

1 **Title:**
2 Viral infections mediate microbial controls on ecosystem responses to global warming
3

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41 **ABSTRACT**

42 Climate change is affecting how energy and matter flow within ecosystems, altering global
43 carbon and nutrient cycles. Microorganisms play a fundamental role in carbon and nutrient
44 cycling and are thus an integral link between ecosystems and climate. Here, we highlight a major
45 black box hindering our ability to anticipate ecosystem climate responses: viral infections within
46 complex microbial food webs. We show how understanding and predicting ecosystem responses
47 to warming could be challenging—if not impossible—without accounting for the direct and
48 indirect effects of viral infections on different microbes (bacteria, fungi, protists) that together
49 perform diverse ecosystem functions. Importantly, understanding how rising temperatures
50 associated with climate change influence viruses and virus-host dynamics is crucial to this task,
51 yet severely understudied. In this perspective, we 1) synthesize existing knowledge about virus-
52 microbe-temperature interactions and 2) identify important gaps to guide future investigations
53 regarding how climate change might alter microbial food web effects on ecosystem functioning.
54 To provide real-world context, we consider how these processes may operate in peatlands—
55 globally significant carbon sinks that are threatened by climate change. We stress that
56 understanding how warming affects biogeochemical cycles in any ecosystem hinges on
57 disentangling complex interactions and temperature responses within microbial food webs.

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64 INTRODUCTION

65 Climate change is warming terrestrial carbon (C) reserves, making them increasingly vulnerable
66 to microbial respiration (Dorrepaal *et al.* 2009; Jassey *et al.* 2015; Page and Baird 2016; Masson-
67 Delmotte *et al.* In Press). Because microbial respiration increases with temperature (Zhou *et al.*
68 2012; Bradford *et al.* 2019; Smith *et al.* 2019; Wieczynski *et al.* 2021), microbes will likely
69 accelerate carbon release at ever increasing rates as Earth warms, creating a positive atmospheric
70 feedback loop not currently represented in predictive models of future climate (Cavicchioli *et al.*
71 2019). However, warming is expected to restructure microbial food webs through changes in
72 species composition (Petchey *et al.* 1999) (but see (Thakur *et al.* 2021)) and species interactions
73 (Lurgi, López and Montoya 2012; Barbour and Gibert 2021). Additionally, microbial impacts on
74 carbon cycling are likely mediated by viral infections of both microbes and their predators
75 (Wilhelm and Suttle 1999; Weitz *et al.* 2015; Fischhoff *et al.* 2020). Despite the increasing
76 recognition that infectious agents like viruses are integral components of food webs (Lafferty *et*
77 *al.* 2008), the role they play in microbial food webs and their associated temperature
78 dependencies remain poorly understood. Identifying and understanding the temperature-
79 dependence of these biotic controls on microbial respiration is paramount to properly forecast
80 current and future ecosystem-climate feedbacks.

81
82 Autotrophic and heterotrophic bacteria, archaea, fungi, and micro-eukaryotes play functionally
83 unique roles in microbial communities as primary producers, nitrogen (N₂)-fixers (diazotrophs),
84 and organic biomass decomposers. For example, microbial autotrophs provide about half of
85 global primary production (Field *et al.* 1998; Litchman *et al.* 2015). Decomposers recycle carbon
86 and nutrients from dead organic matter and act as major carbon emitters by respiring carbon

87 (CO₂ and CH₄) into the atmosphere (Falkowski *et al.* 2000; Canadell *et al.* 2021). The matter
88 recycled by decomposers reaches higher trophic levels through microbial predation—a process
89 known as the “the microbial loop” (Azam *et al.* 1983; Fenchel 2008). Predation by protists is a
90 major source of mortality among microbial primary producers (Geisen *et al.* 2020) and
91 decomposers (Sherr and Sherr 1988; Gao *et al.* 2019) (Fig. 1), that can drastically impact carbon
92 and nutrient cycling by reducing microbial biomass, increasing nutrient turnover, and altering
93 microbial respiration rates (Trap *et al.* 2016; Geisen *et al.* 2018, 2021; Gao *et al.* 2019; Rocca *et*
94 *al.* 2021). Because of these effects, protists have been called the “puppet masters” of the
95 microbiome (Gao *et al.* 2019). Due to changes in underlying physiological processes, protist
96 predation rates are expected to change with warming (DeLong and Lyon 2020), altering species
97 interactions within microbial food webs (DeLong and Lyon 2020; Thakur *et al.* 2021) and
98 influencing microbial biomass and respiration rates (O’Connor *et al.* 2009; Yvon-Durocher and
99 Allen 2012; Geisen *et al.* 2021). This complexity emphasizes the need for a food web
100 perspective to understand microbial responses to changing environmental conditions (Thakur and
101 Geisen 2019).

102

103 Perhaps our biggest oversight in understanding microbial food web responses to global change is
104 the neglected role of viruses, who have also recently been described as “puppet masters” in the
105 microbiome (Breitbart *et al.* 2018). All microbes are potential hosts for viruses, which may affect
106 microbial food web composition and functioning by increasing microbial mortality and, in turn,
107 nutrient cycling (*via* the Viral Shunt) (Fuhrman 1999; Wilhelm and Suttle 1999; Weinbauer
108 2004; Suttle 2005). Viruses are the most abundant biological entities on Earth (Weinbauer 2004;
109 Suttle 2005); therefore, viral mediation of carbon and nutrient flux within microbial food webs is

110 likely widespread, having important consequences for ecosystem functioning at both local and
111 global scales (Fuhrman 1999; Wilhelm and Suttle 1999; Weinbauer 2004; Suttle 2005; Weitz *et*
112 *al.* 2015). Several aspects of the viral infection cycle and virus-host dynamics could potentially
113 be affected by warming (Table 1), yet the effects of temperature on these processes is unclear
114 and severely understudied (Fig. 2), undermining our ability to predict how microbial food webs
115 will respond to global change.

116
117 Although the individual effects of microbes and viruses on ecosystem functioning have been
118 discussed (Azam *et al.* 1983; Fenchel 2008; Quaiser *et al.* 2015; Ballaud *et al.* 2016; Stough *et*
119 *al.* 2017; Gao *et al.* 2019; Geisen *et al.* 2021), we lack a baseline understanding about how these
120 top-down controls jointly influence ecosystem processes within broader microbial food webs and
121 in response to novel climates. Here, we outline the current state of understanding regarding
122 temperature effects on infections within microbial food webs and propose ways to conceptualize
123 and address existing knowledge gaps, with a focus on potential effects of warming on carbon and
124 nutrient cycling. First, we present the current state of knowledge regarding the effects of
125 temperature on viruses and viral infections. Next, we integrate viruses into microbial food webs
126 to discuss how viruses might mediate the effects of warming on food web dynamics and
127 functioning. Finally, to provide real-world context for the potential effects of warming on viral
128 infections within microbial food webs, we conclude by exploring how virus-microbe responses
129 to warming may alter ecosystem processes in *Sphagnum* moss-dominated peatlands, which are
130 particularly vulnerable to future climate change (Page and Baird 2016) and, despite occupying
131 less than 3% of the Earth's surface, store ~25–30% of the world's soil carbon (Yu *et al.* 2010)
132 and produce 5–10% of global atmospheric methane (Blodau 2002).

133

134 **1. TEMPERATURE EFFECTS ON VIRUSES AND VIRAL INFECTIONS**

135 All components of microbial food webs can be infected by viruses. While it is recognized that
136 rising temperatures influence the ecology and physiology of microorganisms across
137 environments (Labbate *et al.* 2016), it is still unclear how the direct and indirect effects of
138 warming will influence viruses, their infection cycles, and how that will ultimately cascade to
139 influence microbial food web functioning. Viral infection occurs in a sequence of steps (Cann
140 2008) (Fig. 2) including 1) host cell encounter, 2) adsorption, 3) introduction of virus or genetic
141 material into the cell, 4) synthesis of viral particles, and 5) assembly and release of viral progeny.
142 Any one, and likely all, of these steps could be temperature dependent (Fig. 2, Table 1, Table
143 S2), but much research is still needed to evaluate the extent and nature of these temperature
144 dependencies. Furthermore, temperature may affect viral production directly by affecting the
145 particle itself (Nagasaki and Yamaguchi 1998) or indirectly by altering host physiology
146 (Kendrick *et al.* 2014). Understanding each of these temperature effects is paramount to
147 determine how warming might impact carbon and nutrient cycling within microbial food webs.
148
149 Increasing temperature can cause a decrease in latent period (time from infection until release of
150 viral progeny) and an increase in burst size (number of viral progeny released) (Hadas *et al.*
151 1997; Nagasaki and Yamaguchi 1998; Demory *et al.* 2017; Maat *et al.* 2017; Piedade *et al.* 2018)
152 (Fig. 2), followed by a reversal of these trends past a virus-specific thermal optimum (T_{opt})
153 (Kimura *et al.* 2008; Demory *et al.* 2017). Temperature effects on burst size and latent period are
154 likely the result of host metabolism and virus synthesis kinetics, but direct evidence is lacking.
155 Based on these findings, we hypothesize that future warming may increase infection and viral

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

179 unresolved (*e.g.*, increasing temperatures may or may not induce lysis (Shan *et al.* 2014)),
180 exposing a crucial gap in our understanding of the temperature-dependencies of viral infection.
181
182 Viral production is linked to host cell physiology (Tomaru, Kimura and Yamaguchi 2014;
183 Demory *et al.* 2017; Maat *et al.* 2017; Piedade *et al.* 2018) because viruses depend on and rewire
184 the metabolism of host cells (Hurwitz, Hallam and Sullivan 2013). However, viral temperature
185 ranges can be independent of, and often surpass, those of their hosts (Seeley and Primrose 1980;
186 Mojica and Brussaard 2014; Tomaru, Kimura and Yamaguchi 2014). Additionally, multiple
187 viruses that infect the same host can have different temperature optima (Tomaru, Kimura and
188 Yamaguchi 2014), potentially promoting niche differentiation and a shift in dominant viral taxa
189 with warming. This suggests that viruses could be less susceptible to extinction under warming
190 than their hosts, but more research is needed to determine the extent of this phenomenon and the
191 resulting impacts on nutrient and carbon cycling.
192
193 Finally, the potential consequences of viral temperature dependencies for microbial food web
194 dynamics and functioning may be complex, context-dependent, and variable across systems. For
195 example, Frenken *et al.* (2020) used aquatic mesocosm experiments to show that, although
196 warming advanced the seasonal timing of viral infection, it did not increase viral abundance or
197 strengthen viral control over host populations. In addition, Danovaro *et al.* (2011) predicted that
198 the effects of warming on viral abundance will vary by oceanic region and that a consistent
199 response to rising temperatures across environments is unlikely. These examples illustrate that
200 the temperature-dependent effects of viruses can manifest in different aspects of viral
201 infection/virus-host interactions and may vary by region. We argue that controlled studies (*e.g.*,

202 mesocosms, synthetic communities) and *in situ* monitoring across diverse environments can aid
203 in identifying and predicting complex viral responses to temperature in different environmental
204 contexts. Moreover, the vast majority of data available for temperature effects on viral dynamics
205 comes from marine environments or a select few model host-virus systems (Table 1),
206 highlighting the need to expand studies to different environments and new systems to better
207 comprehend the influences of virus-microbe interactions on ecosystem processes under warming
208 conditions.

209

210 **2. INTEGRATING VIRAL INFECTIONS WITHIN MICROBIAL FOOD WEBS UNDER** 211 **WARMING**

212 Although viruses are known to impact carbon and nutrient cycling directly, namely *via* the viral
213 shunt (Wilhelm and Suttle 1999; Sullivan, Weitz and Wilhelm 2017), how viruses might mediate
214 microbial responses to warming is poorly understood. Microbes account for a substantial fraction
215 of the biomass on Earth (Bar-On, Phillips and Milo 2018) and place major controls on carbon
216 and nutrient cycling in terrestrial (Schimel and Schaeffer 2012), freshwater (Kayranli *et al.*
217 2010), and marine (Zhang *et al.* 2018) ecosystems worldwide. Microbial communities are
218 complex, functionally-diverse, multi-trophic food webs (Bengtsson, Setälä and Zheng 1996;
219 Petchey *et al.* 1999; Gao *et al.* 2019; Thakur and Geisen 2019) in which energy and matter flow
220 between organisms that occupy different trophic positions and play a variety of functional roles
221 (Fenchel 2008; Steinberg and Landry 2017). Ecosystem responses to climate change are thus
222 likely regulated by changes in overall microbial food web dynamics and organization (Thakur
223 and Geisen 2019; Kuppardt-Kirmse and Chatzinotas 2020). Viruses could play important roles in
224 these changes that depend on i) the relative infection rates of hosts in different functional groups,

225 ii) the temperature dependencies of the viral infection cycle, iii) thermal matching between virus-
226 host pairs, and iv) changes in host physiology, population dynamics, and species interactions
227 associated with viral infection.

228

229 Broadly speaking, how viruses mediate microbial controls on ecosystem responses to warming
230 hinges on how they impact the overall balance of carbon and nutrient uptake (*via* photosynthesis
231 and decomposition), storage in biomass, sequestration in sediment, and release (*via* respiration)
232 (Box 1, Figs. 2, 3). Respiration and decomposition rates are expected to increase with warming
233 (Petchey *et al.* 1999; Kirschbaum 2000; Smith *et al.* 2019) and may be more sensitive to
234 temperature change than photosynthetic rates (Allen, Gillooly and Brown 2005) (although a
235 great deal of variation exists in temperature sensitivities among different microbial groups
236 (Smith *et al.* 2019)). This suggests that warming could tip ecosystems from productivity-
237 dominant carbon sinks (storing carbon in biomass and sediment) to respiration-dominant carbon
238 sources (releasing carbon into the atmosphere) (Yvon-Durocher and Allen 2012). However,
239 increases in microbial primary productivity should at least partially offset this uneven increase in
240 carbon release (Zhou *et al.* 2012; Wyatt *et al.* 2021). Furthermore, warming is expected to alter
241 the biomass and composition of microbial food webs, affecting ecosystem processes like CO₂
242 release *via* respiration (Geisen *et al.* 2021; Rocca *et al.* 2022). How viruses mediate this balance
243 between carbon uptake and release under warming is poorly understood, but will likely involve
244 complex and differential impacts on the dynamics and mortality of hosts that perform different
245 ecosystem functions (Sarmiento *et al.* 2010; Danovaro *et al.* 2011; Vaqué *et al.* 2019). Based on
246 preliminary model results, we hypothesize that warming could strengthen viral controls on
247 decomposers, N-fixers, and protists, leading to reduced microbial biomass, increased nutrient

248 cycling and respiration, shorter mean residence time of carbon in microbial food web
249 compartments, and shifts in the balance of carbon sequestration and release into the atmosphere
250 (Box 1, Fig. B2d). However, the generality of these effects is very difficult to judge given how
251 much uncertainty remains about the effects of temperature on viral infection, virus-host
252 dynamics, and the impacts of viruses on microbial food web structure.

253

254 **3. PEATLANDS AS A MODEL SYSTEM TO STUDY HOW VIRAL INFECTIONS** 255 **MEDIATE MICROBIAL FOOD WEB RESPONSES TO WARMING**

256 We use peatland microbial food webs as a real-world case study to explore how viral infections
257 may influence the effects of microbial activity on carbon and nutrient cycling in a warming
258 world. Peatlands are typically dominated by *Sphagnum* peat mosses, storing more carbon (in
259 both living biomass and peat)—and therefore arguably having a greater influence on global
260 carbon cycling and climate—than any other single genus of plants (Clymo and Hayward 1982;
261 Gorham 1991). While *Sphagnum* plays a primary role in carbon dynamics (Slate, Sullivan and
262 Callaway 2019), it serves a secondary role by insulating permafrost, thus dampening the impacts
263 of rising temperatures on vast amounts of carbon stored in the arctic tundra (Camill and Clark
264 1998). Peatland microbial food webs are uniquely well-suited systems for studying ecosystem
265 responses to global change due to 1) their net impact on the global carbon cycle (Gorham 1991;
266 Dorrepaal *et al.* 2009; Yu *et al.* 2010; Bu *et al.* 2011), 2) the functional diversity of their
267 constituent microbial taxa (Gilbert *et al.* 1998; Trap *et al.* 2016; Geisen *et al.* 2018; Thakur and
268 Geisen 2019), 3) their vulnerability to changes in temperature (Richardson *et al.* 2018; Norby *et*
269 *al.* 2019; Smith *et al.* 2019; Geisen *et al.* 2021), and 4) the ability to grow and study *Sphagnum*
270 moss and associated microbial communities in the laboratory (Altermatt *et al.* 2015; Geisen *et al.*

271 2018; Carrell *et al.* 2019, 2022b) Doing so, however, will require a multifaceted approach—
272 including characterization of microbial communities in the field, microbial experiments in the
273 laboratory, -omics approaches, and mathematical modeling (Singh *et al.* 2010; Geisen *et al.*
274 2017), all of which can benefit from cross-scale integration.

275

276 We propose that the response of *Sphagnum*-dominated peatlands to warming is regulated by
277 poorly understood controls on carbon and nutrient cycling from microbes and viral infections
278 (Fig. 1, Box 1). Microbes play diverse functional roles in peatlands (Gilbert *et al.* 1998; Gilbert
279 and Mitchell 2006; Lara *et al.* 2011; Kostka *et al.* 2016; Carrell *et al.* 2022a) (Fig. 3). For
280 example, bacterial and fungal decomposers are primarily responsible for breaking down dead
281 organic material stored within peatlands (Gilbert *et al.* 1998; Gilbert and Mitchell 2006), a
282 process being accelerated by warming (Dorrepaal *et al.* 2009). Additionally, *Sphagnum*'s ability
283 to persist in harsh peatland habitats with extremely low mineral nitrogen availability depends on
284 symbiotic interactions with microbial associates (Lindo, Nilsson and Gundale 2013; Kostka *et al.*
285 2016; Carrell *et al.* 2022a)—including diazotrophs that colonize the cell surface and water-filled
286 hyaline cells in host plants (Kostka *et al.* 2016) (Fig. 3). Bacterial methanotrophs are also
287 prevalent in boreal peat bogs (Liebner and Svenning 2013; Vile *et al.* 2014) and not only fix N₂,
288 but supply 5%–20% of CO₂ necessary for *Sphagnum* photosynthesis *via* methane oxidation
289 (Larmola *et al.* 2014). *Sphagnum*'s microbial community composition varies widely with climate
290 (Singer *et al.* 2019) and is expected to shift considerably under warming (Carrell *et al.* 2019;
291 Basińska *et al.* 2020), likely altering associated microbial food webs (Bengtsson, Setälä and
292 Zheng 1996; Petchey *et al.* 1999; Geisen *et al.* 2018; Gao *et al.* 2019; Thakur and Geisen 2019).

293

294 Peatland ecosystems also harbor a diverse group of viruses that infect prokaryotes and
295 eukaryotes (Ballaud *et al.* 2016; Emerson *et al.* 2018; Stough *et al.* 2018) and are correlated with
296 overall concentrations of both CO₂ and CH₄ (ter Horst *et al.* 2021). Surprisingly, the inferred
297 frequency of protist infections in the *Sphagnum* microbiome was found to be higher than that of
298 bacterial infection by phages (Stough *et al.* 2018), although the functional role of protist
299 infection in this system remains unclear. Fungal viruses can have considerable downstream
300 ecological consequences by lysing or altering the phenotypes of fungal decomposers, symbionts,
301 or pathogens in *Sphagnum* (Sutela, Poimala and Vainio 2019). In peatlands, viral community
302 composition, abundance, and lifestyle strategies are influenced by environmental factors,
303 including temperature (Ballaud *et al.* 2016; Emerson *et al.* 2018). However, how warming might
304 modify the direct (lytic release of elements) and indirect (altered host phenotype/dynamics and
305 food web processes) effects of viral infections on *Sphagnum*-associated microbial food webs—
306 and carbon and nitrogen cycling in peatlands—is not well understood. Our simple model
307 suggests that viral infections and microbial activity may jointly accelerate the positive effects of
308 warming on C sequestration in peatlands (Box 1, Fig. B2). However, this simple conceptual
309 model is intended as a first attempt to generate hypotheses about the potential impacts of
310 warming, rather than predict future scenarios. Indeed, the mechanisms and parameters governing
311 such interactions between temperature, viruses, protists, and prokaryotes in this model—and the
312 magnitude and direction of resulting changes in carbon cycling—have little empirical
313 verification and will require much more experimental investigation to resolve, thus highlighting
314 the importance of these missing data. A deeper understanding about how these ecological
315 interactions occur in nature and how they are influenced by warming is direly needed, but
316 peatland microbial food webs provide a promising system to begin to develop this understanding.

317

318 CONCLUSIONS

319 Microbial food webs play a central role in the global carbon cycle by processing and storing vast
320 amounts of carbon. We suggest that viral infections within microbial food web components that
321 play distinct functional roles, and their associated temperature-dependencies, could control
322 changes in carbon cycling and storage in response to global warming. We highlight the
323 importance of studying the complex dynamics of microbial food webs to better understand and
324 predict whether rising temperatures will lead to net carbon sequestration or release in globally
325 important ecosystems like *Sphagnum*-dominated peatlands. But we also stress that these
326 ecological interactions and their temperature-dependencies are poorly understood, highlighting
327 several gaps for future research. We propose the following list of questions to serve as a guide
328 moving forward:

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

344

345 Resolving these uncertainties will require a combination of empirical and theoretical analyses
346 that specifically evaluate temperature-dependencies and virus-host interactions within microbial

347 food webs. The effects of these important processes on microbial population dynamics and
348 carbon flow may then shed light on the broader impacts of warming on carbon cycling and
349 storage within and across whole ecosystems.

350

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Box 1.

Climate-driven shifts in nutrient and carbon cycling can be studied using mathematical models that track the collective responses of several essential organisms within microbial food webs (Fig. B1). Each organism plays a unique role in carbon and nutrient cycling depending on its metabolic requirements, trophic mode (autotroph, heterotroph), trophic position, stoichiometry, temperature sensitivity, etc. The fate of carbon—storage in biomass, storage in sediment, or respiration into the atmosphere—is therefore controlled by the composition and organization of microbial food webs. Here we develop a conceptual model describing a simplified, example microbial food web from the *Sphagnum*-dominated peatland system and examine potential impacts of warming on ecosystem functioning.

Organisms

- **Decomposers** like heterotrophic bacteria and fungi recycle dead organic matter produced primarily by plants (C uptake) and are major contributors to microbial respiration (C release) and soil organic carbon via mortality (C sequestration).
- **Nitrogen-fixers** like cyanobacteria, methanogenic archaea, and some heterotrophic bacteria transform atmospheric nitrogen (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.

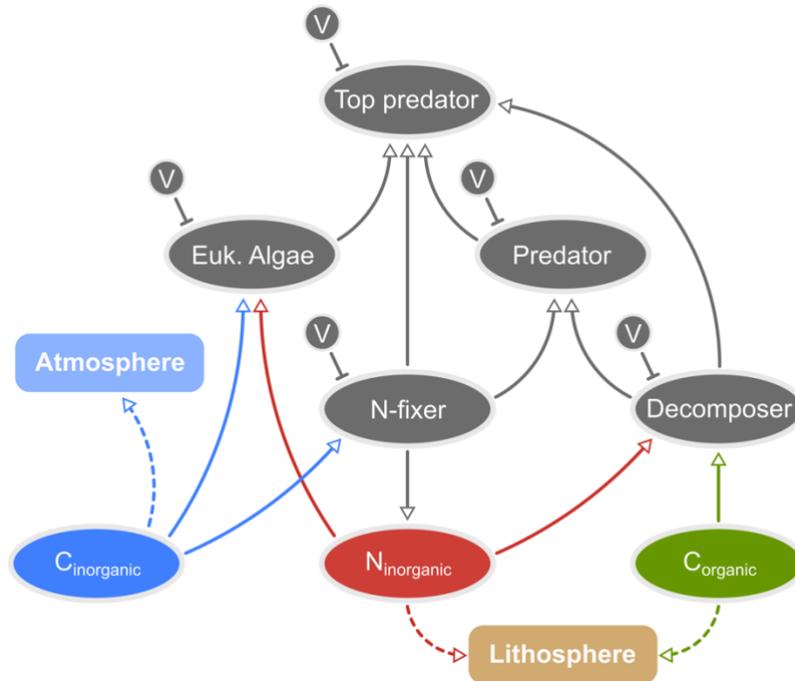


Figure B1. Hypothetical microbial food web in *Sphagnum* peatlands including organisms and nitrogen and carbon flow. Arrows represent flow between components. Each type of organism consumes elements or other organisms based on its unique stoichiometric requirements and is also subject to infection by 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 $\sim 0.32\text{eV}$ (Allen, Gillooly and Brown 2005; López-Urrutia *et al.* 2006; O'Connor *et al.* 2009; Yvon-Durocher and Allen 2012)) than respiration and predation ($\sim 0.65\text{eV}$ (Brown *et al.* 2004; Dell, Pawar and Savage 2011, 2014)), while mortality lies somewhere in between ($\sim 0.45\text{eV}$ (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.

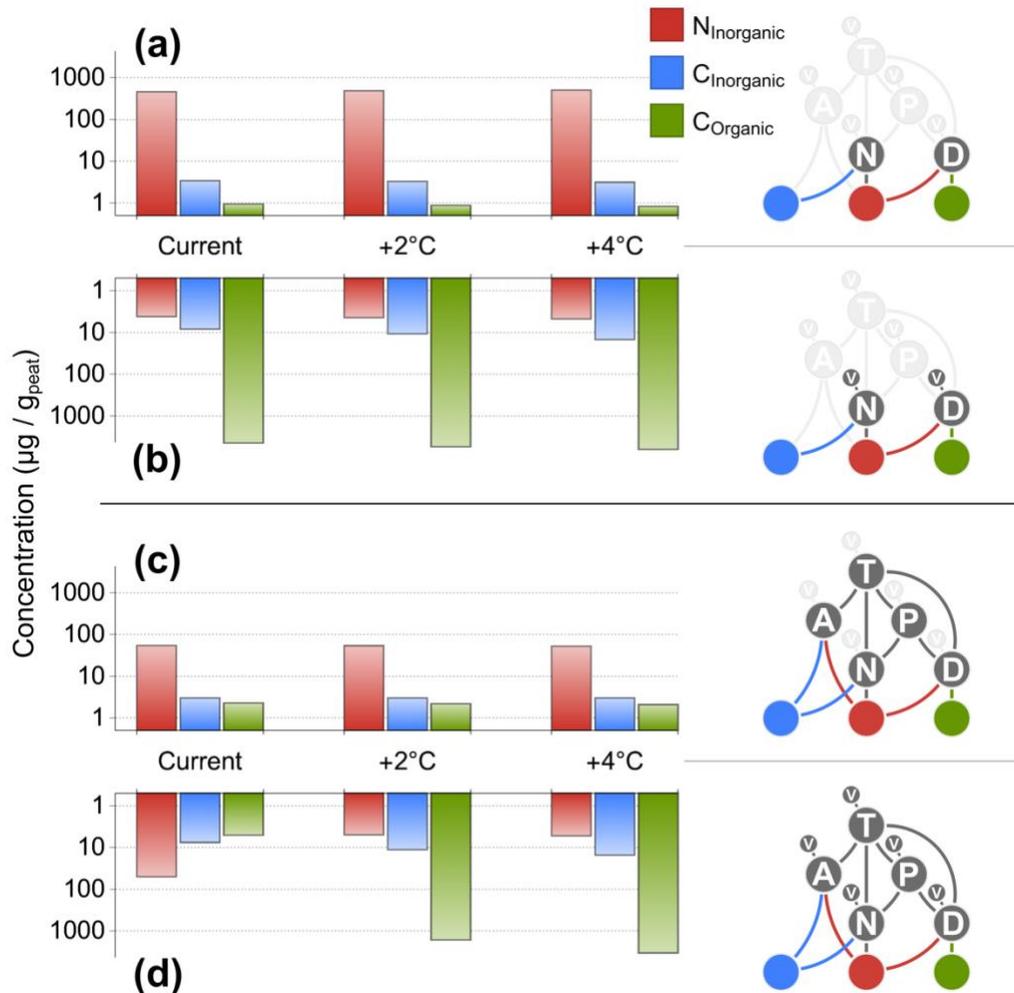


Figure B2. The effects of warming on equilibrium concentrations of nitrogen and carbon in the model microbial food web from Fig. B1. Four scenarios are shown to assess the influences of different food web components: (a) non-protists only (N + D), (b) non-protists + viruses (N + D + V), (c) non-protists + 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
		- <i>Heterosigma akashiwo</i> (H93616, NM96) / Hav (HaV01, HaV08) (Lab) (Nagasaki and Yamaguchi 1998) ²
	Decreases with temperature	- <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

		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> / <i>S. aureus</i> phage (Lab) (Krueger and Fong 1937) ¹³
Virus abundance	Temperature effects unclear	- 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> 2011 ¹⁸ ; Williamson <i>et al.</i> 2017 ¹⁹)
Lysis thermal range	Temperature effects are host-dependent	- <i>Heterosigma akashiwo</i> (H93616, NM96) / HaV (HaV01, HaV08) (Lab) (Nagasaki and Yamaguchi 1998) ²
		- Bacteriophage 9A isolated from Arctic seawater (Lab) (Wells and Deming 2006) ³
		- <i>Escherichia coli</i> / coliphage isolates from the River Swift (Lab) (Seeley and Primrose 1980) ⁵
		- Metadata (Mojica and Brussaard 2014)
Virus-induced host mortality	Increases with temperature	- North Atlantic Ocean (Field) (Mojica <i>et al.</i> 2016)

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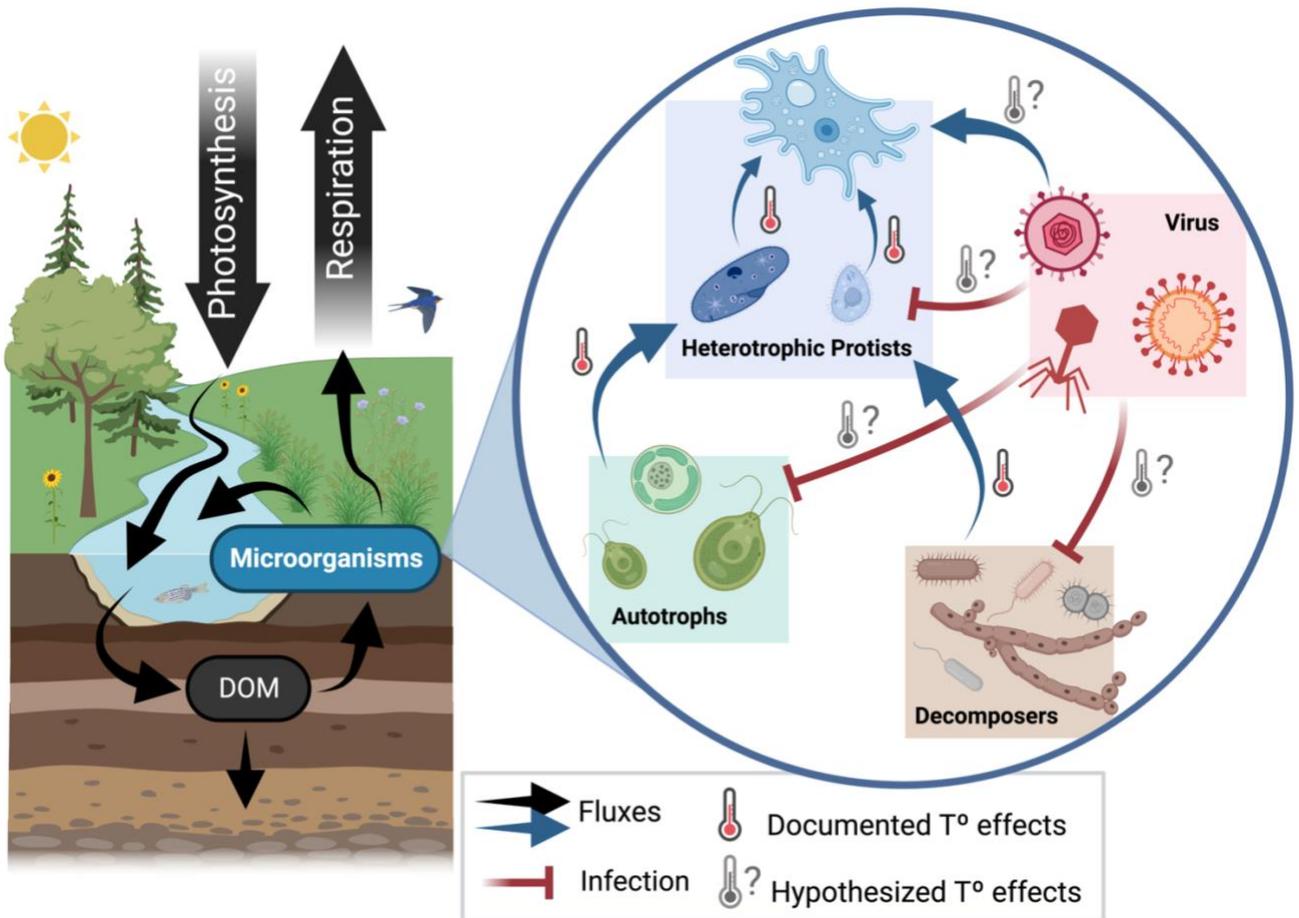
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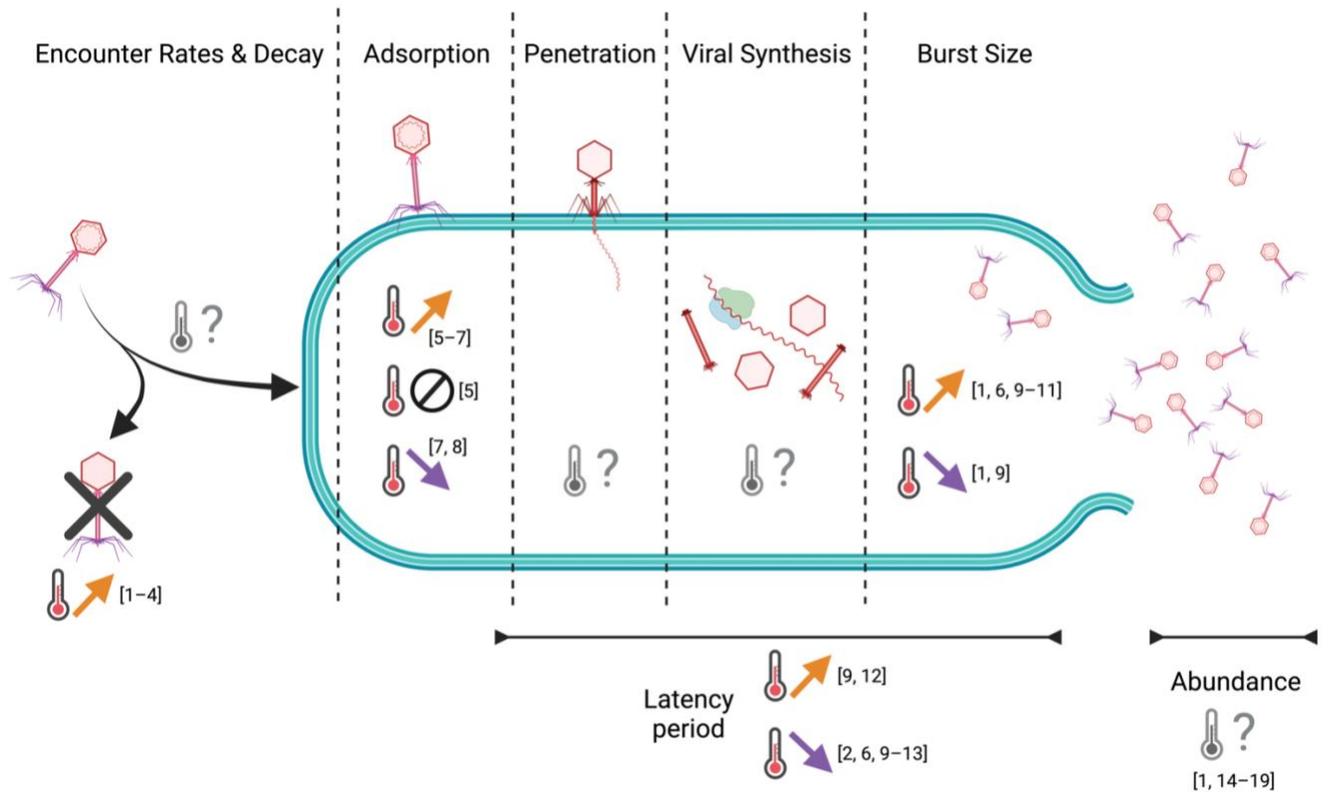
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401 **FIGURES**





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414 **Figure 2.** Stages of the viral lytic infection cycle and published temperature effects. Orange

415 arrows indicate a positive effect, purple arrows indicate a negative effect, and interdictory

416 symbols indicate no effect with warming. Gray thermometers indicate stages of the viral

417 infection cycle that either have no published experimental data or published effects are

418 confounded by other environmental/biological factors (*e.g.* abundances from field studies).

419 Numbers correspond to references in Table 1. More details from these studies can be found in

420 Table S2.

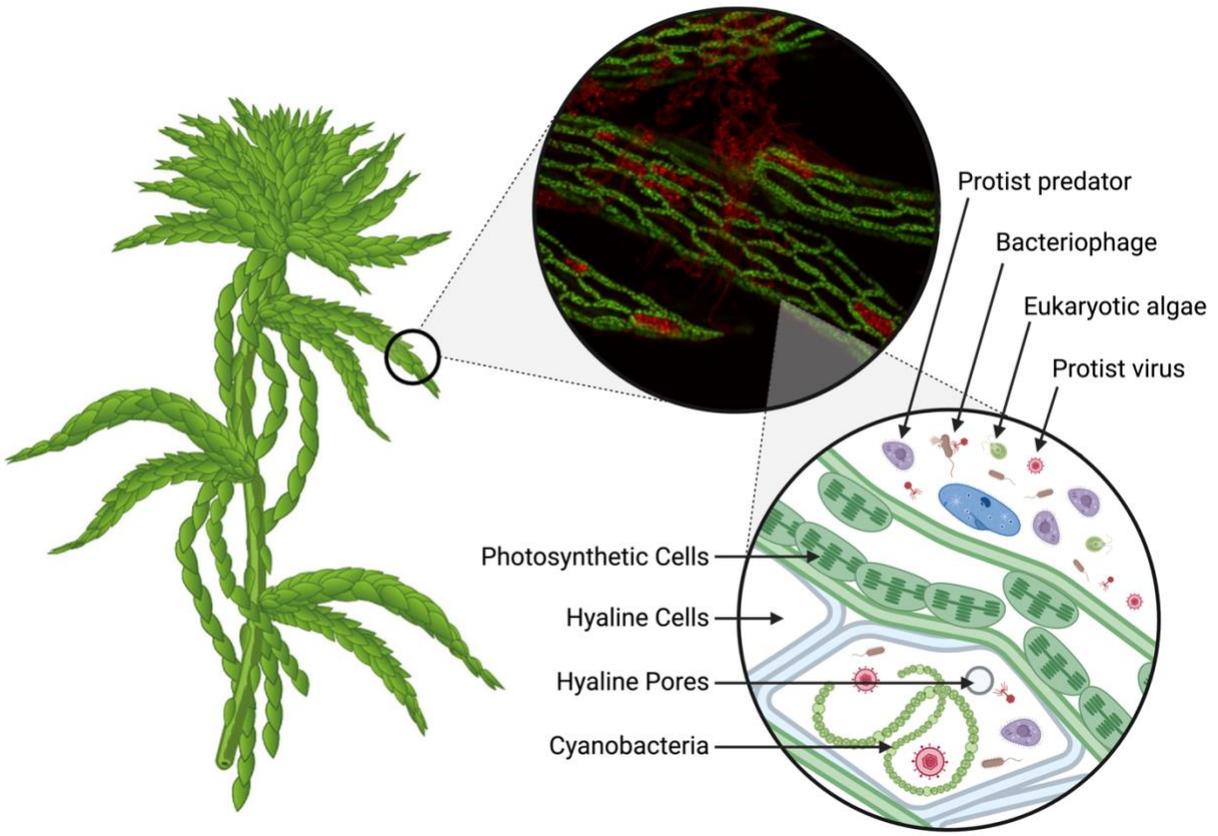
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427 **Figure 3.** *Sphagnum* moss and associated microbial food web. Microbial species inhabit both
 428 water-filled hyaline cells of *Sphagnum* tissue and the external aquatic habitat. First inset shows
 429 cyanobacteria (in red) living inside *Sphagnum* tissue (in green, image taken using a Zeiss LSM
 430 710 laser scanning confocal microscope, image credit: Andrea Timm and Collin Timm).

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