

**Viral infections mediate microbial food web controls on the global carbon cycle under warming**

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## ABSTRACT

Climate warming will likely disrupt the flow of matter and energy within ecosystems, threatening the global carbon balance. Microorganisms are fundamental components of carbon cycling and are thus integral to ecosystem climate responses. However, ecosystem responses to warming are uncertain due to the functional and trophic complexity of microbial food webs. Here, we expose two major black boxes hindering our ability to anticipate ecosystem climate responses: viral infection and predation by microbial predators. We review current knowledge and uncover critical gaps in knowledge about how warming will impact these important top-down controls on the global carbon cycle. Understanding and predicting ecosystem responses to climate change will require disentangling complex direct and indirect responses within microbial food webs.

## INTRODUCTION

Climate change is warming terrestrial carbon (C) reserves, making them increasingly vulnerable to microbial respiration<sup>1-4</sup>. Because microbial respiration increases with temperature<sup>5-8</sup>, microbes will likely release previously inaccessible carbon pools at ever increasing rates as Earth warms, creating a large positive atmospheric feedback not currently represented in predictive models of future climate<sup>9</sup>. Microbial responses to warming may be especially important in *Sphagnum* moss-dominated peatlands which are particularly vulnerable to future climate change<sup>3</sup> and, despite occupying less than 3% of the Earth's surface, store ~25% of the world's soil carbon<sup>10</sup> and produce 5-10% of global atmospheric methane<sup>11</sup>. Warming is also expected to restructure microbial food webs through species losses<sup>12</sup> (but see<sup>13</sup>) and changes in species interactions<sup>1</sup>.

Identifying and understanding the temperature-dependence of these biotic controls on microbial respiration is thus paramount to properly forecast future climates.

While bacterial and fungal communities play central roles as decomposers and N<sub>2</sub>-fixers, the carbon and nutrients these organisms recycle reach higher trophic levels through predation—a process known as the “the microbial loop”<sup>16,17</sup>. Predation from protists is a major source of mortality among bacteria and fungi<sup>18,19</sup> (Fig. 1), significantly impacting carbon cycling by reducing decomposer biomass, increasing nutrient turnover, and influencing microbial respiration rates<sup>19–23</sup>. Because of these effects, protists have been called the “puppet masters” of the soil microbiome<sup>19</sup>. Protist predation rates are expected to increase with temperature<sup>24</sup>, altering protist-decomposer interactions<sup>13,24</sup> and influencing microbial biomass and respiration rates<sup>23,25,26</sup>. Changes in predation patterns with warming may lead to shifts in the make-up of decomposer communities, in turn impacting system-critical nitrogen (N<sub>2</sub>)-fixation rates and C sequestration. Furthermore, protist consumers are themselves preyed upon by larger organisms in a temperature-dependent manner<sup>24</sup>. This added complexity<sup>27</sup> emphasizes the need for a food web perspective to understand microbial processes under changing environmental conditions.

Protists and their prey are also infected by viruses, which likely mediate protist effects on microbial food webs<sup>28–30</sup> (Fig. 1). Because viruses play critical roles in microbial mortality and nutrient cycling<sup>28–31</sup>, they too have been deemed “puppet masters” of the microbiome<sup>32</sup>. Viruses are the most abundant biological entities on Earth<sup>28,30</sup>, therefore viral mediation of protist control on microbes is likely widespread, having important consequences for ecosystem function at both local and global scales<sup>28–31,33</sup>. Viral dynamics are regulated by temperature (Table 2), yet how

warming may influence viral mediation of protists is severely understudied (Fig. 1). This lack of understanding impairs our ability to predict how microbial food webs will respond to global warming.

Although the direct impacts of protists and viruses on ecosystem function have been discussed independently<sup>16,17,19,23,34–36</sup>, we lack a baseline understanding about how these top-down controls jointly influence ecosystem processes within broader microbial food webs and novel climates. Here, we outline the state of the art and propose ways to conceptualize and address existing knowledge gaps (Table 1), with a specific focus on potential impacts of warming on carbon and nutrient cycling.

## **TEMPERATURE EFFECTS ON MICROBIAL FOOD WEBS**

We now recognize that microbial communities are complex, functionally-diverse, multi-trophic food webs<sup>12,19,27,37</sup>. These food webs control carbon and nutrient cycling as energy and matter flows between microbes that occupy different trophic positions and play different functional roles<sup>17,38</sup>. Ecosystem responses to climate change are thus likely regulated by overall microbial food web organization, the relative abundances of autotrophs (cyanobacteria and eukaryotic algae) and heterotrophs (decomposers and microbial predators), differences in diet and predation rates among predators, the prevalence of omnivory, and the number of trophic levels<sup>27,39</sup>. For example, protist species affect the biomass and composition of bacterial prey communities, which in turn influences ecosystem processes like CO<sub>2</sub> release *via* respiration—but these interactions are likely to change with warming<sup>22,23</sup>. Predation by protists at higher trophic levels may potentially counter these effects *via* trophic cascades<sup>27</sup>. Carbon and nutrient flows can also

be rerouted by mixotrophic protists<sup>40</sup>—which are ubiquitous across ecosystems<sup>2</sup>, simultaneously occupy multiple trophic levels, and exhibit flexibility in both energy acquisition strategies (relative dependence on phototrophy vs. phagotrophy)<sup>41</sup> and stoichiometry<sup>42</sup>. Finally, although viruses are known to impact carbon and nutrient cycling, namely *via* the viral shunt<sup>29</sup>, how viruses might mediate microbial responses to warming at different trophic levels is poorly understood (Table 1).

Warming may also alter how species interact due to temperature-driven reductions in body size (*i.e.*, the temperature-size rule)<sup>43,44</sup> that effectively rewire patterns of flow within food webs<sup>14,15</sup>. For example, shrinking protists may begin to favor smaller prey (*e.g.*, solitary bacteria or yeasts) over larger prey (*e.g.*, larger or colony forming bacteria, eukaryotic algae, and small heterotrophic protists), with consequences for N<sub>2</sub>-fixation rates, decomposition rates, and nutrient cycling. As global warming is expected to alter the composition and structure of microbial food webs<sup>14,15,45,46</sup>, understanding the causes and consequences of this reorganization is critical to predicting possible changes in overall function (Table 1).

Anticipating the effects of warming on microbial food webs ultimately hinges on understanding how temperature alters the flow of materials between organisms. This flow is controlled by two main mechanistic constraints that are both likely to change under warming: 1) the metabolic/stoichiometric requirements of consumers and 2) assimilation efficiency ( $\epsilon$ ), *i.e.*, the fraction of ingested resource biomass ( $I$ ) that is used for metabolism and production ( $R$ ) ( $\epsilon=R/I$ ). Consumers require certain amounts of essential elements (*e.g.*, C, N, P) to survive and reproduce<sup>47</sup>. As metabolic demands typically increase with temperature<sup>48</sup>, warming may favor

consumption of prey with more carbon relative to other essential elements (*e.g.*, N, P)<sup>49</sup>. Such constraints may be mitigated or exacerbated by stoichiometric flexibility under warming—flexible prey (*e.g.*, bacteria or algae) may become more or less nutritious to consumers according to climate-induced changes in elemental ratios<sup>50</sup>, while flexible consumers (*i.e.*, mixotrophs) may alleviate elemental constraints by changing either trophic modes or internal stoichiometry. Although ingestion and metabolic rates are both expected to increase with temperature<sup>48</sup>, assimilation efficiency can either decrease<sup>51</sup> or increase<sup>52</sup>, so it is unclear how efficiency might alter carbon and nutrient cycling with warming. Whether and how the temperature-dependence of these trophic constraints differs within and among microbial food web components (*e.g.*, fungi, bacteria, and protists) is unknown.

The overall balance of carbon and nutrient uptake (*via* photosynthesis), storage in biomass, sequestration in sediment, and release (*via* respiration) will likely shift based on microbial food web responses to warming (Box 1, Figs. B1, B2). Respiration rates are significantly more sensitive to temperature change than photosynthetic rates<sup>53</sup>, although increases in microbial primary productivity could at least partially offset this uneven increase in carbon released by respiration<sup>5,54</sup>. Additionally, decomposition rates are expected to increase with warming<sup>7,12,55</sup>, especially for lower quality litter, which is more sensitive to temperature change<sup>56</sup>. Together, this suggests that warming may tip the balance of microbe dominated ecosystems from productivity-dominant carbon sinks (storing carbon in biomass and sediment) to respiration-dominant carbon sources (releasing carbon into the atmosphere)<sup>26</sup>. However, how viruses mediate this balance between carbon uptake (photosynthesis) and release (respiration) under warming is still

relatively unknown (Table 1) but will likely involve complex and differential impacts on the dynamics and mortality of hosts that perform different ecosystem functions<sup>57–59</sup>.

## **TEMPERATURE EFFECTS ON VIRUSES AND VIRAL INFECTIONS**

While rising temperatures are recognized to influence microorganisms across environments<sup>60</sup>, it is not clear how global warming will alter viral mediation of food web dynamics. All compartments of microbial food webs are infected by viruses: bacteria are infected by bacteriophages, fungi by mycoviruses, and protists by giant viruses, among others. Consequently, the unique functions of these different food web compartments will be mediated by viral infections. Moreover, all of these host-virus interactions have the potential to be temperature dependent, which may ultimately decide the way in which temperature determines how carbon is cycled within food webs. We hypothesize that warming may strengthen viral controls on decomposers, N-fixers, and protists, leading to reduced 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, we lack a basic understanding of how temperature influences viral life cycles and the outcomes of infection. Viral infection occurs in a sequence of steps<sup>61</sup> (Fig. 2) which include 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 2, Table S1). Temperature may affect viral production both indirectly (by altering host physiology<sup>62</sup>) or directly by affecting the

particle itself<sup>63</sup>. Well documented effects include a decrease in latent period (time from infection until release of viral progeny) and increases in burst size (number of viral progeny released) with increasing temperature<sup>63–67</sup> (Fig. 2), followed by a reversal of these trends past a virus-specific thermal optimum ( $T_{opt}$ )<sup>65,68</sup>. Temperature effects on burst size and latent period are likely the result of virus synthesis kinetics, but direct evidence is lacking. At suboptimal *in situ* temperatures, warming may increase infection and viral production, while systems already near or at  $T_{opt}$  should produce fewer viruses or undergo complete shutdown of viral propagation.

The effects of temperature on other aspects of the viral life cycle, however, remain poorly understood (Table 1, Fig. 2). Encounter rates between viruses and hosts depend on virus and host densities<sup>69</sup>, host cell size, and host motility<sup>70</sup>. Host cell sizes<sup>43,71,72</sup> and population densities<sup>73,74</sup> often decrease while motility increases<sup>75–79</sup> with temperature. Consequently, warming could have positive or negative effects on virus-host encounter rates, although experimental evidence is lacking (Fig. 2). Evidence suggests that adsorption can increase<sup>64,80</sup>, decrease<sup>62</sup>, or remain unchanged<sup>80</sup> with temperature, depending on the host-virus pair (Table 2, Fig. 2). While cell membranes are more fluid and permeable at higher temperatures<sup>81,82</sup>, whether this alters viral infection is unknown. We are also unaware of studies that directly link temperature and virus synthesis rates (Fig. 2). And while many studies have reported seasonal changes in viral abundances<sup>83–86</sup>, confounding factors such as nutrient availability and predation obscure the direct effects of temperature on viral infection cycles. Lastly, viral life strategies other than lytic (*e.g.*, lysogeny in prokaryotes and/or latency in multicellular eukaryotes) are ecologically important<sup>36</sup>, and likely exhibit unique trends with temperature that are currently unresolved (*e.g.*,



increasing temperatures may induce lysis<sup>87</sup>), thus highlighting the need to resolve the unknown and poorly understood temperature-dependencies of viral infection (Table 1) .

Finally, viral production is linked to host cell physiology<sup>65–67,88</sup>, which is unsurprising given that infection induces the metabolic reprogramming of host cells<sup>89</sup>. However, viral temperature ranges can be independent of, and often surpass those of, their hosts<sup>80,88,90</sup>. Additionally, multiple viruses that infect the same host can have different temperature optima<sup>88</sup>, potentially promoting niche differentiation and a shift in dominant viral taxa with warming. This suggests that viruses, and their effects on nutrient and carbon cycling, may be less susceptible to warming than their hosts, but more research is needed.

## PEATLANDS AS A MODEL SYSTEM

We focus on peatland microbial food webs as a case study to assess how viral infections may influence the effects of microbial grazing and predation on carbon and nutrient cycling in a warming world. *Sphagnum* mosses dominate peatlands, storing more carbon (in both biomass and peat)—and therefore arguably having a greater impact on global carbon cycling and climate—than any other single genus of plants<sup>91,92</sup>. While *Sphagnum* plays a primary role in carbon dynamics<sup>93</sup>, it also serves a secondary role by insulating permafrost, thus dampening the impacts of rising temperatures on vast amounts of carbon stored in the arctic tundra<sup>94</sup>. Peatland microbial food webs are uniquely well-suited systems for studying how warming will influence the global carbon cycle due to 1) their importance in the global carbon cycle<sup>1,10,92,95</sup>, 2) the functional diversity of their constituent taxa<sup>20,21,27,96</sup>, 3) their sensitivity to changes in temperature<sup>7,23,97,98</sup>, and 4) the ability to grow *Sphagnum* moss and associated communities in the

laboratory<sup>21,99,100</sup>. 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<sup>101,102</sup>, all of which can be performed at local or global scales and in the laboratory or in the field.

We propose that the response of *Sphagnum*-dominated peatlands to warming is regulated by poorly understood controls on carbon and nutrient cycling from protists and viral infections (Fig. 1, Box 1). These microbes play diverse trophic and functional roles both within and outside the living tissue<sup>96,103–105</sup> (Fig. 3). For example, *Sphagnum*'s unique ability to persist in harsh peatland habitats with extremely low mineral nitrogen availability depends on symbiotic interactions with microbial associates<sup>105,106</sup>—including a variety of N<sub>2</sub>-fixing microbes (diazotrophs) that colonize the cell surface and water-filled hyaline cells in host plants<sup>105</sup> (Fig. 3). Bacterial methanotrophs are also prevalent in boreal peat bogs<sup>107,108</sup> and not only fix N<sub>2</sub>, but supply 5%–20% of CO<sub>2</sub> in photosynthesis *via* methane oxidation<sup>109</sup>. *Sphagnum*'s microbial community composition varies widely with climate<sup>110</sup> and is expected to shift considerably under warming<sup>100,111</sup>, likely altering the associated microbial food webs<sup>12,19,21,27,37</sup>. A simple model that incorporates predation by protists shows some potential ways that top-down control on *Sphagnum* microbiomes might strongly impact overall peatland C uptake, sequestration, and release (Box 1).

Peatland ecosystems also harbor a diverse group of viruses that infect prokaryotes and eukaryotes<sup>34,112,113</sup>. Surprisingly, the inferred frequency of protist infections in the *Sphagnum* microbiome was found to be higher than that of bacterial infection by phages<sup>112</sup>, although the functional role of protist infection in this system remains unclear. Viruses of fungi can have

considerable downstream ecological consequences by lysing or altering the phenotypes of fungal decomposers, symbionts, or pathogens in *Sphagnum*<sup>114</sup>. In peatlands, viral community composition, lifestyle strategies, and a variety of infection stages are influenced by environmental factors, including temperature<sup>34,113</sup>. 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 (Table 1). Preliminary modeling suggests that viral infections and protist predation may jointly accelerate the effects of warming on C sequestration in peatlands (Box 1, Fig. B2), but a deeper understanding on how these ecological interactions occur in nature and how they are influenced by temperature is direly needed.

## CONCLUSIONS

We synthesize multiple lines of evidence suggesting that viral infections, predation by protists, and their associated temperature-dependencies will control changes in carbon and nutrient cycling in microbial food webs in response to warming. We propose that microbial food web components play distinct roles in response to increasing temperatures and that their joint effects could increase the total amount of carbon stored and respired by microbes under warming. We also stress that these ecological interactions—and their associated temperature-dependencies—are poorly understood, highlighting several gaps for future research. Microbial food webs play a central role in the global carbon cycle due to the vast amount of carbon they store as biomass and route to the lithosphere and atmosphere. We highlight the importance of studying the complex dynamics of microbial food webs to better understand and predict whether rising temperatures

274 will lead to net carbon sequestration or release in globally important ecosystems like *Sphagnum*-  
275 dominated peatlands.

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**Box 1.**

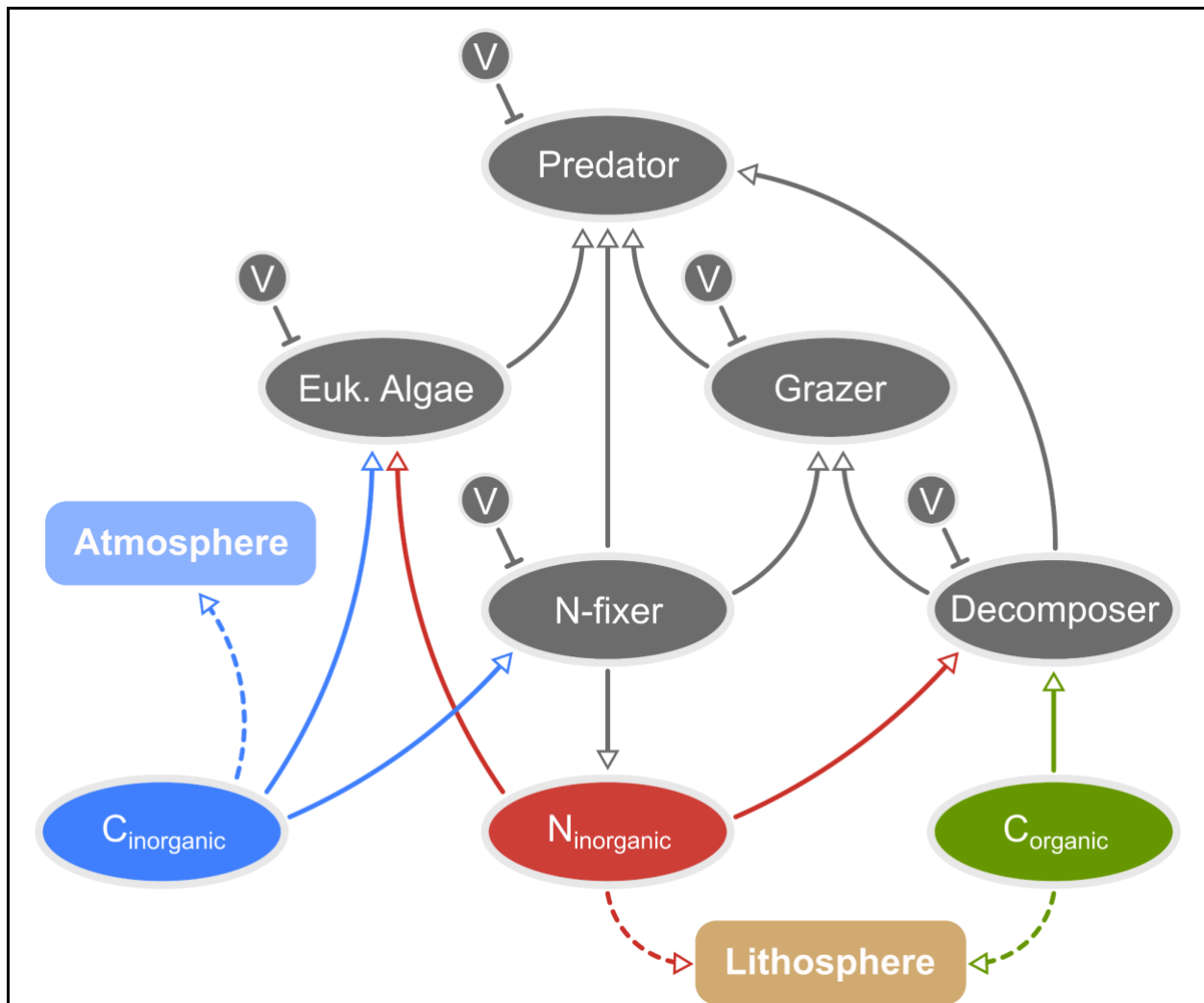
Climate-driven shifts in nutrient and carbon cycling can be studied using mathematical models that track the collective responses of several essential organisms within microbial food webs (Figure B1). Each organism plays a unique role in carbon and nutrient cycling depending on its metabolic requirements, 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 describe an 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<sub>2</sub>) into biologically usable forms that are metabolically required by all organisms and photosynthetic nitrogen-fixers also require carbon dioxide for photosynthesis (C uptake).
- **Grazers** 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 grazer biomass (C uptake). We use the term “grazers” for simplicity here and to differentiate these from protists that also eat other protists (termed “predators” below).
- **Eukaryotic algae** include protists that use carbon dioxide for photosynthesis (C uptake) and may represent a significant offset to microbial respiration.
- **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<sub>2</sub>) 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.



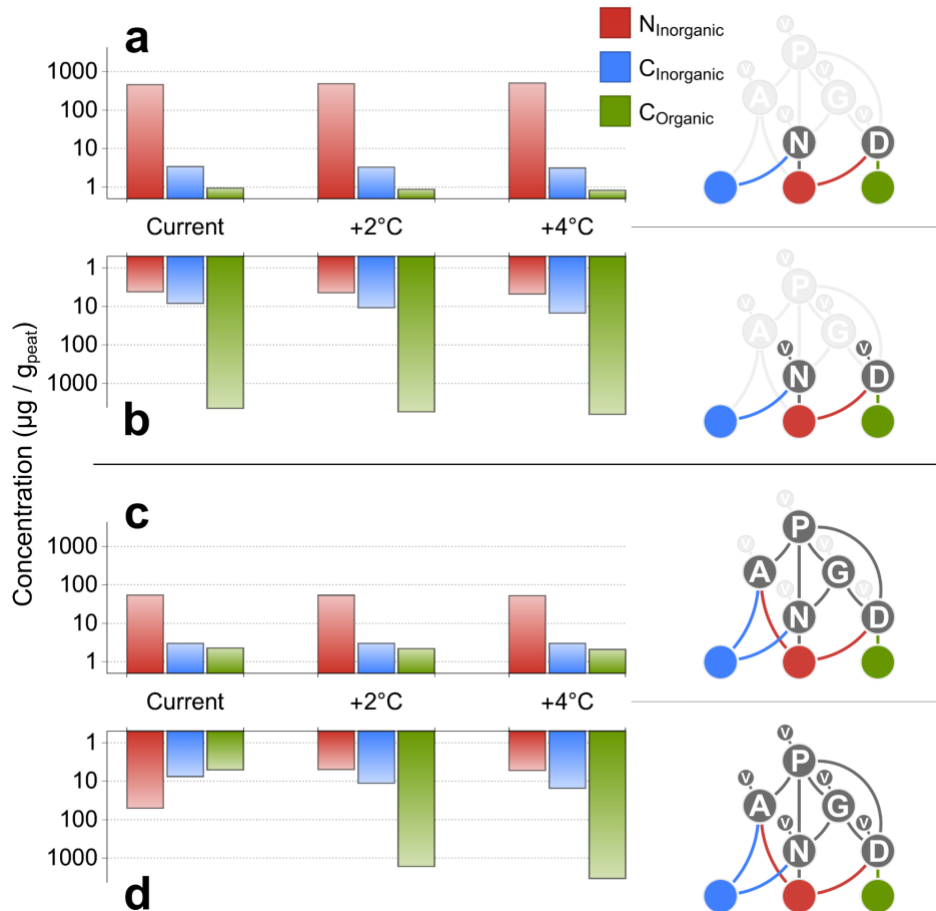
**Figure B1.** Hypothetical microbial food web in *Sphagnum* peatlands including organisms and nitrogen and carbon flow. Arrows represent flow between components. Each type of organism consumes elements or other organisms based on its unique stoichiometric requirements and is also subject to infection 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&2). However, photosynthesis is generally less sensitive to increases in temperature (activation energy of  $\sim 0.32\text{eV}^{25,26,53,115}$ ) than respiration and predation ( $\sim 0.65\text{eV}^{48,75,76}$ ), while mortality lies somewhere in between ( $\sim 0.45\text{eV}^{48,73}$ ).

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.

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 (Table 1, Figs. 1&2), possible changes in size across taxa that could change predation rates<sup>44</sup>, and temperature-dependence at all stages of viral infection (Table 2). In this perspective we advocate that it is important to investigate these unknowns to more accurately predict ecosystem responses to climate change.



**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 + G + P), and (d) all organisms and viruses.

<p style="text-align: center;"><b><u>Temperature effects on microbial food webs</u></b></p> <p>1) How will the unique temperature responses of functionally and trophically diverse microbes collectively regulate carbon (and nutrient) cycling under warming?</p> <p>2) How will microbial food webs, and therefore ecosystem flux, be rewired by warming?</p> <p>3) Does the temperature-dependence of metabolic constraints differ among microbial food web components? Will decomposers, N-fixers, and autotrophic or heterotrophic protists respond differently?</p> <p>4) Will warming shift microbial carbon balance toward more photosynthesis (carbon uptake) or more respiration (carbon release), and how might predation by protists and viral infections alter this shift?</p> <p style="text-align: center;"><b><u>Temperature effects on viruses and viral infections</u></b></p> <p>5) How will warming impact different aspects of the viral infection cycle, including both host-dependent and host-independent processes?</p> <p>6) How will warming influence the direct (<i>via</i> cell lysis) and indirect (<i>via</i> host population dynamics) functions of viruses in carbon and nutrient cycling?</p> <p>7) How will mismatches between virus and host temperature niches and sensitivities affect virus-host interactions under warming?</p>
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311 **Table 2.** Select published studies of temperature effects on viruses. A more detailed description  
 312 of each study, including summarized results, can be found in Table S1.

Process	Temperature Effects	Location or Host-Virus System
Viral decay	Increases with temperature	<ul style="list-style-type: none"> <li>- Backwater system of Danube River (Field)<sup>116</sup></li> <li>- <i>Heterosigma akashiwo</i> (H93616, NM96) / Hav (HaV01, HaV08) (Lab)<sup>63</sup></li> <li>- Bacteriophage 9A isolated from Arctic seawater (Lab)<sup>117</sup></li> <li>- Samples from Western Pacific Ocean (Lab)<sup>118</sup></li> </ul>
		<ul style="list-style-type: none"> <li>- Escherichia coli / coliphage isolates from the River Swift (Lab)<sup>80</sup></li> <li>- Escherichia coli / T4 (Lab)<sup>64</sup></li> <li>- Chaetoceros tenuissimus / Cten DNAV and Cten RNAV (Lab)<sup>88</sup></li> </ul>
Adsorption	Decreases with temperature	<ul style="list-style-type: none"> <li>- Emiliana huxleyi CCMP374 / EhV86 (Lab)<sup>62</sup></li> <li>- Chaetoceros tenuissimus / Cten DNAV and Cten RNAV (Lab)<sup>88</sup></li> </ul>
	No effect of temperature	<ul style="list-style-type: none"> <li>- Escherichia coli / coliphage isolates from the River Swift (Lab)<sup>80</sup></li> </ul>
	Increases with temperature	<ul style="list-style-type: none"> <li>- Backwater system of Danube River (Field)<sup>116</sup></li> <li>- Escherichia coli / T4 (Lab)<sup>64</sup></li> <li>- Micromonas sp. MicA, MicB, MicC / MicVA, MicVB, MicVC (Lab)<sup>65</sup></li> <li>- Micromonas polaris / MpoV (Lab)<sup>66</sup></li> <li>- Micromonas polaris strain RCC2257, strain RCC2258 / Mpov-45T (Lab)<sup>67</sup></li> </ul>
Burst size	Decreases with temperature	<ul style="list-style-type: none"> <li>- Backwater system of Danube River (Field)<sup>116</sup></li> <li>- Micromonas sp. MicA, MicB, MicC / MicVA, MicVB, MicVC (Lab)<sup>65</sup></li> </ul>
	Increases with temperature	<ul style="list-style-type: none"> <li>- Escherichia coli / coliphage (Lab)<sup>119</sup></li> <li>- Micromonas sp. MicA, MicB, MicC / MicVA, MicVB, MicVC (Lab)<sup>65</sup></li> </ul>
Latency period	Decreases with temperature	<ul style="list-style-type: none"> <li>- <i>Heterosigma akashiwo</i> (H93616, NM96) / Hav (HaV01, HaV08) (Lab)<sup>63</sup></li> <li>- Escherichia coli / T4 (Lab)<sup>64</sup></li> <li>- Staphylococcus aureus / S. aureus phage (Lab)<sup>120</sup></li> <li>- Escherichia coli / coliphage (Lab)<sup>119</sup></li> <li>- Micromonas sp. MicA, MicB, MicC / MicVA, MicVB, MicVC (Lab)<sup>65</sup></li> <li>- Micromonas polaris / MpoV (Lab)<sup>66</sup></li> <li>- Micromonas polaris strain RCC2257, strain RCC2258 / Mpov-45T (Lab)<sup>67</sup></li> </ul>

Virus abundance	Temperature effects unclear	- Backwater system of Danube River (Field) <sup>116</sup>
		- Southern Beaufort Sea and Amundsen Gulf (Field) <sup>84</sup>
		- Lake Pavin (Field) <sup>83</sup>
		- Japanese paddy field (Field) <sup>86</sup>
		- Michigan agricultural soils (Field) <sup>85</sup>
Lysis thermal range	Temperature effects are host-dependent	- Metadata <sup>59,121</sup>
		- <i>Heterosigma akashiwo</i> (H93616, NM96) / Hav (HaV01, HaV08) (Lab) <sup>63</sup>
		- Bacteriophage 9A isolated from Arctic seawater (Lab) <sup>117</sup>
		- Escherichia coli / coliphage isolates from the River Swift (Lab) <sup>80</sup>
		- Metadata <sup>90</sup>
Virus-induced host mortality	Increases with temperature	- North Atlantic Ocean (Field) <sup>122</sup>

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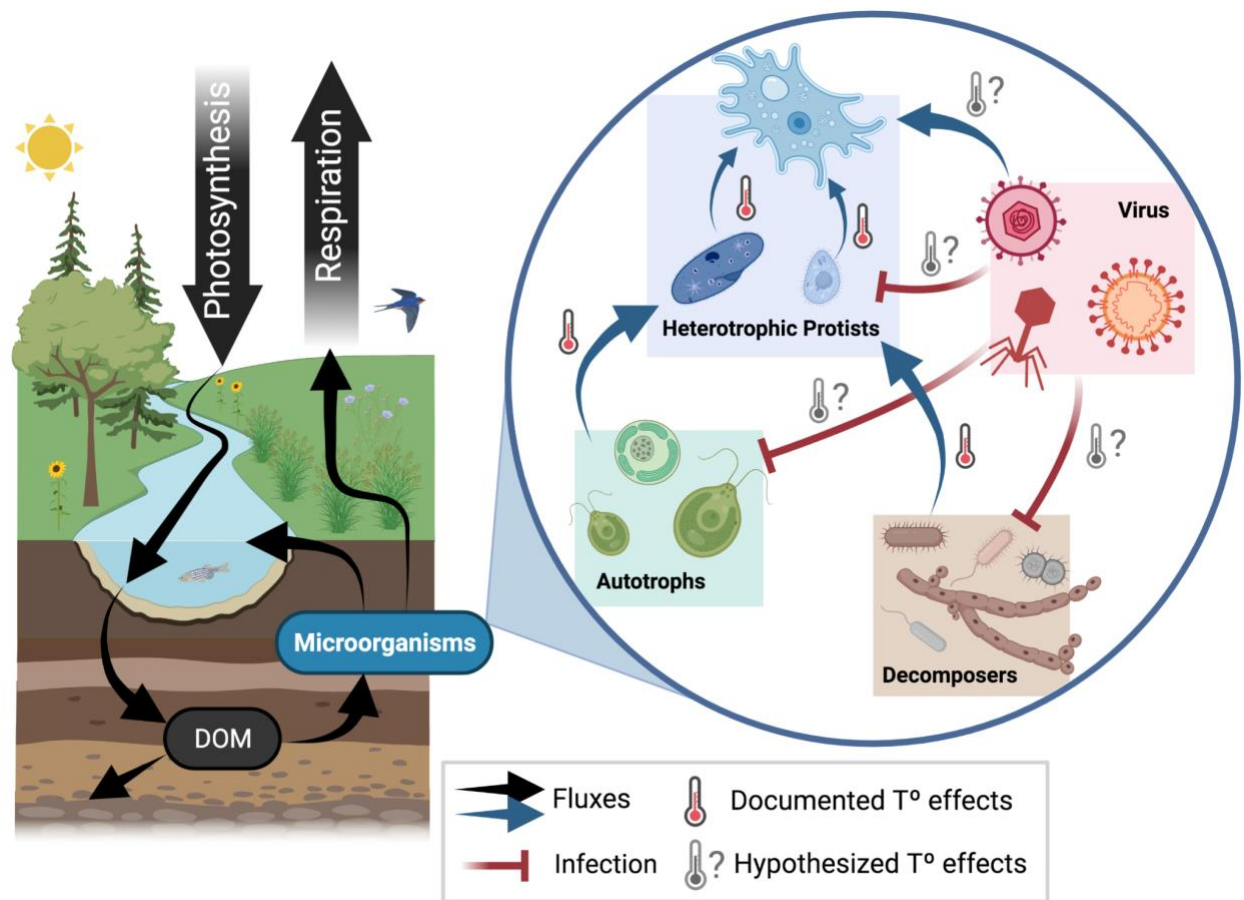
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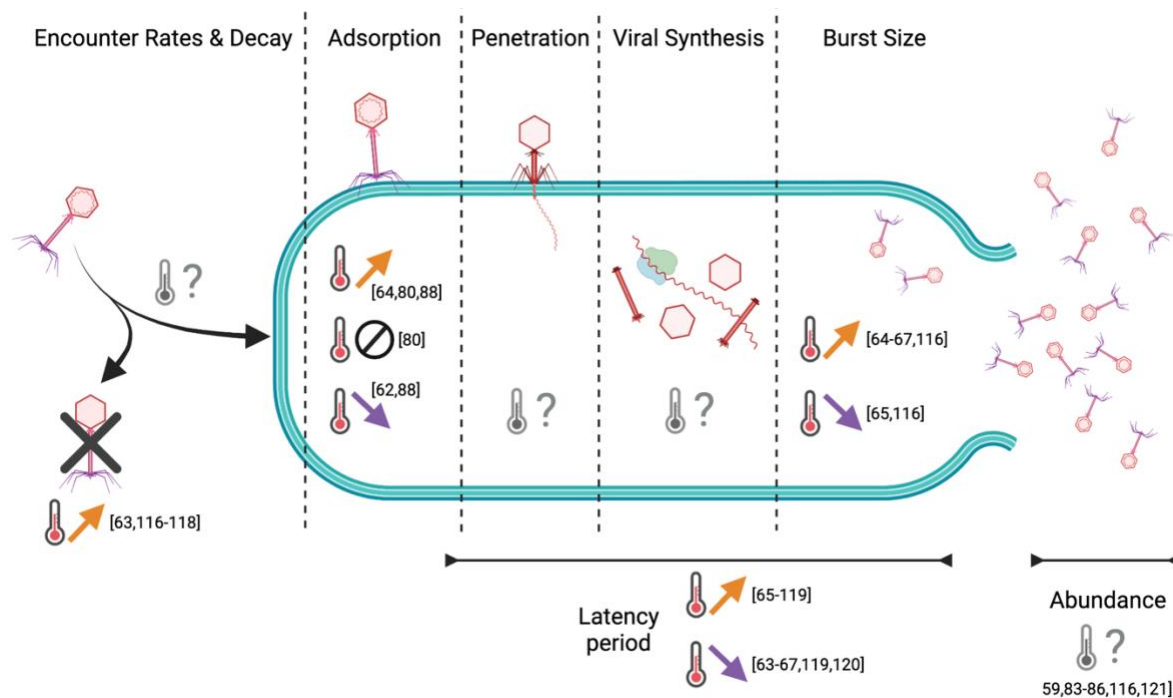
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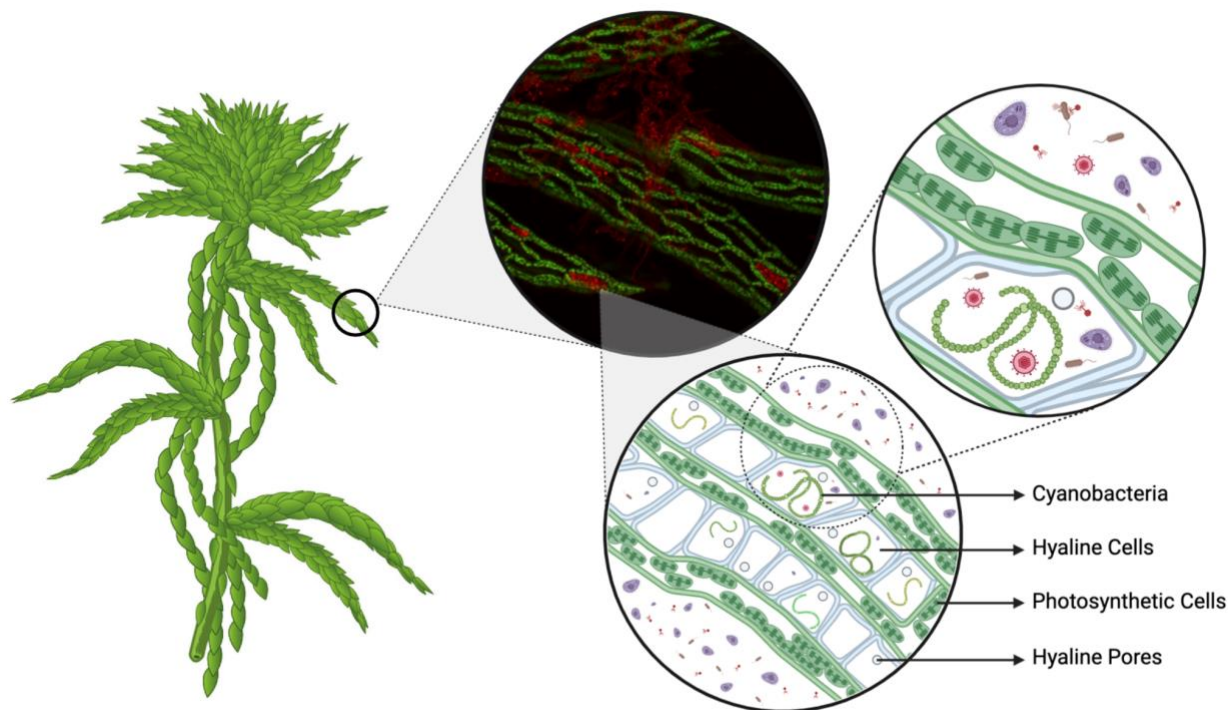
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**Figure 1.** Conceptual diagram outlining the documented and hypothesized temperature effects on processes influencing global carbon cycling, including the impacts of decomposers (heterotrophic bacteria and fungi), autotrophs (cyanobacteria and eukaryotic algae), heterotrophic protists that consume all organisms, and viruses that infect all organisms.



**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). More details from these studies can be found in Table S1.



**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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