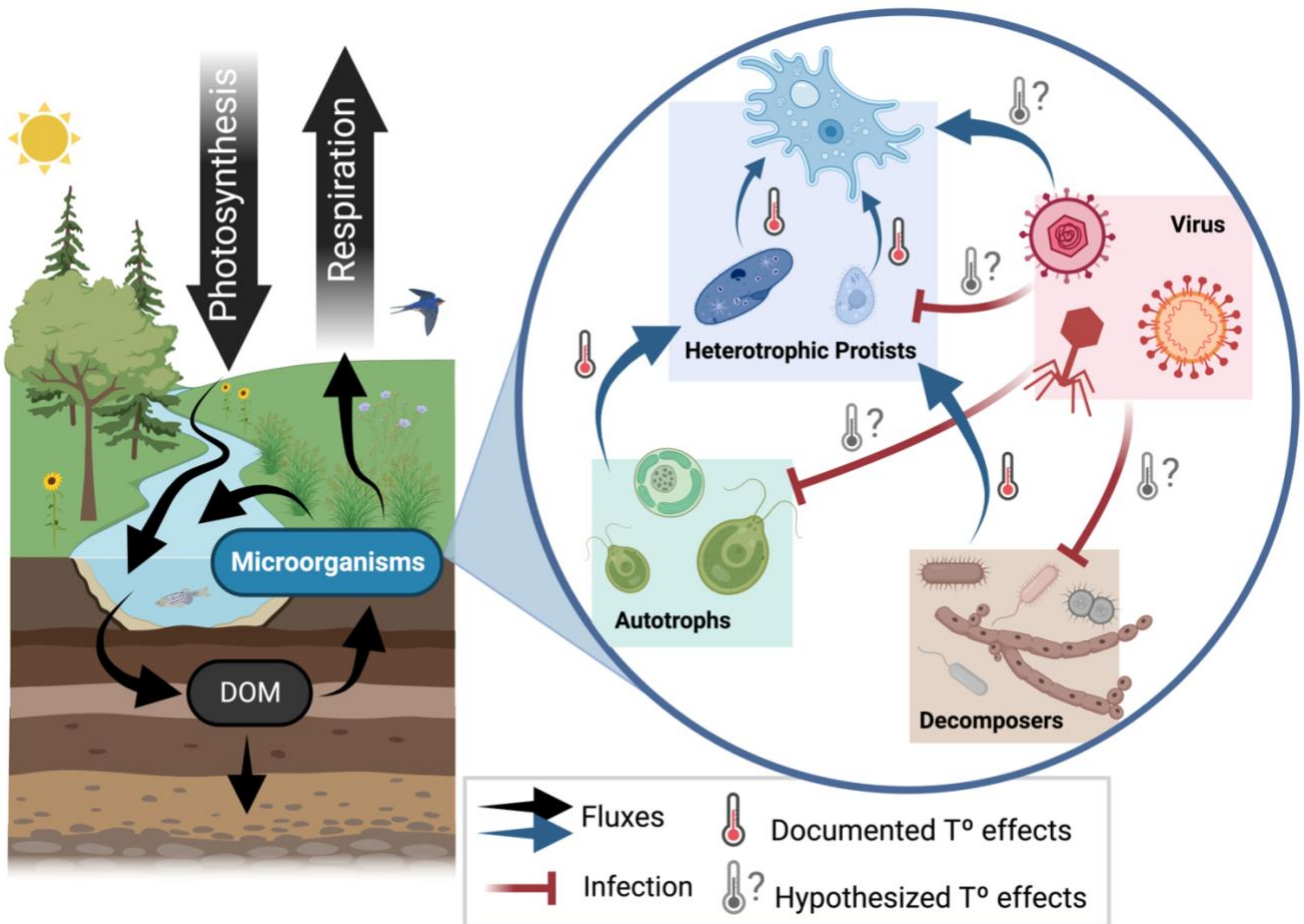


Figure 1. Conceptual diagram outlining the documented and hypothesized temperature effects on processes influencing global carbon cycling, including the impacts of decomposers (heterotrophic bacteria, archaea, and fungi), autotrophs (cyanobacteria and eukaryotic algae), heterotrophic protists that consume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

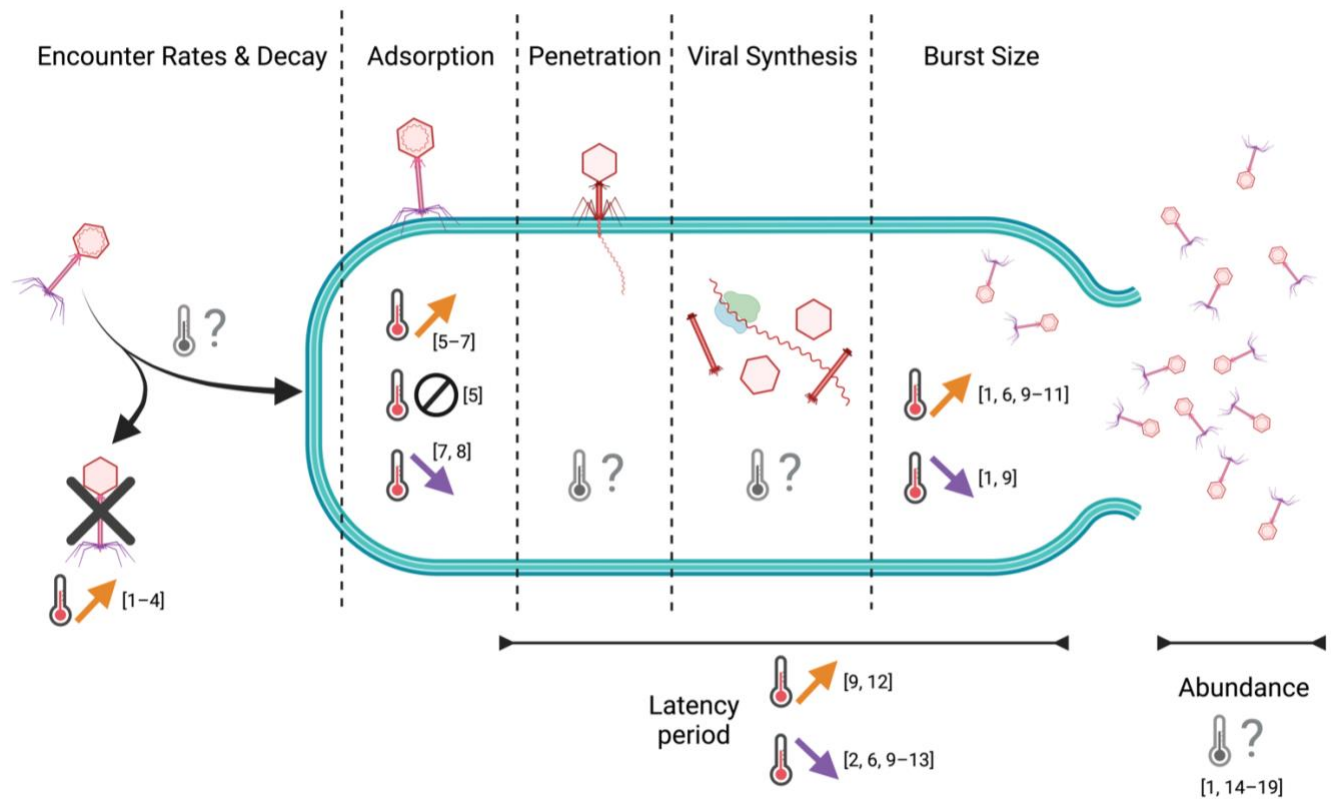


Figure 2. Stages of the viral lytic infection cycle and published temperature effects. Orange arrows indicate a positive effect, purple arrows indicate a negative effect, and interdictory symbols indicate no effect with warming. Gray thermometers indicate stages of the viral infection cycle that either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

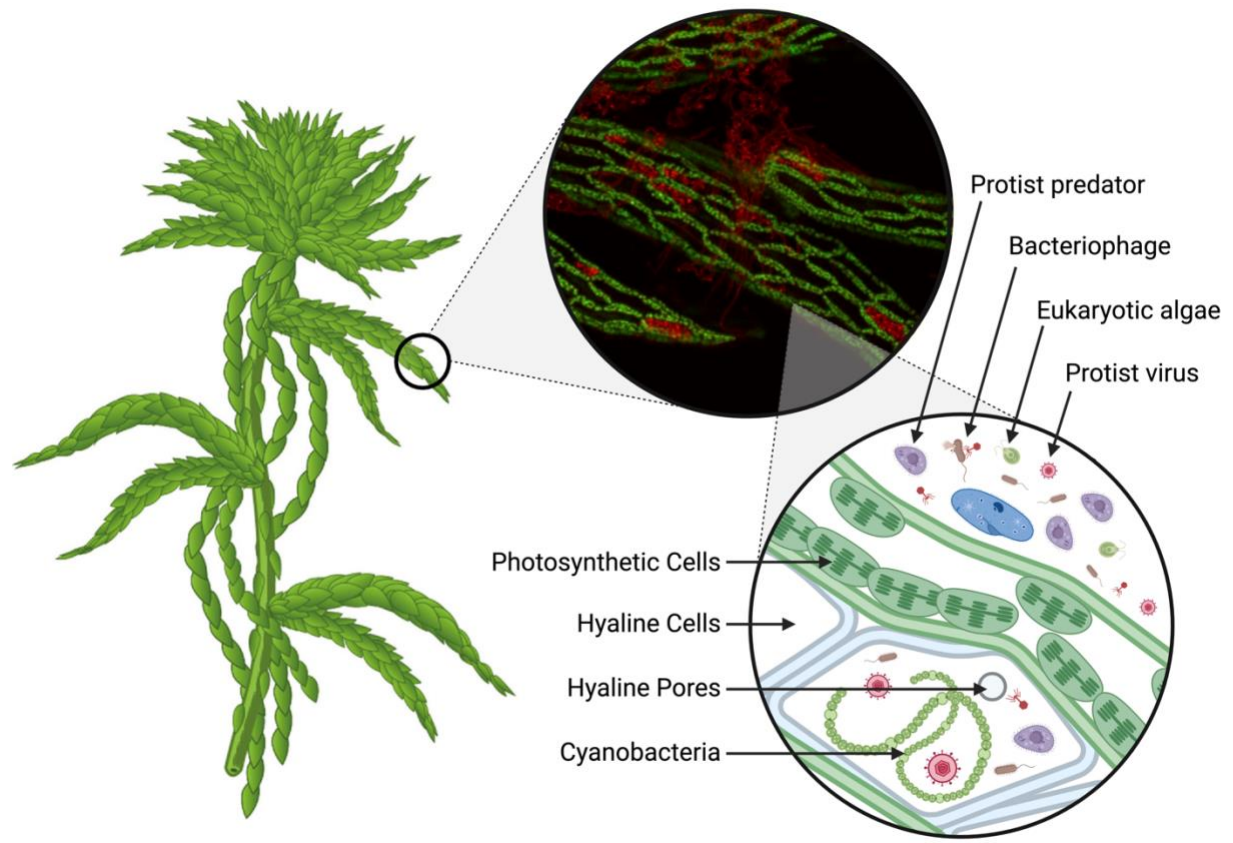


Figure 3. *Sphagnum* moss and associated microbial food web. Microbial species inhabit both water-filled hyaline cells of *Sphagnum* tissue and the external aquatic habitat. First inset shows cyanobacteria (in red) living inside *Sphagnum* tissue (in green, image taken using a Zeiss LSM 710 laser scanning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

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