

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

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47 **ABSTRACT**

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

58

59 **INTRODUCTION**

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

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

71

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

85

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

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

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96 Although the direct impacts of protists and viruses on ecosystem function have been discussed  
97 independently<sup>16,17,19,23,34–36</sup>, we lack a baseline understanding about how these top-down controls  
98 jointly influence ecosystem processes within broader microbial food webs and novel climates.

99 Here, we outline the state of the art and propose ways to conceptualize and address existing  
100 knowledge gaps (Table 1), with a specific focus on potential impacts of warming on carbon and  
101 nutrient cycling.

102

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

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

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

121

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

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

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

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

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

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

164 While rising temperatures are recognized to influence microorganisms across environments<sup>60</sup>, it  
165 is not clear how global warming will alter viral mediation of food web dynamics. All  
166 compartments of microbial food webs are infected by viruses: bacteria are infected by  
167 bacteriophages, fungi by mycoviruses, and protists by giant viruses, among others.  
168 Consequently, the unique functions of these different food web compartments will be mediated  
169 by viral infections. Moreover, all of these host-virus interactions have the potential to be  
170 temperature dependent, which may ultimately decide the way in which temperature determines  
171 how carbon is cycled within food webs. We hypothesize that warming may strengthen viral  
172 controls on decomposers, N-fixers, and protists, leading to reduced biomass, increased nutrient  
173 cycling and respiration, shorter mean residence time of carbon in microbial food web  
174 compartments, and shifts in the balance of carbon sequestration and release into the atmosphere  
175 (Box 1, Fig. B2d).

176

177 However, we lack a basic understanding of how temperature influences viral life cycles and the  
178 outcomes of infection. Viral infection occurs in a sequence of steps<sup>61</sup> (Fig. 2) which include 1)  
179 host cell encounter, 2) adsorption, 3) introduction of virus or genetic material into the cell, 4)  
180 synthesis of viral particles, and 5) assembly and release of viral progeny. Any one, and likely all,  
181 of these steps could be temperature-dependent (Fig. 2, Table 2, Table S1). Temperature may  
182 affect viral production both indirectly (by altering host physiology<sup>62</sup>) or directly by affecting the

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

190  
191 The effects of temperature on other aspects of the viral life cycle, however, remain poorly  
192 understood (Table 1, Fig. 2). Encounter rates between viruses and hosts depend on virus and host  
193 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>  
194 often decrease while motility increases<sup>75-79</sup> with temperature. Consequently, warming could have  
195 positive or negative effects on virus-host encounter rates, although experimental evidence is  
196 lacking (Fig. 2). Evidence suggests that adsorption can increase<sup>64,80</sup>, decrease<sup>62</sup>, or remain  
197 unchanged<sup>80</sup> with temperature, depending on the host-virus pair (Table 2, Fig. 2). While cell  
198 membranes are more fluid and permeable at higher temperatures<sup>81,82</sup>, whether this alters viral  
199 infection is unknown. We are also unaware of studies that directly link temperature and virus  
200 synthesis rates (Fig. 2). And while many studies have reported seasonal changes in viral  
201 abundances<sup>83-86</sup>, confounding factors such as nutrient availability and predation obscure the  
202 direct effects of temperature on viral infection cycles. Lastly, viral life strategies other than lytic  
203 (*e.g.*, lysogeny in prokaryotes and/or latency in multicellular eukaryotes) are ecologically  
204 important<sup>36</sup>, and likely exhibit unique trends with temperature that are currently unresolved (*e.g.*,

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

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

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## 216 **PEATLANDS AS A MODEL SYSTEM**

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

228 laboratory<sup>21,99,100</sup>. Doing so, however, will require a multifaceted approach—including  
229 characterization of microbial communities in the field, microbial experiments in the laboratory, -  
230 omics approaches, and mathematical modeling<sup>101,102</sup>, all of which can be performed at local or  
231 global scales and in the laboratory or in the field.

232

233 We propose that the response of *Sphagnum*-dominated peatlands to warming is regulated by  
234 poorly understood controls on carbon and nutrient cycling from protists and viral infections (Fig.  
235 1, Box 1). These microbes play diverse trophic and functional roles both within and outside the  
236 living tissue<sup>96,103–105</sup> (Fig. 3). For example, *Sphagnum*'s unique ability to persist in harsh peatland  
237 habitats with extremely low mineral nitrogen availability depends on symbiotic interactions with  
238 microbial associates<sup>105,106</sup>—including a variety of N<sub>2</sub>-fixing microbes (diazotrophs) that colonize  
239 the cell surface and water-filled hyaline cells in host plants<sup>105</sup> (Fig. 3). Bacterial methanotrophs  
240 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  
241 photosynthesis *via* methane oxidation<sup>109</sup>. *Sphagnum*'s microbial community composition varies  
242 widely with climate<sup>110</sup> and is expected to shift considerably under warming<sup>100,111</sup>, likely altering  
243 the associated microbial food webs<sup>12,19,21,27,37</sup>. A simple model that incorporates predation by  
244 protists shows some potential ways that top-down control on *Sphagnum* microbiomes might  
245 strongly impact overall peatland C uptake, sequestration, and release (Box 1).

246

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

251 considerable downstream ecological consequences by lysing or altering the phenotypes of fungal  
252 decomposers, symbionts, or pathogens in *Sphagnum*<sup>114</sup>. In peatlands, viral community  
253 composition, lifestyle strategies, and a variety of infection stages are influenced by  
254 environmental factors, including temperature<sup>34,113</sup>. However, how warming might modify the  
255 direct (lytic release of elements) and indirect (altered host phenotype/dynamics and food web  
256 processes) effects of viral infections on *Sphagnum*-associated microbial food webs—and carbon  
257 and nitrogen cycling in peatlands—is not well understood (Table 1). Preliminary modeling  
258 suggests that viral infections and protist predation may jointly accelerate the effects of warming  
259 on C sequestration in peatlands (Box 1, Fig. B2), but a deeper understanding on how these  
260 ecological interactions occur in nature and how they are influenced by temperature is direly  
261 needed.

262

## 263 **CONCLUSIONS**

264 We synthesize multiple lines of evidence suggesting that viral infections, predation by protists,  
265 and their associated temperature-dependencies will control changes in carbon and nutrient  
266 cycling in microbial food webs in response to warming. We propose that microbial food web  
267 components play distinct roles in response to increasing temperatures and that their joint effects  
268 could increase the total amount of carbon stored and respired by microbes under warming. We  
269 also stress that these ecological interactions—and their associated temperature-dependencies—  
270 are poorly understood, highlighting several gaps for future research. Microbial food webs play a  
271 central role in the global carbon cycle due to the vast amount of carbon they store as biomass and  
272 route to the lithosphere and atmosphere. We highlight the importance of studying the complex  
273 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.**

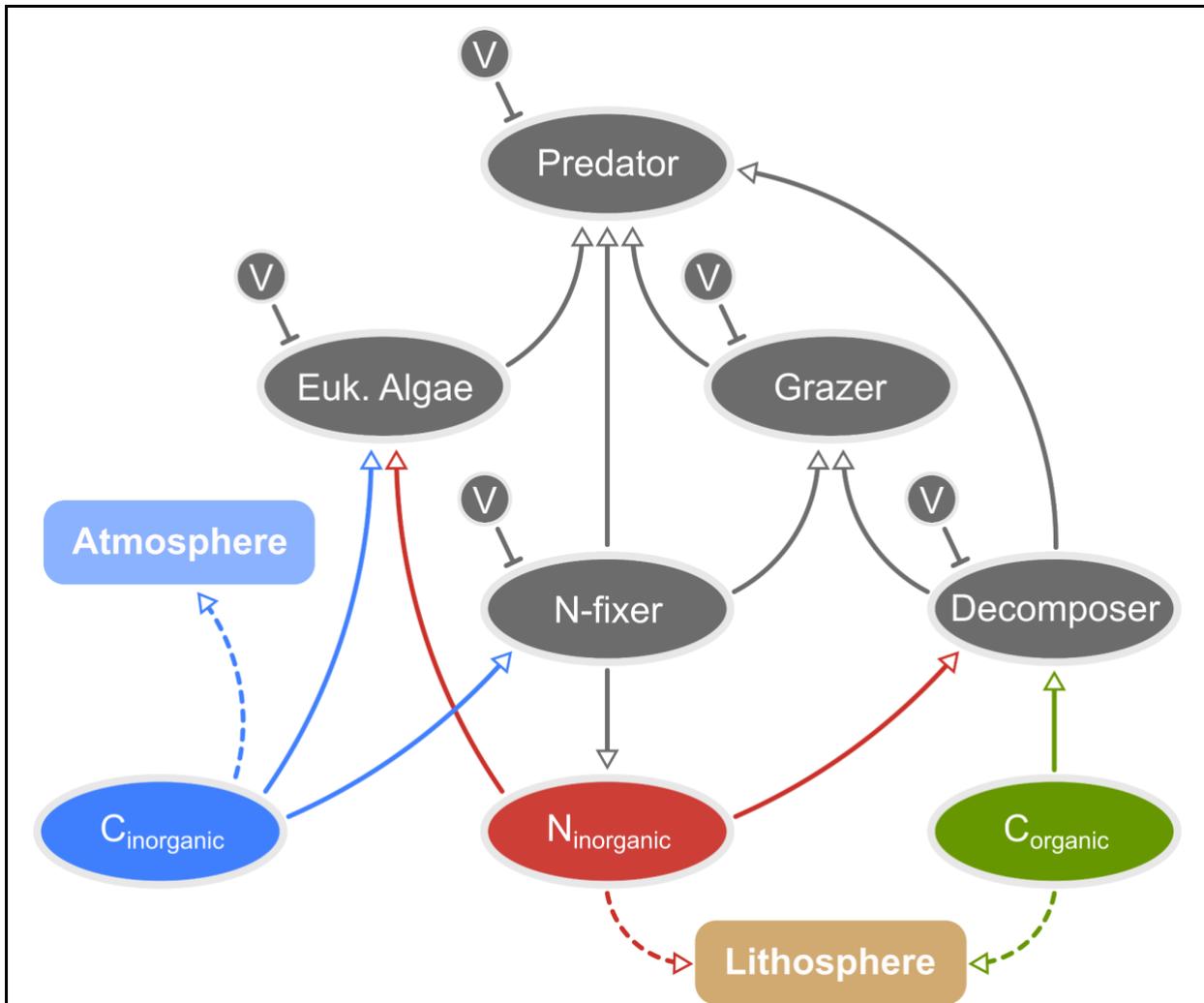
Climate-driven shifts in nutrient and carbon cycling can be studied using mathematical models that track the collective responses of several essential organisms within microbial food webs (Figure B1). Each organism plays a unique role in carbon and nutrient cycling depending on its metabolic requirements, 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.



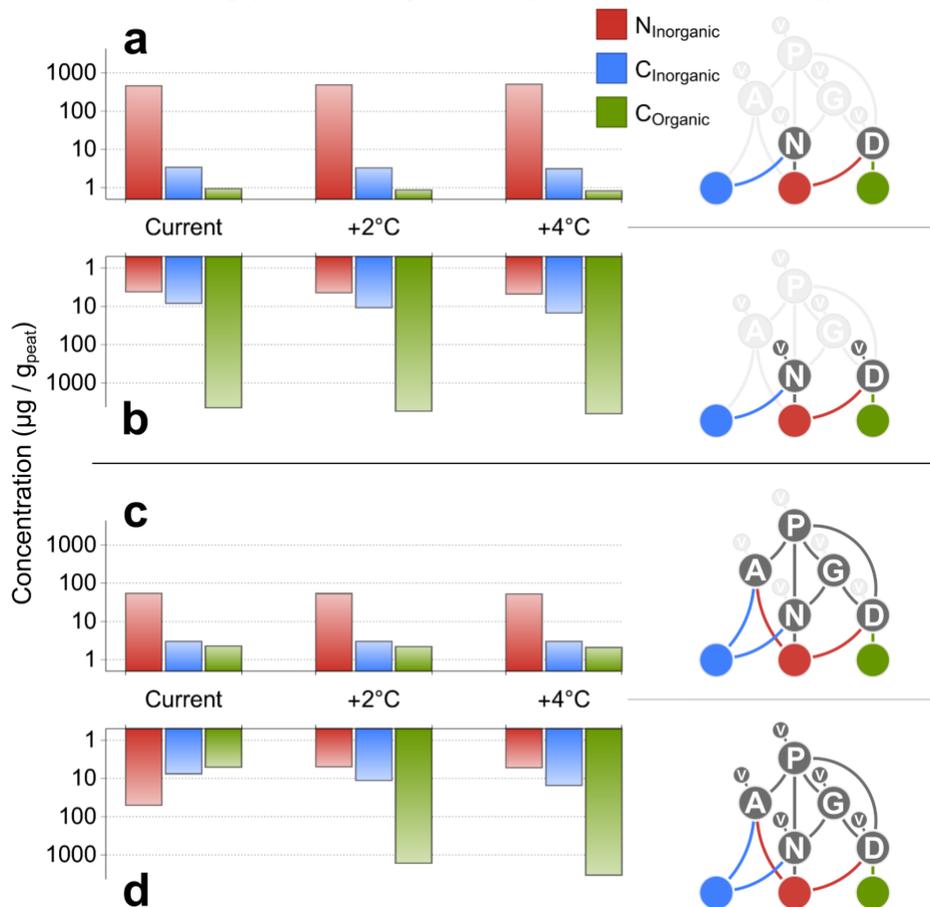
**Figure B1.** Hypothetical microbial food web in *Sphagnum* peatlands including organisms and nitrogen and carbon flow. Arrows represent flow between components. Each type of organism consumes elements or other organisms based on its unique stoichiometric requirements and is also subject to infection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

299 Table 1. Outstanding questions

**Temperature effects on microbial food webs**

- 1) How will the unique temperature responses of functionally and trophically diverse microbes collectively regulate carbon (and nutrient) cycling under warming?
- 2) How will microbial food webs, and therefore ecosystem flux, be rewired by warming?
- 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?
- 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?

**Temperature effects on viruses and viral infections**

- 5) How will warming impact different aspects of the viral infection cycle, including both host-dependent and host-independent processes?
- 6) How will warming influence the direct (*via* cell lysis) and indirect (*via* host population dynamics) functions of viruses in carbon and nutrient cycling?
- 7) How will mismatches between virus and host temperature niches and sensitivities affect virus-host interactions under warming?

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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	- Backwater system of Danube River (Field) <sup>116</sup> - <i>Heterosigma akashiwo</i> (H93616, NM96) / Hav (HaV01, HaV08) (Lab) <sup>63</sup> - Bacteriophage 9A isolated from Arctic seawater (Lab) <sup>117</sup> - Samples from Western Pacific Ocean (Lab) <sup>118</sup>
		Increases with temperature
Adsorption	Decreases with temperature	- Emiliana huxleyi CCMP374 / EhV86 (Lab) <sup>62</sup> - Chaetoceros tenuissimus / Cten DNAV and Cten RNAV (Lab) <sup>88</sup>
	No effect of temperature	- Escherichia coli / coliphage isolates from the River Swift (Lab) <sup>80</sup>
	Increases with temperature	- Backwater system of Danube River (Field) <sup>116</sup> - Escherichia coli / T4 (Lab) <sup>64</sup> - Micromonas sp. MicA, MicB, MicC / MicVA, MicVB, MicVC (Lab) <sup>65</sup> - Micromonas polaris / MpoV (Lab) <sup>66</sup> - Micromonas polaris strain RCC2257, strain RCC2258 / Mpov-45T (Lab) <sup>67</sup>
Burst size	Decreases with temperature	- Backwater system of Danube River (Field) <sup>116</sup> - Micromonas sp. MicA, MicB, MicC / MicVA, MicVB, MicVC (Lab) <sup>65</sup>
	Increases with temperature	- Escherichia coli / coliphage (Lab) <sup>119</sup> - Micromonas sp. MicA, MicB, MicC / MicVA, MicVB, MicVC (Lab) <sup>65</sup>
Latency period	Decreases with temperature	- <i>Heterosigma akashiwo</i> (H93616, NM96) / Hav (HaV01, HaV08) (Lab) <sup>63</sup> - Escherichia coli / T4 (Lab) <sup>64</sup> - Staphylococcus aureus / S. aureus phage (Lab) <sup>120</sup> - Escherichia coli / coliphage (Lab) <sup>119</sup> - Micromonas sp. MicA, MicB, MicC / MicVA, MicVB, MicVC (Lab) <sup>65</sup> - Micromonas polaris / MpoV (Lab) <sup>66</sup> - Micromonas polaris strain RCC2257, strain RCC2258 / Mpov-45T (Lab) <sup>67</sup>

Virus abundance	Temperature effects unclear	<ul style="list-style-type: none"> <li>- Backwater system of Danube River (Field)<sup>116</sup></li> <li>- Southern Beaufort Sea and Amundsen Gulf (Field)<sup>84</sup></li> <li>- Lake Pavin (Field)<sup>83</sup></li> <li>- Japanese paddy field (Field)<sup>86</sup></li> <li>- Michigan agricultural soils (Field)<sup>85</sup></li> <li>- Metadata<sup>59,121</sup></li> </ul>
Lysis thermal range	Temperature effects are host-dependent	<ul style="list-style-type: none"> <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>- <i>Escherichia coli</i> / coliphage isolates from the River Swift (Lab)<sup>80</sup></li> <li>- Metadata<sup>90</sup></li> </ul>
Virus-induced host mortality	Increases with temperature	<ul style="list-style-type: none"> <li>- North Atlantic Ocean (Field)<sup>122</sup></li> </ul>

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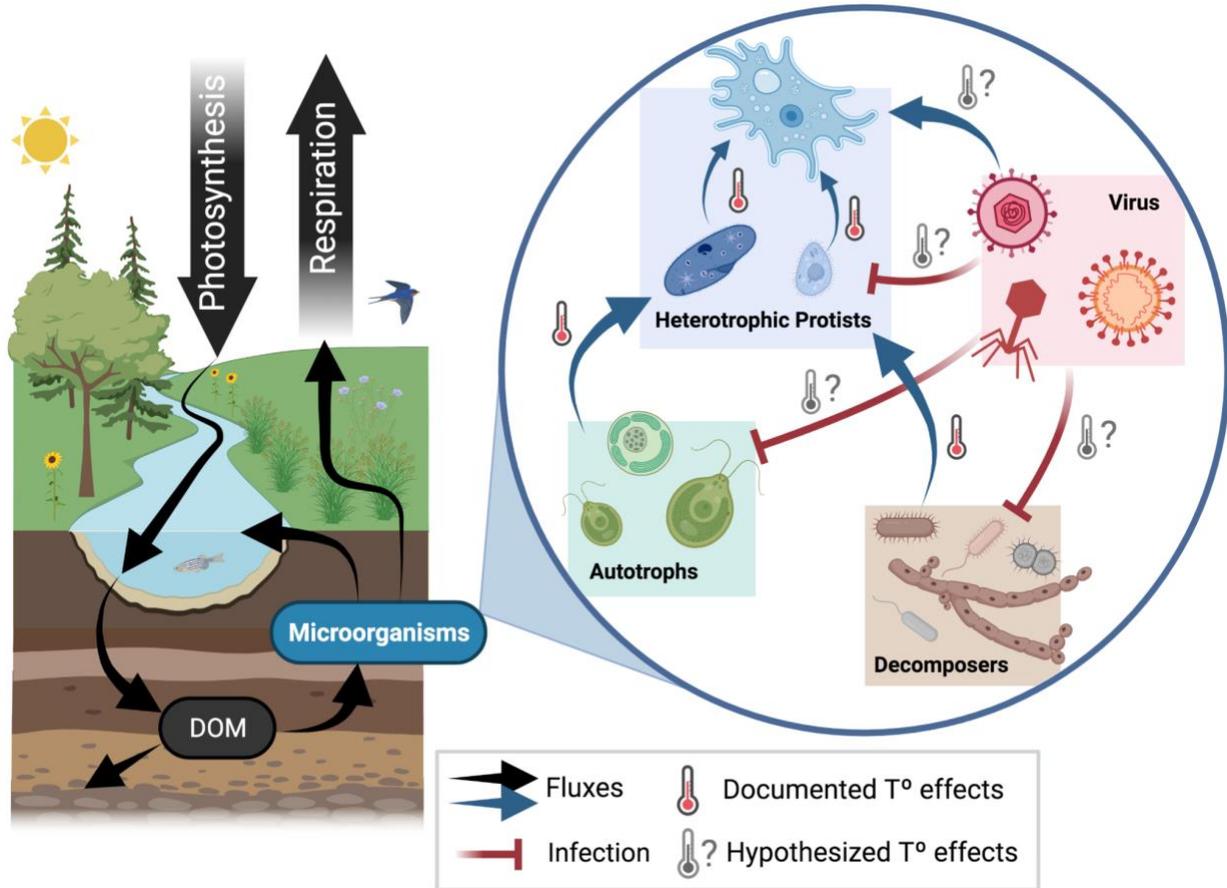
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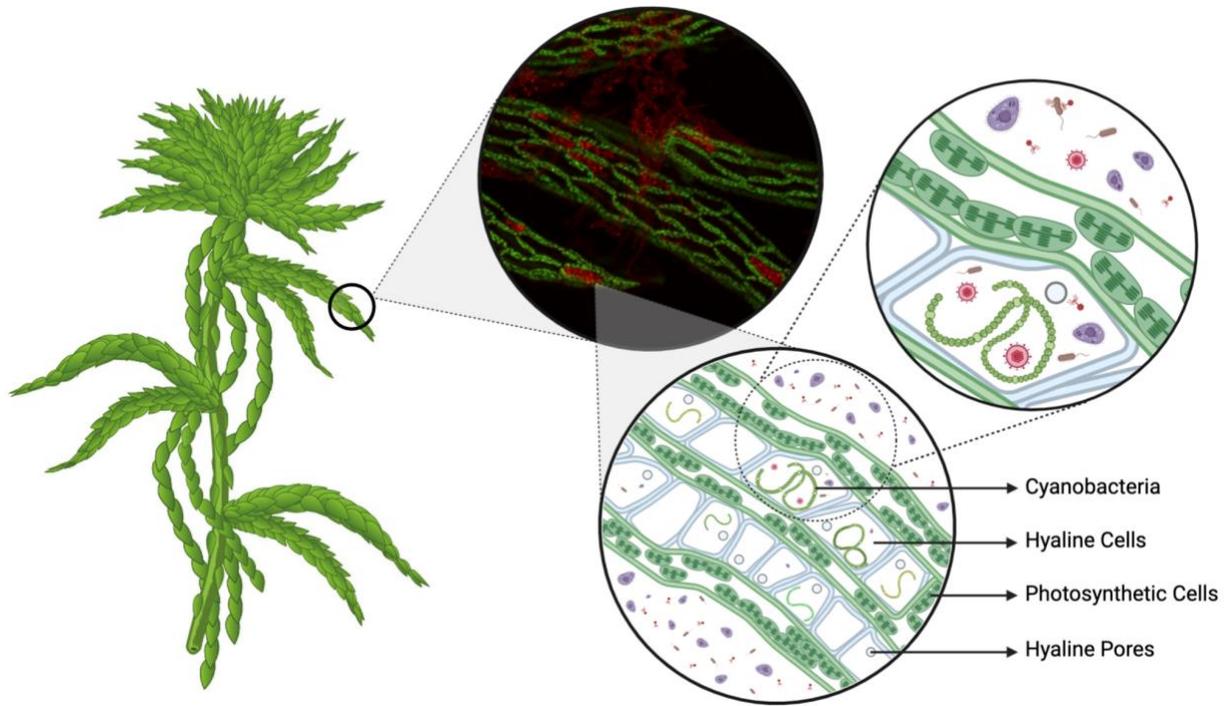
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 330 **Figure 1.** Conceptual diagram outlining the documented and hypothesized temperature effects  
 331 on processes influencing global carbon cycling, including the impacts of decomposers  
 332 (heterotrophic bacteria and fungi), autotrophs (cyanobacteria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

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355 **Figure 3.** *Sphagnum* moss and associated microbial food web. Microbial species inhabit both  
 356 water-filled hyaline cells of *Sphagnum* tissue and the external aquatic habitat. First inset shows  
 357 cyanobacteria (in red) living inside *Sphagnum* tissue (in green, image taken using a Zeiss LSM  
 358 710 laser scanning confocal microscope, image credit: Andrea Timm and Collin Timm).

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