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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 are80 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.

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

Rapid advances in genetic characterisation of the structure and functions of microbial communities offer the potential for transformative progress in these areas, but the scale and speed of methodological and conceptual advances in studying ecosystem functions is a challenge for peatland scientists. Advances in this area require multidisciplinary collaborations between peatland scientists, data scientists and microbiologists and ultimately, collaboration with the modelling community. Developing a process-based understanding of the resilience and recovery of peatlands to perturbations, such as climate extremes, fires, and drainage, will be key to meeting climate 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.

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

In 2019, a series of four workshops (funded by NERC UK) were held at The University of
Manchester to map our current understanding of the role of the microbial community on
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**

2.1 What is peatland resilience, and in what ways does understanding the microbial systemunderpin it?

As major stores and sources of carbon and greenhouse gases, peatlands play a key role in regulating the climate. Thus, the nature of their functional response to climate change, and the ways in which peatland management has in the past and can in the future mediate this 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., 2010). 157

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

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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?

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

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grasslands, although vegetation still shapes microbial communities and the response of
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; Jassey 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 (Jassey 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

microbes function on both sides of opposite processes, demonstrating that questions of
microbial functioning in healthy peatlands are likely not to have simple answers. By identifying
microbial processes and their constraints, it may be possible to predict and influence the
direction in which peatland processes proceed, and we may gain insight into feedback loops
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).

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

vegetation shifts or the microbial loop will be important for informing models of peatland C-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 (Megonigal 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).

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

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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 the acidity, wetness and anaerobiosis that exists (Malik et al., 2018). This slow growth partly limits microbial decomposition thereby maintaining high levels of organic matter. Peat drainage and liming remove the conditions that are responsible for slow microbial growth thereby causing increased decomposition and rapid losses of carbon. Therefore, peat formation and degradation 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

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

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

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

Measurement of gas flux from peatland surfaces derived from microbial decomposition of organic matter commonly demonstrates localised hotspots of methane production (Dinsmore et al., 2009), which are not explained by macro-level variation in physical parameters. Micro-scale drivers of microbial metabolism may be important here, which would be best understood through a focus on the microbial system. While it may not be possible to include all microbial 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 of382 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; Largeron 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

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

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

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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).

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

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

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

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

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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
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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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