

1 **Towards a microbial process-based understanding of the resilience of**
2 **peatland ecosystem service provisioning – a research agenda**

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78 **Highlights**

- 79 . Although microbes are key to peatland function the underpinning processes are
80 unclear
- 81 . Microbial characterisation is needed across a range of sites, depths and conditions
- 82 . Temporal and spatial changes in microbial communities need to be linked to
83 functions
- 84 . Potential to use microbiome as a monitoring tool for peatland restoration
85 progress
- 86 . Enhancing microbial communities could improve peatland resilience

87 **Keywords**

88 Peat; Resilience; Microbiology; Carbon Cycling; Peatland Restoration and Management

89

90 **Abstract**

91 Peatlands are wetland ecosystems with great significance as natural habitats and as major
92 global carbon stores. They have been subject to widespread exploitation and degradation with
93 resulting losses in characteristic biota and ecosystem functions such as climate regulation.
94 More recently, large-scale programmes have been established to restore peatland ecosystems
95 and the various services they provide to society. Despite significant progress in peatland
96 science and restoration practice, we lack a process-based understanding of how soil microbiota
97 influence peatland functioning and mediate the resilience and recovery of ecosystem services,
98 to perturbations associated with land use and climate change.

99 We argue that there is a need to: in the *short-term*, characterise peatland microbial communities
100 across a range of spatial and temporal scales and develop an improved understanding of the
101 links between peatland habitat, ecological functions and microbial processes; in the *medium*
102 *term*, define what a successfully restored 'target' peatland microbiome looks like for key carbon
103 cycle related ecosystem services and develop microbial-based monitoring tools for assessing
104 restoration needs; and in the *longer term*, to use this knowledge to influence restoration
105 practices and assess progress on the trajectory towards 'intact' peatland status.

106 Rapid advances in genetic characterisation of the structure and functions of microbial
107 communities offer the potential for transformative progress in these areas, but the scale and
108 speed of methodological and conceptual advances in studying ecosystem functions is a
109 challenge for peatland scientists. Advances in this area require multidisciplinary collaborations
110 between peatland scientists, data scientists and microbiologists and ultimately, collaboration
111 with the modelling community.

112 Developing a process-based understanding of the resilience and recovery of peatlands to
113 perturbations, such as climate extremes, fires, and drainage, will be key to meeting climate
114 targets and delivering ecosystem services cost effectively.

115

116 **1.0 Introduction**

117 Peatlands are the largest store of terrestrial carbon (Joosten et al. 2016), yet many have
118 become net sources of carbon emissions due to land use change, erosion, acid deposition,
119 drainage and fire. Peatland restoration is a cost-effective method of lowering emissions and
120 removing carbon from the atmosphere, costing between GBP 6 – 29 per tCO₂e (Moxey, 2011)
121 and a number of restoration projects have been completed around the world (Bonn et al., 2014).
122 While examples of successful methods for peatland restoration and recovery of ecological
123 functions such as climate mitigation can now be demonstrated (Günther et al., 2020), the role of
124 the microbiome in the restoration process and its influence on ecosystem resilience to external
125 pressures is not adequately understood.

126 Carbon cycling in peatlands is fundamentally driven by microbial processes (Andersen et al.,
127 2013) and just the upper 1.5 m of peat contains 3-4 tonnes per ha of microbial biomass
128 (Dobrovol'skaya et al., 2017). Although microbial processes drive carbon transformations in
129 peatlands, our current understanding of the controls on these systems is mostly based on the
130 dynamics of variables such as water-table depth and temperature. In fact, microbial processes
131 are still mostly a 'black box' where we only know how the inputs to the system affect the
132 outputs, but we do not know the processes involved inside the microbial 'black box'.

133 In 2019, a series of four workshops (funded by NERC UK) were held at The University of
134 Manchester to map our current understanding of the role of the microbial community on
135 peatland ecosystems services, and define research questions which could develop a microbial

136 process-based understanding of the resistance and recovery of peatland systems to
137 perturbations. Participants were a diverse group of peatland scientists, microbiologists,
138 modellers and restoration practitioners as well as representatives from governmental and non-
139 governmental organisations. In this commentary we develop the key ideas emerging from four
140 days of discussion with over 50 participants to define a research agenda for progress in this
141 area.

142 **2.0 Discussion**

143 *2.1 What is peatland resilience, and in what ways does understanding the microbial system* 144 *underpin it?*

145 As major stores and sources of carbon and greenhouse gases, peatlands play a key role in
146 regulating the climate. Thus, the nature of their functional response to climate change, and the
147 ways in which peatland management has in the past and can in the future mediate this
148 response, are important components of peatland-climate feedbacks.

149 Resilience can be defined as ‘the capacity of a system to absorb disturbance and reorganize
150 while undergoing change so as to still retain essentially the same function, structure, identity,
151 and feedbacks’ (Walker et al., 2004). What makes a system resilient is key to our understanding
152 of how peatlands have responded in the past and may respond to future changes in
153 management, deposition chemistry and climatic conditions. Resilient peatlands maintain their
154 long-term carbon sequestration function (and the associated ecosystem services) under a
155 changing climate or land use. This resilience mitigates the risk of degradation of the peatland
156 carbon store and release of significant amounts of carbon to the atmosphere (Billett et al.,
157 2010).

158 Although peatlands are naturally resilient systems, as evidenced by their persistence despite
159 numerous external pressures, resistance and recovery concepts are highly relevant in the
160 context of degraded peatlands. For example, UK peatlands are highly modified ecosystems due

161 to a range of anthropogenic impacts and consequent degradation and erosion (Evans et al.,
162 2006). Extensive restoration and rehabilitation efforts are now under way, particularly in the
163 uplands and at former peat extraction sites (Grand-Clement et al., 2015; Juottonen et al. 2012;
164 Lunt et al., 2010; Parry et al., 2014), meaning there is an urgency to understanding if, and how
165 quickly, ecosystem functions can be restored after disturbance. It is possible that peatlands may
166 move between a number of alternative stable states; e.g. due to past management, pollution or
167 climatic events (Scheffer et al., 1993). Climate change and/or management could push a
168 peatland into a new stable state representing either a safe operating space for carbon storage
169 or a completely different system that is a net source of greenhouse gases.

170 The scale of future climate change may present an existential threat to UK peatlands with the
171 potential to move peatlands out of their natural bioclimatic envelope into new states, in which
172 carbon sequestration and storage may no longer be maintained (Gallego-Sala et al., 2010).
173 However, we do not know which of the key carbon cycle related peatland functions are resilient
174 to these changes. Further research is needed to define resilience in terms of peatland carbon,
175 microbiological and eco-hydrological functions, and to identify particularly susceptible peatlands
176 (e.g. types or location) and whether tipping points exist for abrupt shifts to alternative states that
177 could cause a cascade of failures in ecosystem function.

178 *2.1 What microbial processes are key to peatland function?*

179 In peatlands and most other soil systems, plants are a vital and highly controlling feature of the
180 environment, and therefore plant-microbe interactions are often considered to “drive” the soil
181 microbiome and its functionality (Robroek et al., 2015). However, peatlands are somewhat
182 unusual in this respect because of multiple factors that decrease the potential of vascular plants
183 to strongly influence the ecosystem (e.g. deep peat depth, waterlogging, low nutrient
184 availability). This means that microbes are likely to be relatively more important in peatlands
185 from a functional perspective compared to other temperate ecosystems like woodlands and

186 grasslands, although vegetation still shapes microbial communities and the response of
187 greenhouse gas fluxes to warming in the upper layers (Ward et al., 2015, 2013).

188 The role that plant communities play on peatland processes through their tight links with
189 microbes has been intensively studied. Plant removal experiments attest a key role for plant
190 community composition in peatland carbon cycling (Kuiper et al., 2014; Robroek et al., 2015;
191 Ward et al., 2013), and highlight its importance to microbial community composition and
192 microbial-based processes (Bragazza et al., 2013; Jassej et al., 2014). Although peatlands
193 have been perceived as remarkably stable in terms of microbial species composition (Backéus,
194 1972; Rydin and Barber, 2001), evidence is mounting that species interactions are affected
195 (Breeuwer et al., 2009), and biological diversity is decreasing (Field et al., 2014) as a result of
196 changing environmental conditions. Depending on the type of shifts in the plant community
197 composition, corresponding changes in soil microbial community functional trait composition
198 may enhance or mediate the effects of plant community change on ecosystem functions (Díaz
199 et al., 2007). Recent findings that microbial community composition turnover far exceeds
200 turnover in the plant community composition (Robroek et al., 2020) only highlights that we
201 urgently need to improve our understanding on how this affects plant-soil processes and
202 ecosystem functions. The most recognised function of microbes in peatlands is their role in
203 decomposition and stabilisation of organic carbon, the balance of which in comparison with
204 primary productivity determines the net flux of carbon. Microbes are also intimately involved in
205 the success of vascular and non-vascular plants (e.g. mosses) on peatlands and therefore,
206 through numerous symbioses and interactions, they support the primary production which
207 underpins the existence of biologically diverse carbon sequestering peatlands. Some peatland
208 microbes are also capable of photosynthesis, either as obligate phototrophs or mixotrophs
209 (Jassej et al., 2015), and therefore directly contribute to carbon uptake from the atmosphere
210 (although the magnitude of this uptake remains largely unknown). These examples show how

211 microbes function on both sides of opposite processes, demonstrating that questions of
212 microbial functioning in healthy peatlands are likely not to have simple answers. By identifying
213 microbial processes and their constraints, it may be possible to predict and influence the
214 direction in which peatland processes proceed, and we may gain insight into feedback loops
215 that can enhance resilience of ecosystem functions to perturbations.

216 Microbiological research has so far focused on the characterisation of taxonomy and community
217 structure rather than the functionality and contribution to peatland ecosystem services and
218 resilience (Andersen et al., 2013). Whilst it is important to differentiate “who is there?”, the most
219 important question from a practical point of view is “what do they do?” (Greslehner, 2020). The
220 relationships between microbiome community structure and functions are complex,
221 incorporating interactions between species, both abundant and rare (Jousset et al., 2017; Rivett
222 and Bell, 2018), and the matter of functional redundancy, which means that community structure
223 does not directly infer function (Robroek et al., 2017). Ultimately, recovery and resilience of a
224 peatland is likely to be closely linked to gene abundance and activity rather than species
225 presence or absence. Therefore, a focus on measurement of microbial phenotypic
226 characteristics or traits like community growth rate and carbon use efficiency is more likely to
227 provide a mechanistic link of microbial processes to C cycling in peatlands. Understanding the
228 ecosystem implications of microbial processes needs an integrated approach linking taxonomy,
229 function and process rate measurements (Hall et al., 2018).

230 Microbes do not exist in isolation, but rather they adapt and respond to their surroundings, and
231 furthermore their activities cause fundamental changes in the micro-environment which
232 commonly results in macroscopic effects of relevance to the ecosystem as a whole. When this
233 happens, microbes can be described as ecosystem engineers and this is certainly the case in
234 peatlands. For example, aerobic microbial respiration depletes oxygen in waterlogged peat,

235 leading to the development of anoxic conditions and a shift to anaerobic metabolism, which is a
236 major factor in stabilising the carbon store in peatlands (Ingram, 1978).

237 We believe microbiological assessments are an undervalued tool in understanding peatland
238 ecosystem functions and drivers of change. For example, the microbiological response to
239 environmental changes can be much more rapid than changes in plant and animal communities,
240 as a consequence of short generation times and their evolutionary potential (Logue et al., 2015).
241 Microbial responses to external and internal stressors may therefore be utilised as rapid
242 indicators as peatland systems approach potential tipping points (i.e. changes in substrate
243 availability and redox conditions) or may assist in identifying limiting factors in peatlands
244 recovering from degradation and enhancing resilience to future changes. Adaptive responses
245 occur both at the individual level (e.g. adaptation of a species to drought conditions) and at the
246 community level (e.g. replacement of a community member with an organism which is already
247 drought-adapted) (Potter et al., 2017). This is one reason why community surveys are unlikely
248 to yield proper understanding of the microbial contributions to processes, and we need to
249 understand mechanistically how microbes interact with the environment.

250 Understanding links between vegetation shifts and microbial composition and functioning will be
251 key to better understanding interrelationships between above- and belowground processes in
252 peatland systems, their resilience to environmental change and recovery from degradation.
253 Changes in the dominance of mycorrhizal associated plants such as ericaceous shrubs can
254 have a significant impact on decomposition rates in peatlands, likely driven in part by
255 competitive interactions between ericoid mycorrhizas and saprotrophic free-living fungi (Ward et
256 al., 2015, 2013). The presence of ericoid or ectomycorrhizal fungi is associated with a wider C:N
257 ratio in litter and inhibition of decomposition processes by saprotrophic fungi (Averill et al.,
258 2014). The extent to which global change factors such as N deposition and climate warming
259 alter competitive interactions between mycorrhizal and free-living fungi either directly or via

260 vegetation shifts or the microbial loop will be important for informing models of peatland C-
261 cycling.

262 Different microbial groups play different roles in the decomposition of organic matter in
263 peatlands, a key example being the tendency for fungi to have greater extracellular enzyme
264 activity than bacteria (Bragazza et al., 2015). Research has shown that these communities
265 change during restoration and in response to changing conditions (Andersen et al., 2010; Elliott
266 et al., 2015), however, it is unclear how this change in the microbiome affects the resilience and
267 overall function of a peatland. Knowledge regarding gradients in microbiological community
268 structure across peat depth, vegetation types and severity of degradation or recovery following
269 peatland restoration is currently lacking. Of particular interest is the gradient through depth as
270 this may be key to our understanding of the acrotelm/catotelm model of peatlands (and
271 haplotelmic model in severely degraded areas) and its role in the carbon balance of a peatland
272 (Clymo, 1984). In particular, the potential change with depth of electron acceptor availability
273 (Meronigal and Rabenhorst, 2013) and recalcitrance of carbon sources (Putkinen et al., 2009)
274 may be key controls on carbon cycling by methanotrophic species. Climate change may alter
275 the hydrological functioning of peatlands, as does restoration, where raising the water table is
276 the desired outcome. Understanding the community structure and function of obligate and
277 facultative anaerobic taxa is important as restoration practices such as gully blocking can create
278 overall wetter soil conditions, including ponds, with potential impacts on methane emissions
279 (e.g. Cooper et al., 2014) and water quality (e.g. Peacock et al., 2018).

280 In addition to understanding the importance of changing redox conditions, leading to altered
281 pools of electron acceptors, a deeper understanding of the ability of the microbial community to
282 access specific electron donors is critical to modeling community functional response to
283 changing conditions. We know that peat organic chemistry, such as the proportion and identity
284 of o-alkyl (mainly carbohydrates) and aromatic groups, will affect the degree to which different

285 suites of hydrolytic and oxidative enzymes will be effective at mobilizing substrates. We also
286 know that this chemistry changes in response to initial substrate quality, degree of
287 decomposition, and drainage history (Limpens et al., 2008). Microbes differ vastly in their ability
288 to attack substrates of different complexity. Under oxic conditions aerobic microorganisms may
289 attack more complex substrates using oxidative enzymes, yet their ability to do so is constrained
290 both evolutionarily and environmentally. For example, as noted above regarding mycorrhizal
291 fungi, because they are in direct contact with host sugars, they are less likely to be carbon
292 limited, and more likely to be using enzymes to mobilize organically bound nutrients, especially
293 N, rather than C. To do this they mobilize a suite of oxidative and hydrolytic enzymes, with the
294 presumed goal of mining N from organic matter, e.g., by breaking up protein-polyphenol
295 complexes (Lindahl and Tunlid, 2015; Read, 1991). By contrast, saprotrophs have a dual goal of
296 mobilizing carbon and nutrient substrates, and so are constrained by carbon quality on the one
297 hand, and nutrient availability on the other. Mutualist and saprotroph evolutionary history
298 constrains the suite of enzymes available to do this work, e.g., class II peroxidases as a tool for
299 degrading lignocellulose are limited to a subset of Basidiomycota. Therefore, the Ascomycota
300 and primitive Basidiomycota symbiotic with Ericaceae possess a broad suite of oxidative and
301 hydrolytic enzymes, but do not possess Class II peroxidases, limiting their ability to degrade
302 certain aromatic and amorphous substrates such as lignin. Yet they still effectively mobilize N
303 from many substrates. In the absence of ericoid mycorrhizal competition, saprotrophic fungi with
304 broader enzymatic potential, e.g., possession of class II peroxidases, could shift peatland
305 carbon cycling in a different trajectory (see Tedersoo & Bahram (2019) for review).

306 *2.2 Timescales of microbial response to changes in the peatland system*

307 Understanding the interactions of rapid transformations and longer-term trajectories of microbial
308 changes is important with regards to peatland ecosystem functions. At weekly timescales there
309 is an understanding surrounding the behavior of water tables and carbon fluxes (Waddington et

310 al., 2015), but there is a lack of understanding about microbial behavior at this short timescale.
311 Consequently, the importance of short-term change as a component of long-term resilience is
312 poorly understood. We do, however, know that longer-term processes such as drought are
313 important (Hicks Pries et al., 2015). Concepts such as the enzymic latch mechanism (Freeman
314 et al., 2001) indicate that significant lags in ecosystem function to these events are possible.
315 The responses of microbial communities to these changes and the ways in which they control or
316 mitigate lagged responses is a fundamental aspect in understanding the impact of the
317 microbiota on resilience of the peatland.

318 The resilience of peatlands, their tipping points and reaction to long-term climate change is only
319 partially understood, particularly when factoring in multiple stressors. Peatland resilience is likely
320 to occur where there are negative feedbacks, e.g. the negative feedbacks between
321 decomposition and water table depth (Waddington et al. 2015). Tipping points may be reached
322 as a result of extreme droughts (Jassey et al., 2018), flooding, pollution events and fire.
323 Identifying if some stressors are more influential than others in creating system tipping points
324 and whether there is a cascade effect linked to microbially-driven plant-soil processes may be
325 key to predicting future trajectories. Focussed experiments on microbial response to
326 combinations and ordering of stressors represent a clear research need in this context.

327 Microbial growth and turnover in peatlands are very slow, attributable to various factors linked to
328 the acidity, wetness and anaerobiosis that exists (Malik et al., 2018). This slow growth partly
329 limits microbial decomposition thereby maintaining high levels of organic matter. Peat drainage
330 and liming remove the conditions that are responsible for slow microbial growth thereby causing
331 increased decomposition and rapid losses of carbon. Therefore, peat formation and degradation
332 can occur at different time scales reflecting microbial growth and activity.

333 In terms of peatland restoration, the effects and timescales of response on water table (e.g.
334 Holden et al., (2011)), fluvial carbon fluxes (e.g. Wilson et al., (2011)), vegetation (e.g. Hancock
335 et al., (2018); Putkinen et al., (2018)) and wider ecosystem service delivery (e.g. Alderson et al.,
336 2019) have been characterised for a range of approaches (drain blocking, gully reprofiling,
337 forestry removal, etc) and sites. Yet, we still do not know enough about the impact on microbial
338 communities and specific carbon cycle pathways linked to, for example, water quality aspects
339 (i.e. specific carbon compounds causing issues and costs in water treatment). The impact on
340 these communities of more extreme restoration measures such as changing the pH of the peat
341 (by liming) during restoration is likely to be important. However, to allow us to identify responses
342 to, and consequences of, restoration effects on the microbiome we need to define the baseline
343 microbial definitions of 'intact' and 'degraded' systems. The speed of response of microbial
344 communities to restoration represents an important avenue of research together with
345 investigating the palaeo-record to understand longer-term changes.

346 2.3 Incorporating microbial understanding into peatland modelling

347 Current peatland statistical and process-based models are mainly driven by physical variables
348 such as rainfall and temperature, which affect macroscopic properties such as vegetation and
349 water-table depth, and these in turn act as key controls on plant and microbial functions such as
350 net primary productivity and organic matter decomposition (Strack and Waddington, 2007;
351 Worrall et al., 2009). Such models rely on empirical relationships between physical variables
352 and ecosystem functioning. Where environmental change pushes system parameters beyond
353 previous observations, or causes combinations of conditions not previously observed, then it
354 may be difficult to predict processes using proxy drivers, which rely on correlations not fully
355 understood at the process level. For example, long term lower water tables in peatlands may
356 lead to cracking of surface peats (Evans and Warburton, 2010), so that, potentially, measured
357 water table does not relate linearly to peat moisture at the micropore level experienced by

358 microbes. This would lead to a non-linearity in the relations between water table and gas flux.
359 This example highlights the need for process-level understanding at a microbial scale (in this
360 case an understanding of direct microbial response to changing water balance).

361 Furthermore, models in which carbon dynamics are driven by water tables typically use long
362 term mean water tables (monthly or annual) as drivers. Synoptic scale change in long-term
363 hydrometeorological conditions, and particularly changes in the frequency of floods and
364 droughts, may not be properly represented at these time scales. Changes in carbon metabolism
365 can occur at these shorter timescales and microbial processes can introduce lags into the
366 system (e.g. enzyme latch mechanism). Similarly, there are lags in methanogenesis which
367 might be induced through microbial dormancy during drought periods (Freeman et al., 2002).

368 We therefore require models that operate at a higher time resolution (daily or shorter) and
369 incorporate underlying microbial processes and dynamics. Such models will be possible when
370 the key organism groups, their functions, habitat and activity ranges are known. For example, a
371 key requirement is that peatland models accurately partition gaseous carbon losses between
372 methane and CO₂. To achieve this they must include, for example, plant-mediated transfer of
373 CH₄ which varies on sub-daily timescales (e.g. Poindexter et al., 2016), and microbial
374 information such as methanogenic/methanotroph ratios.

375 Measurement of gas flux from peatland surfaces derived from microbial decomposition of
376 organic matter commonly demonstrates localised hotspots of methane production (Dinsmore et
377 al., 2009), which are not explained by macro-level variation in physical parameters. Micro-scale
378 drivers of microbial metabolism may be important here, which would be best understood
379 through a focus on the microbial system. While it may not be possible to include all microbial
380 knowledge gained at the micro-scale in large-scale or global models, this knowledge can give

381 confidence that representative response curves in models are appropriate across a range of
382 conditions.

383 2.4 What is possible now and how can we progress modelling work in this area?

384 In contrast to most peatland models, large-scale Earth system models (ESMs) tend to operate
385 at approximately hourly timesteps, which are relevant for microbial processes. In addition, they
386 usually include a process-based representation of water and energy dynamics. This provides
387 the potential to introduce microbial dynamics both implicitly and explicitly into such models as
388 JULES (Joint UK Land Environment Simulator) (Gedney et al., 2019; Chadburn et al., under
389 review) among others (e.g. Oh et al., 2020) However, the low spatial resolution (typically 50 km)
390 of ESMs is problematic since grid cells are larger than the typical size of many peatlands.

391 Therefore, despite peatlands being represented as a 'grid cell fraction' in some models (Stocker
392 et al., 2014; Langeron et al., 2018), lateral processes in peatlands cannot be resolved at a global
393 scale. On the other hand, in peatland-specific models with higher spatial resolution but monthly
394 or annual timesteps, incorporating microbial processes can be equally challenging because the
395 temporal dynamics are not adequately resolved.

396 Once the appropriate spatial and temporal scales are resolved in models, to progress the
397 incorporation of microbial knowledge in peatland modelling, experimental evidence is required
398 to define peatland function response curves outside the envelope of previously observed
399 environmental conditions. This experimental work will need to be supported by long-term
400 monitoring to identify peatland systems that are moving out of their functional envelope
401 (precariousness). Recovery from severe fire and peatland restoration are useful study cases in
402 this goal, however we also need to capture a possible point beyond no return such as water
403 repellency after prolonged peat cracking which may create an alternative stable state(s). Tracer
404 studies and sensing of fluxes and chemical conditions (e.g. redox and electron acceptor
405 concentrations) are also required to understand the complex and dynamic microbe-electron

406 acceptor system and complimentary functional gene studies are required alongside
407 measurement of these drivers. Critically, new experiments in this area should be co-designed by
408 interdisciplinary teams so that they develop response curves which are directly applicable to
409 refining existing models.

410 The rapid development of omics techniques for studying microbial taxonomy and function is a
411 current research frontier that has the potential to develop understanding of microbial control of
412 carbon cycling to the point where model incorporation is possible. One interesting approach is to
413 consider simplification of microbial omics datasets into key microbial traits that determine
414 ecosystem process rates and fluxes (Fry et al. 2019; Malik et al., 2020). The rapid evolution of
415 genomic techniques is both a challenge and an opportunity in this area. The need for higher
416 resolution studies and for the integration of studies of microbial structure and microbial function
417 has been recognised for some years, yet there has been relatively little progress in the last
418 decade. In part, this is because peatland scientists and practitioners with interests in microbial
419 processes have often been unable to keep up with the rapidity of change in genetic
420 instrumentation and analysis. Therefore, progress in this area clearly will also requires
421 interdisciplinary approaches bringing together the expertise of microbial ecologists and peatland
422 scientists.

423 *2.5 Remote sensing (RS) of microbial communities or their proxies*

424 Several ecological studies have already demonstrated the importance of plant community
425 composition and plant physiological and functional traits, as drivers of belowground microbial
426 communities and their function. For example, plant community composition has been shown to
427 play a significant role in regulating short-term litter decomposition and shaping belowground
428 peatland communities (Ward et al. 2015; Robroek et al. 2015); similarly, plant chemical
429 composition (e.g. leaf nitrogen, lignin, and polyphenols) is a trait that affects litter chemistry and
430 soil nutrient availability. Remote sensing has previously been used to retrieve a number of these

431 potential aboveground proxies. For example spectral signatures of the vegetation surface have
432 been used to translate reflected light into maps of species richness in anthropogenic peatlands
433 using satellite data (Castillo-Riffart et al., 2017), whereas airborne hyperspectral or high spatial
434 resolution drone data have been used to identify key peatland species (Harris and Bryant,
435 2009), species compositions (Harris et al., 2015; Lehmann et al., 2016), plant growth forms
436 (Schmidtlein et al., 2012) and functional groups (Cole et al., 2014; Harris et al., 2015;
437 McPartland et al., 2019; Räsänen et al., 2019) with reasonable accuracy. It should be noted,
438 however, that although communities associated with vegetation types may have common
439 features, they still vary in taxonomic and functional composition in response to climate (Singer
440 et al., 2019; Reczuga et al., 2020).

441 Canopy chemical traits such as chlorophyll, N, lignin and polyphenolics can also be measured
442 by imaging spectroscopy (e.g. (Asner and Martin, 2016; Madritch et al., 2014; Schweiger et al.,
443 2018), although their retrieval across peatland ecosystems has received less attention
444 (Kalacska et al., 2015). Nevertheless, despite the potential, there are few examples of linking
445 RS data to belowground peatland properties, with those that have exclusively focused on
446 estimating C stocks (Lopatin et al., 2019). The sparsity of such studies is perhaps in part due to
447 the need to integrate knowledge across disparate scientific disciplines, but also because several
448 challenges remain before remote sensing can be reliably employed to generate belowground
449 predictions (Madritch et al., 2020).

450 Microbial processes occur at the microscopic scale and remote sensing can only pick up the
451 aggregate of many processes which are occurring in diverse micro-niches within the pixel,
452 whether that be 1 m or 1 km square. Microbes operate on a different scale, so it is a challenge
453 to meaningfully observe their activities from a distance. Nevertheless, without the regional and
454 global-scale perspectives offered up through remote sensing, any understanding of microbial
455 processes is likely to be limited in its scope and scale of application. Understanding at what

456 scale it is acceptable to aggregate variables such as plant community structure, nitrogen
457 availability, soil moisture, water table availability and peatland type to achieve meaningful inputs
458 to a peatland microbial model will be a key challenge in this area.

459 A promising potential solution to this problem is to make use of habitat suitability and distribution
460 models (HSDMs), which can be used to infer species distributions (and their actions) across
461 multiple scales. The techniques are not fully established in ecology but there is a recognised
462 need to address this (Elith and Leathwick, 2009), which in our view would be a valuable step
463 forwards. A framework for applying HSDMs to soil microbes has been proposed by Lembrechts
464 et al (2020). In short, a nested sampling design is proposed whereby different points in the
465 landscape are measured to provide different amounts of detail. The points for which more detail
466 is obtained are used to model the detail in the less well analysed locations. Thus, with relatively
467 low sampling effort a high level of detail can be inferred at the landscape scale, and it becomes
468 possible to understand processes such as carbon storage and nutrient cycling at the scales
469 relevant to human experience and global budgets. These kinds of techniques may bridge the
470 gap between common sampling practices and the scale at which microbial communities
471 operate.

472 Once process-level understanding of vegetation-microbial community links has been
473 established, we may then be able to use existing remote sensing technology as indirect proxies
474 for microbial behaviours, communities and processes (e.g. detecting and characterising plant
475 communities) and through developing new approaches (e.g. to remotely sense soil moisture).
476 Remote sensing is also important in measuring peatland habitat condition and resilience to
477 climate change (e.g. shrinkage and expansion rates over time/season, e.g. (Alshammari et al.,
478 2018), monitoring recovery after stress has been applied (e.g. vegetation re-establishment (Cole
479 et al., 2013) or water content and gross primary productivity (Lees et al., 2020)) and assessing

480 fire damage extent (Millin-Chalabi et al., 2014) and estimating gas fluxes (Artz et al., 2017; Lees
481 et al., 2018; McMorrow et al., 2004).

482 Remote sensing can also be used as a key part of experimental design to allow us to target
483 sites or areas of interest for specific ground-based research, dependent on the research
484 question e.g. identifying areas within a peatland that exhibit extreme characteristics or
485 behaviours such as methane hotspots (e.g. Elder et al., 2020). Detecting hotspots could be
486 useful for targeted investigation of microbial communities and the environmental factors leading
487 to enhanced microbial activity. This is potentially important in terms of developing field
488 understanding of microbial controls on peatland function at smaller temporal and spatial scales.

489 *2.6 Required knowledge to incorporate microbial processes into restoration practice*

490 There is some understanding of mechanistic contributions of the microbial community to
491 peatland functioning e.g. methanogenic vs methanotrophic respiration and relationships with
492 abiotic processes. The past decade of peatland restoration has produced many datasets
493 recording factors affecting, for example, methane production. However, we have relatively little
494 associated data on microbial community structure and function. What data we do have suggests
495 high variability of microbial communities in undamaged sites, suggesting there may be issues in
496 scaling up any data collected (Griffiths et al., 2011). The large-scale manipulation of peatlands
497 over these timescales means that chronosequence studies of microbial function offer a
498 promising method to develop understanding of microbial responses to, and controls on,
499 restoration success.

500 Vegetation and restoration gradients are a key driver of the spatial and temporal variability of
501 microbial community structure and function (Dobrovol'skaya et al., 2019; Putkinen et al., 2018;
502 Elliott et al., 2015). Vegetation mosaics change through restoration processes and have
503 implications for re-wetting and methane emissions, affecting the balance of methanotrophs and

504 methanogens and substrate quality (e.g. Juottonen et al., 2012; Reumer et al., 2018). It is highly
505 likely therefore, that the microbial community is transformed through restoration, however, at
506 present we do not have enough data to draw clear conclusions.

507 There are also some observations that suggest that microbial ecology could be an important
508 factor in restoration success, for example using *Sphagnum* from local donor sites was found to
509 be more effective than micro-propagated material in establishing *Sphagnum* cover (Crouch,
510 2018). This could be one piece of evidence in resolving the 'chicken and egg' problem of
511 whether microbes drive restoration processes (and success vs failure) or if they simply respond
512 to abiotic conditions and vegetation development. Further understanding is needed on the
513 dynamic relationship between vegetation, microbes and abiotic factors (e.g. Hamard et al.
514 (2019). There is some suggestion that the beneficial microbes are already present but need the
515 right conditions to promote their growth (Baas-Becking, 1934), in which case restoration may
516 need to focus on promoting these conditions. Resolving this question could inform restoration
517 practice either by developing microbial inoculations as part of the restoration process, or in
518 defining the conditions which will promote a 'good' and healthy microbial community.

519 We do not yet know how the microbiome responds to unusual hydrological conditions (beyond
520 testate amoeba records) and whether this may affect our current grasp of the water table and
521 ecosystem function relationship. Characterising just the 'normal' community might not be
522 enough if we also need to understand the parts of the microbial community adapted to more
523 extreme conditions. Both 'normal' and 'extreme condition' microbiota are likely to be present in a
524 resilient system. Finally, there are additional interactions between soil fauna and microbes that
525 are currently not understood (e.g. Cole et al., 2002). It may be more fruitful to assess the state
526 of a peat ecosystem and the success of restorative approaches using microbial functional or
527 phenotypic indicators as they are more tightly coupled with ecosystem process rates.

528

529 *2.7 A research agenda for studies of peatland function and microbial processes*

530 Through a series of four workshops we have developed and prioritised a set of research
531 questions which provide an agenda for progressing the research frontiers described in this
532 commentary. Our aim is to help the academic and practitioner communities better understand
533 peatland ecosystem functioning and the role microbial processes may play in peatland
534 resilience, and to potentially move to using the microbial community as a monitoring tool,
535 support mechanism and/or end goal. The research questions presented below were developed
536 and refined throughout the workshops and prioritised through a series of participant votes.

537 Table 1: Prioritised research questions developed from the four workshops

538

539

540 The questions given the most priority are the high-level questions concerning what
541 characteristic peatland biota communities look like and how they change. How does this affect
542 carbon balance and how does it affect or support practical peatland restoration? Beneath these
543 are more detailed questions about the nature of microbial processes at different temporal and
544 spatial scales and the nature of the links between peatland function and microbial communities
545 and processes. Arguably, progress on these questions will also be necessary to answer the
546 higher-level questions, and particularly to understand longer term resilience of peatland carbon
547 stores, but the prioritisation emphasises the 'real world' importance of this research.

548 Understanding peatland microbial systems is not an arcane academic interest but is an
549 important applied aspect of peatland science which is required to underpin the developing
550 understanding of the recovery and resilience of peatlands as vital terrestrial carbon stores in a
551 rapidly changing world.

552 **3.0 Conclusions**

553 Developing a process-based understanding of the resilience of peatlands will be key to meeting
554 nature and climate targets and cost-effective delivery of ecosystem services. In this regard, the
555 ability to alter the microbial community to favour net carbon sequestering conditions, alongside
556 benefits to other ecosystem services, could be a powerful tool; however, our current
557 understanding is still some way off being able to do this. In order to develop our knowledge and
558 aid peatland restoration and management practice, we first need to be able to characterise
559 peatland microbial communities and their functions in different types of peatlands, and in
560 different states of modification/degradation, and recognise what a 'good' community looks like
561 and what role this plays in ecosystem functioning. This would allow us to assess the usefulness
562 of microbial techniques to promote restoration of peatland function and to the development of
563 monitoring tools to streamline indication of restoration success. Ultimately such process-based
564 understanding will be fundamental to applied ecological work supporting the resilience of
565 peatlands under conditions of rapid climate change and other pressures.

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573 **Clare H. Robinson:** conceptualisation, writing – original draft, writing – review and editing,
574 funding acquisition. **Martin G. Evans:** conceptualisation, writing – original draft, writing – review
575 and editing, funding acquisition. **All other authors:** writing – review and editing.

576

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