



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

Jonathan P. Ritson^{a,*}, Danielle M. Alderson^a, Clare H. Robinson^b, Alexandra E. Burkitt^c, Andreas Heinemeyer^d, Andrew G. Stimson^e, Angela Gallego-Sala^f, Angela Harris^g, Anne Quillet^h, Ashish A. Malikⁱ, Beth Cole^j, Bjorn J.M. Robroek^k, Catherine M. Heppell^l, Damian W. Rivett^m, Dave M. Chandlerⁿ, David R. Elliott^o, Emma L. Shuttleworth^a, Erik Lilleskov^p, Filipa Cox^q, Gareth D. Clay^a, Iain Diack^r, James Rowson^s, Jennifer Pratscher^t, Jonathan R. Lloyd^b, Jonathan S. Walker^u, Lisa R. Belyea^l, Marc G. Dumont^v, Mike Longden^w, Nicholle G.A. Bell^x, Rebekka R.E. Artz^y, Richard D. Bardgett^z, Robert I. Griffiths^{aa}, Roxane Andersen^{ab}, Sarah E. Chadburn^{ac}, Simon M. Hutchinson^{ad}, Susan E. Page^j, Tim Thom^{ae}, William Burn^d, Martin G. Evans^a

^a School of Environment Education and Development, The University of Manchester, Oxford Road, Manchester M13 9PL, UK

^b Department of Earth & Environmental Sciences, The University of Manchester, Williamson Building, Oxford Road, Manchester M13 9PL, UK

^c Department of Environment & Geography, University of York, YO10 5NG, UK

^d Stockholm Environment Institute, Department of Environment & Geography, York YO10 5NG, UK

^e North Pennines AONB Partnership, Weardale Business Centre, The Old Co-op building, 1 Martin Street, Stanhope, County Durham DL13 2UY, UK

^f Department of Geography, University of Exeter, Laver, North Park Road, Exeter EX4 4QE, UK

^g Department of Geography, The University of Manchester, Manchester M13 9PL, UK

^h Department of Geography and Environmental Science, University of Reading, Whiteknights RG6 6AB, UK

ⁱ School of Biological Sciences, University of Aberdeen, Aberdeen AB24 3UU, UK

^j School of Geography, Geology and the Environment, University of Leicester, LE1 7RH, UK

^k Dept. of Aquatic Ecology & Environmental Biology, Institute for Water and Wetlands Research, Radboud University, Nijmegen, the Netherlands

^l School of Geography, Queen Mary University of London, Mile End Road, London E1 4NS, UK

^m Department of Natural Sciences, Manchester Metropolitan University, Manchester, UK

ⁿ Moors for the Future Partnership, The Moorland Centre, Fieldhead, Edale, Derbyshire S33 7ZA, UK

^o Environmental Sustainability Research Centre, University of Derby, Derby DE22 1GB, UK

^p USDA Forest Service, Northern Research Station, Houghton, MI 49931, USA

^q Department of Earth and Environmental Sciences, University of Manchester, M13 9PL, UK

^r Natural England, Parkside Court, Hall Park Way, Telford, Shropshire TF3 4LR, UK

^s Department of Geography and Geology, Edge Hill University, St Helens Road, Ormskirk Lancs L39 4QP, UK

^t School of Energy, Geoscience, Infrastructure and Society, The Lyell Centre, Heriot-Watt University, Edinburgh EH14 4AP, UK

^u College of Science, Swansea University, Swansea SA2 8PP, UK

^v School of Biological Sciences, University of Southampton, Southampton SO17 1BJ, UK

^w Lancashire Wildlife Trust, 499-511 Bury new road, Bolton BL2 6DH, UK

^x School of Chemistry, University of Edinburgh, King's Buildings, David Brewster Road, Edinburgh EH93FJ, UK

^y Ecological Sciences, The James Hutton Institute, Craigiebuckler, Aberdeen AB15 8QH, UK

^z Department of Earth and Environmental Sciences, The University of Manchester, Manchester M13 9PT, UK

^{aa} Centre for Ecology & Hydrology, Deiniol Road, Bangor LL57 2UW, UK

^{ab} Environmental Research Institute, University of the Highlands and Islands, Castle St., Thurso KW14 7JD, UK

^{ac} College of Engineering, Mathematics and Physical Sciences, University of Exeter, Stocker Road, Exeter EX4 4PY, UK

^{ad} School of Science, Engineering and Environment, University of Salford, Salford M5 4WT, UK

^{ae} Yorkshire Peat Partnership, Yorkshire Wildlife Trust, Unit 23, Skipton Auction Mart, Gargrave Road, Skipton, North Yorkshire BD23 1UD, UK

HIGHLIGHTS

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

* Corresponding author.

E-mail address: jonny.ritson@manchester.ac.uk (J.P. Ritson).

ARTICLE INFO

Article history:

Received 24 August 2020

Received in revised form 12 October 2020

Accepted 24 October 2020

Available online 10 November 2020

Editor: Jose Julio Ortega-Calvo

Keywords:

Peat

Resilience

Microbiology

Carbon cycling

Peatland restoration and management

ABSTRACT

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

© 2020 Elsevier B.V. All rights reserved.

1. Introduction

Peatlands are the largest store of terrestrial carbon (Joosten et al., 2016), yet many have become net sources of carbon emissions due to land use change, erosion, acid deposition, drainage and fire. Peatland restoration is a cost-effective method of lowering emissions and removing carbon from the atmosphere, costing between GBP 6–29 per tCO₂e (Moxey, 2011) and a number of restoration projects have been completed around the world (Bonn et al., 2014). While examples of successful methods for peatland restoration and recovery of ecological functions such as climate mitigation can now be demonstrated (Günther et al., 2020), the role of the microbiome in the restoration process and its influence on ecosystem resilience to external 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 t per ha of microbial biomass (Dobrovolskaya 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 process-based understanding of the resistance and recovery of peatland systems to perturbations. Participants were a diverse group of peatland scientists, microbiologists, modellers and restoration practitioners as well as representatives from governmental and non-governmental organisations. In this commentary we develop the key ideas emerging from four days of discussion with over 50 participants to define a research agenda for progress in this area.

2. Discussion

2.1. What is peatland resilience, and in what ways does understanding the microbial system underpin 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.

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

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

either a safe operating space for carbon storage or a completely different system that is a net source of greenhouse gases.

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

2.2. 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., 2015a, 2015b). 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 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).

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

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

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

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

Different microbial groups play different roles in the decomposition of organic matter in peatlands, a key example being the tendency for fungi to have greater extracellular enzyme activity than bacteria

(Bragazza et al., 2015). Research has shown that these communities change during restoration and in response to changing conditions (Andersen et al., 2010; Elliott et al., 2015), however, it is unclear how this change in the microbiome affects the resilience and overall function of a peatland. Knowledge regarding gradients in microbiological community structure across peat depth, vegetation types and severity of degradation or recovery following peatland restoration is currently lacking. Of particular interest is the gradient through depth as this may be key to our understanding of the acrotelm/catotelm model of peatlands (and haplotelmic model in severely degraded areas) and its role in the carbon balance of a peatland (Clymo, 1984). In particular, the potential change with depth of electron acceptor availability (Meronigal and Rabenhorst, 2013) and recalcitrance of carbon sources (Putkinen et al., 2009) may be key controls on carbon cycling by methanotrophic species. Climate change may alter the hydrological functioning of peatlands, as does restoration, where raising the water table is the desired outcome. Understanding the community structure and function of obligate and facultative anaerobic taxa is important as restoration practices such as gully blocking can create overall wetter soil conditions, including ponds, with potential impacts on methane emissions (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 modelling 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 suites of hydrolytic and oxidative enzymes will be effective at mobilizing substrates. We also know that this chemistry changes in response to initial substrate quality, degree of decomposition, and drainage history (Limpens et al., 2008). Microbes differ vastly in their ability to attack substrates of different complexity. Under oxic conditions aerobic microorganisms may attack more complex substrates using oxidative enzymes, yet their ability to do so is constrained both evolutionarily and environmentally. For example, as noted above regarding mycorrhizal fungi, because they are in direct contact with host sugars, they are less likely to be carbon limited, and more likely to be using enzymes to mobilize organically bound nutrients, especially N, rather than C. To do this they mobilize a suite of oxidative and hydrolytic enzymes, with the presumed goal of mining N from organic matter, e.g., by breaking up protein-polyphenol complexes (Lindahl and Tunlid, 2015; Read, 1991). By contrast, saprotrophs have a dual goal of mobilizing carbon and nutrient substrates, and so are constrained by carbon quality on the one hand, and nutrient availability on the other. Mutualist and saprotroph evolutionary history constrains the suite of enzymes available to do this work, e.g., class II peroxidases as a tool for degrading lignocellulose are limited to a subset of Basidiomycota. Therefore, the Ascomycota and primitive Basidiomycota symbiotic with Ericaceae possess a broad suite of oxidative and hydrolytic enzymes, but do not possess Class II peroxidases, limiting their ability to degrade certain aromatic and amorphous substrates such as lignin. Yet they still effectively mobilize N from many substrates. In the absence of ericoid mycorrhizal competition, saprotrophic fungi with broader enzymatic potential, e.g., possession of class II peroxidases, could shift peatland carbon cycling in a different trajectory (see Tedersoo and Bahram (2019) for review).

2.3. Timescales of microbial response to changes in the peatland system

Understanding the interactions of rapid transformations and longer-term trajectories of microbial changes is important with regards to peatland ecosystem functions. At weekly timescales there is an understanding surrounding the behavior of water tables and carbon fluxes (Waddington et al., 2015), but there is a lack of understanding about

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

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

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.

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

2.4. Incorporating microbial understanding into peatland modelling

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

2.5. What is possible now and how can we progress modelling work in this area?

In contrast to most peatland models, large-scale Earth system models (ESMs) tend to operate at approximately hourly timesteps, which are relevant for microbial processes. In addition, they usually include a process-based representation of water and energy dynamics. This provides the potential to introduce microbial dynamics both implicitly and explicitly into such models as JULES (Joint UK Land Environment Simulator) (Gedney et al., 2019; Chadburn et al., under review) among others (e.g. Oh et al., 2020). However, the low spatial resolution (typically 50 km) of ESMs is problematic since grid cells are larger than the typical size of many peatlands. Therefore, despite peatlands being represented as a 'grid cell fraction' in some models (Stocker et al., 2014; Llargeron et al., 2018), lateral processes in peatlands cannot be resolved at a global scale. On the other hand, in peatland-specific models with higher spatial resolution but monthly or annual timesteps, incorporating microbial processes can be equally challenging because the temporal dynamics are not adequately resolved.

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

dynamic microbe-electron 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.

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

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

Canopy chemical traits such as chlorophyll, N, lignin and polyphenolics can also be measured by imaging spectroscopy (e.g. (Asner and Martin, 2016; Madritch et al., 2014; Schweiger et al., 2018)), although their retrieval across peatland ecosystems has received less attention (Kalacska et al., 2015). Nevertheless, despite the potential, there are few examples of linking RS data to belowground peatland properties, with those that have exclusively focused on estimating C stocks (Lopatin et al., 2019). The sparsity of such studies is perhaps in part due to the need to integrate knowledge across disparate scientific disciplines, but also because several challenges remain before remote sensing can be reliably employed to generate belowground 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 scale it is acceptable to aggregate variables such as plant community structure, nitrogen availability, soil moisture, water table availability and peatland type to achieve meaningful inputs to a peatland microbial model will be a key challenge in this area.

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

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

2.7. Required knowledge to incorporate microbial processes into restoration practice

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

Vegetation and restoration gradients are a key driver of the spatial and temporal variability of microbial community structure and function (Dobrovolskaya 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 methanogens and substrate quality (e.g. Juottonen et al., 2012; Reumer et al., 2018). It is highly likely therefore, that the microbial community is transformed through restoration, however, at present we do not have enough data to draw clear conclusions.

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

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

Table 1
Prioritised research questions developed from the four workshops.

High priority questions	Medium priority questions	Low priority questions
Are there differences in microbial communities between net carbon sink and source sites and can we define keystone groups as well as an 'ideal' state?	What are the links between plants and microbes (chicken and egg in terms of order of influence during restoration)? This would likely include inoculation experiments, recovery from stress, resilience and persistence	What is the speed of response of the microbiome to stresses, restoration and management including lags, turnover dynamics and trajectory?
Can microbial intervention (e.g. inoculation or promoting a desirable community) enhance restoration practice, and if so via what method?	Does microbial understanding explain the residual variance in the proxies we use to understand peatland carbon functioning (e.g. water table)?	What is the contribution of the microbiome to ecosystem response to extreme shock?
How does the microbial community change with respect to time, space and depth at a site as well as with peatland condition across sites?	What are the timescales and trajectories of microbial processes linked to carbon loss?	What functional groups relate to ecosystem function? Redundancy, DNA, RNA
Can we link carbon cycle functions to particular microbial groups?	Does microbiome change impact peat structure and what are the feedbacks? Are there situations where natural recovery of microbial biota won't happen?	What is the heterogeneity of microbial communities and functions?

2.8. A research agenda for studies of peatland function and microbial processes

Through a series of four workshops we have developed and prioritised a set of research questions which provide an agenda for progressing the research frontiers described in this commentary. Our aim is to help the academic and practitioner communities better understand peatland ecosystem functioning and the role microbial processes may play in peatland resilience, and to potentially move to using the microbial community as a monitoring tool, support mechanism and/or end goal. The research questions presented below were developed and refined throughout the workshops and prioritised through a series of participant votes (Table 1).

The questions given the most priority are the high-level questions concerning what characteristic peatland biota communities look like and how they change. How does this affect carbon balance and how does it affect or support practical peatland restoration? Beneath these are more detailed questions about the nature of microbial processes at different temporal and spatial scales and the nature of the links between peatland function and microbial communities and processes. Arguably, progress on these questions will also be necessary to answer the higher-level questions, and particularly to understand longer term resilience of peatland carbon stores, but the prioritisation emphasises the 'real world' importance of this research. Understanding peatland microbial systems is not an arcane academic interest but is an important applied aspect of peatland science which is required to underpin the developing understanding of the recovery and resilience of peatlands as vital terrestrial carbon stores in a rapidly changing world.

3. Conclusions

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

CRediT author contribution statement

Jonathan P. Ritson: conceptualisation, writing - original draft, writing - review and editing. **Danielle M. Alderson:** conceptualisation, writing - original draft, writing - review and editing. **Clare H. Robinson:** conceptualisation, writing - original draft, writing - review and editing, funding acquisition. **Martin G. Evans:** conceptualisation, writing - original draft, writing - review and editing, funding acquisition. **All other authors:** writing - review and editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors acknowledge funding through the UK Natural Environment Research Council as part of the UK Climate Resilience Programme (grant number NE/5016724/1). The authors would also like to thank all the attendees of the workshops for their valuable contributions.

References

- Alderson, D.M., Evans, M.G., Shuttleworth, E.L., Pilkington, M., Spencer, T., Walker, J., Allott, T.E.H., 2019. Trajectories of ecosystem change in restored blanket peatlands. *Sci. Total Environ.* 665, 785–796. <https://doi.org/10.1016/j.scitotenv.2019.02.095>.
- Alshammari, L., Large, D.J., Boyd, D.S., Sowter, A., Anderson, R., Andersen, R., Marsh, S., 2018. Long-term peatland condition assessment via surface motion monitoring using the ISBAS DInSAR technique over the Flow Country, Scotland. *Remote Sens.* 10. <https://doi.org/10.3390/rs10071103>.
- Andersen, R., Grasset, L., Thormann, M.N., Rochefort, L., Francez, A.J., 2010. Changes in microbial community structure and function following Sphagnum peatland restoration. *Soil Biol. Biochem.* 42, 291–301. <https://doi.org/10.1016/j.soilbio.2009.11.006>.
- Andersen, R., Chapman, S.J., Artz, R.R.E., 2013. Microbial communities in natural and disturbed peatlands: a review. *Soil Biol. Biochem.* 57, 979–994. <https://doi.org/10.1016/j.soilbio.2012.10.003>.
- Artz, R.R.E., Donaldson-Selby, G., Poggio, L., Donnelly, D., Aitkenhead, M.J., 2017. *Comparison of Remote Sensing Approaches for Detection of Peatland Drainage in Scotland*. Asner, G.P., Martin, R.E., 2016. Spectranomics: emerging science and conservation opportunities at the interface of biodiversity and remote sensing. *Glob. Ecol. Conserv.* 8, 212–219. <https://doi.org/10.1016/j.gecco.2016.09.010>.
- Averill, C., Turner, B.L., Finzi, A.C., 2014. Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature* 505, 543–545. <https://doi.org/10.1038/nature12901>.
- Baas-Becking, L.G.M., 1934. *Geobiologie of inleiding tot de milieukunde*. W.P. Van Stockum & Zoon, The Hague, the Netherlands.
- Backéus, I., 1972. Bog vegetation re-mapped after sixty years, studies on Skagershultamossen, Central Sweden. *Oikos* 23, 384–393.
- Billett, M.F., Charman, D.J., Clark, J.M., Evans, C.D., Evans, M.G., Ostle, N.J., Worrall, F., Burden, A., Dinsmore, K.J., Jones, T., McNamara, N.P., Parry, L., Rowson, J.G., Rose, R., 2010. Carbon balance of UK peatlands: current state of knowledge and future research challenges. *Clim. Res.* 45, 13–29.
- Bonn, A., Reed, M.S., Evans, C.D., Joosten, H., Bain, C., Farmer, J., Emmer, I., Couwenberg, J., Moxey, A., Artz, R., Tanneberger, F., Unger, M., Von, Smyth, M., Birnie, D., 2014. Investing in nature: developing ecosystem service markets for peatland restoration. *Ecosyst. Serv.* 9, 54–65. <https://doi.org/10.1016/j.ecoser.2014.06.011>.
- Bragazza, L., Parisod, J., Buttler, A., Bardgett, R.D., 2013. Biogeochemical plant-soil microbe feedback in response to climate warming in peatlands. *Nat. Clim. Chang.* 3, 273–277. <https://doi.org/10.1038/nclimate1781>.
- Bragazza, L., Bardgett, R.D., Mitchell, E.A.D., Buttler, A., 2015. Linking soil microbial communities to vascular plant abundance along a climate gradient. *New Phytol.* 205, 1175–1182. <https://doi.org/10.1111/nph.13116>.
- Breeuwer, A., Robroek, B.J.M., Limpens, J., Heijmans, M.M.P.D., Schouten, M.G.C., Berendse, F., 2009. Decreased summer water table depth affects peatland vegetation. *Basic Appl. Ecol.* 10, 330–339. <https://doi.org/10.1016/j.baae.2008.05.005>.
- Castillo-Riffart, I., Galleguillos, M., Lopatin, J., Perez-Quezada, J.F., 2017. Predicting vascular plant diversity in anthropogenic peatlands: comparison of modeling methods with free satellite data. *Remote Sens.* 9. <https://doi.org/10.3390/rs9070681>.
- Clymo, R.S., 1984. The limits to peat bog growth. *Philos. Trans. R. Soc. London. B, Biol. Sci.* 303, 605–654. <https://doi.org/10.1098/rstb.1984.0002>.
- Cole, L., Bardgett, R.D., Ineson, P., Hobbs, P.J., 2002. Enchytraeid worm (Oligochaeta) influences on microbial community structure, nutrient dynamics and plant growth in blanket peat subjected to warming. *Soil Biol. Biochem.* 34, 83–92. [https://doi.org/10.1016/S0038-0717\(01\)00159-6](https://doi.org/10.1016/S0038-0717(01)00159-6).
- Cole, B., Mc Morrow, J., Evans, M., 2013. Empirical modelling of vegetation abundance from airborne hyperspectral data for upland peatland restoration monitoring. *Remote Sens.* 6, 716–739. <https://doi.org/10.3390/rs6010716>.
- Cole, B., Mc Morrow, J., Evans, M., 2014. Spectral monitoring of moorland plant phenology to identify a temporal window for hyperspectral remote sensing of peatland. *ISPRS J. Photogramm. Remote Sens.* 90, 49–58. <https://doi.org/10.1016/j.isprsjprs.2014.01.010>.
- Cooper, M.D.A., Evans, C.D., Zielinski, P., Levy, P.E., Gray, A., Peacock, M., Norris, D., Fenner, N., Freeman, C., 2014. Infilled ditches are hotspots of landscape methane flux following peatland re-wetting. *Ecosystems* 17. <https://doi.org/10.1007/s10021-014-9791-3>.
- Crouch, T., 2018. *Kinder Scout Sphagnum Trials: 2018 Update Report*. Edale, UK.
- Díaz, S., Lavorel, S., De Bello, F., Quétier, F., Grigulis, K., Robson, T.M., 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *Proc. Natl. Acad. Sci. U. S. A.* 104, 20684–20689. <https://doi.org/10.1073/pnas.0704716104>.
- Dinsmore, K.J., Skiba, U.M., Billett, M.F., Rees, R.M., Drewer, J., 2009. Spatial and temporal variability in CH₄ and N₂O fluxes from a Scottish ombrotrophic peatland: implications for modelling and up-scaling. *Soil Biol. Biochem.* 41, 1315–1323. <https://doi.org/10.1016/j.soilbio.2009.03.022>.
- Dobrovol'skaya, T.G., Golovchenko, A.V., Yakushev, A.V., Yurchenko, E.N., Manucharov, N.A., Chernov, I.Y., 2017. Bacterial complexes of a high moor related to different elements of microrelief. *Eurasian Soil Sci.* 50, 470–475. <https://doi.org/10.1134/S1064229317040020>.

- Dobrovolskaya, T.G., Golovchenko, A.V., Yurchenko, E.N., Kostina, N.V., 2019. Composition of bacterial communities of the main types of bog plants. *Moscow Univ. Soil Sci. Bull.* 74, 40–43. <https://doi.org/10.3103/s0147687419010046>.
- Elder, C.D., Thompson, D.R., Thorpe, A.K., Hanke, P., Walter Anthony, K.M., Miller, C.E., 2020. Airborne mapping reveals emergent power law of Arctic methane emissions. *Geophys. Res. Lett.* 47. <https://doi.org/10.1029/2019GL085707>.
- Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst.* 40, 677–697. <https://doi.org/10.1146/annurev.ecolsys.110308.120159>.
- Elliott, D.R., Caporn, S.J.M., Nwaishi, F., Nilsson, R.H., Sen, R., 2015. Bacterial and fungal communities in a degraded ombrotrophic peatland undergoing natural and managed re-vegetation. *PLoS One* 10, 1–20. <https://doi.org/10.1371/journal.pone.0124726>.
- Evans, M., Warburton, J., 2010. *Geomorphology of Upland Peat: Erosion, Form and Landscape Change*.
- Evans, M., Warburton, J., Yang, J., 2006. Eroding blanket peat catchments: global and local implications of upland organic sediment budgets. *Geomorphology* 79, 45–57.
- Field, C.D., Dise, N.B., Payne, R.J., Britton, A.J., Emmett, B.A., Helliwell, R.C., Hughes, S., Jones, L., Lees, S., Leake, J.R., Leith, I.D., Phoenix, G.K., Power, S.A., Sheppard, L.J., Southon, G.E., Stevens, C.J., Caporn, S.J.M., 2014. The role of nitrogen deposition in widespread plant community change across semi-natural habitats. *Ecosystems* 17, 864–877. <https://doi.org/10.1007/s10021-014-9765-5>.
- Freeman, C., Ostle, N., Kang, H., 2001. An enzymic “latch” on a global carbon store. *Nature* 409, 149. <https://doi.org/10.1038/35051650>.
- Freeman, C., Nevison, G.B., Kang, H., Hughes, S., Reynolds, B., Hudson, J.A., 2002. Contrasted effects of simulated drought on the production and oxidation of methane in a mid-Wales wetland. *Soil Biol. Biochem.* 34, 61–67. [https://doi.org/10.1016/S0038-0717\(01\)00154-7](https://doi.org/10.1016/S0038-0717(01)00154-7).
- Fry, E.L., De Long, J.R., Álvarez Garrido, L., Alvarez, N., Carrillo, Y., Castañeda-Gómez, L., Chomel, M., Dondini, M., Drake, J.E., Hasegawa, S., Hortal, S., Jackson, B.G., Jiang, M., Lavalley, J.M., Medlyn, B.E., Rhymes, J., Singh, B.K., Smith, P., Anderson, I.C., Bardgett, R.D., Baggs, E.M., Johnson, D., 2019. Using plant, microbe, and soil fauna traits to improve the predictive power of biogeochemical models. *Methods Ecol. Evol.* 10, 146–157. <https://doi.org/10.1111/2041-210X.13092>.
- Gallego-Sala, A.V., Clark, J.M., House, J.I., Orr, H.G., Prentice, I.C., Smith, P., Farewell, T., Chapman, S.J., 2010. Bioclimatic envelope model of climate change impacts on blanket peatland distribution in Great Britain. *Clim. Res.* 45, 151–162. <https://doi.org/10.3354/cr00911>.
- Gedney, N., Huntingford, C., Comyn-Platt, E., Wiltshire, A., 2019. Significant feedbacks of wetland methane release on climate change and the causes of their uncertainty. *Environ. Res. Lett.* 14. <https://doi.org/10.1088/1748-9326/ab2726>.
- Grand-Clement, E., Anderson, K., Smith, D., Angus, M., Luscombe, D.J., Gatis, N., Bray, L.S., Brazier, R.E., 2015. New approaches to the restoration of shallow marginal peatlands. *J. Environ. Manag.* 161, 417–430. <https://doi.org/10.1016/j.jenvman.2015.06.023>.
- Greslehner, G.P., 2020. Microbiome structure and function: a new framework for interpreting data. *BioEssays* 42, 1–8. <https://doi.org/10.1002/bies.201900255>.
- Griffiths, R.I., Thomson, B.C., James, P., Bell, T., Bailey, M., Whiteley, A.S., 2011. The bacterial biogeography of British soils. *Environ. Microbiol.* 13, 1642–1654. <https://doi.org/10.1111/j.1462-2920.2011.02480.x>.
- Günther, A., Barthelmes, A., Huth, V., Joosten, H., Jurasinski, G., Koesch, F., Couwenberg, J., 2020. Prompt rewetting of drained peatlands reduces climate warming despite methane emissions. *Nat. Commun.* 11, 1–5. <https://doi.org/10.1038/s41467-020-15499-z>.
- Hall, E.K., Bernhardt, E.S., Bier, R.L., Bradford, M.A., Boot, C.M., Cotner, J.B., del Giorgio, P.A., Evans, S.E., Graham, E.B., Jones, S.E., Lennon, J.T., Locey, K.J., Nemergut, D., Osborne, B.B., Rocca, J.D., Schimel, J.P., Waldrop, M.P., Wallenstein, M.D., 2018. Understanding how microbiomes influence the systems they inhabit. *Nat. Microbiol.* 3, 977–982. <https://doi.org/10.1038/s41564-018-0201-z>.
- Hamard, S., Robroek, B.J.M., Allard, P.M., Signarbieux, C., Zhou, S., Saesong, T., de Baaker, F., Buttler, A., Chiapusio, G., Wolfender, J.L., Bragazza, L., Jassey, V.E.J., 2019. Effects of Sphagnum leachate on competitive Sphagnum microbiome depend on species and time. *Front. Microbiol.* 10, 1–17. <https://doi.org/10.3389/fmicb.2019.02042>.
- Hancock, M.H., Klein, D., Andersen, R., Cowie, N.R., 2018. Vegetation response to restoration management of a blanket bog damaged by drainage and afforestation. *Appl. Veg. Sci.* 21, 167–178. <https://doi.org/10.1111/avsc.12367>.
- Harris, A., Bryant, R.G., 2009. A multi-scale remote sensing approach for monitoring northern peatland hydrology: present possibilities and future challenges. *J. Environ. Manag.* 90, 2178–2188. <https://doi.org/10.1016/j.jenvman.2007.06.025>.
- Harris, A., Charnock, R., Lucas, R.M., 2015. Hyperspectral remote sensing of peatland floristic gradients. *Remote Sens. Environ.* 162, 99–111. <https://doi.org/10.1016/j.rse.2015.01.029>.
- Hicks Pries, C.E., Van Logtestijn, R.S.P., Schuur, E.A.G., Natali, S.M., Cornelissen, J.H.C., Aerts, R., Dorrepaal, E., 2015. Decadal warming causes a consistent and persistent shift from heterotrophic to autotrophic respiration in contrasting permafrost ecosystems. *Glob. Chang. Biol.* 21, 4508–4519. <https://doi.org/10.1111/gcb.13032>.
- Holden, J., Wallace, Z.E., Lane, S.N., McDonald, A.T., 2011. Water table dynamics in undisturbed, drained and restored blanket peat. *J. Hydrol.* 402, 103–114. <https://doi.org/10.1016/j.jhydrol.2011.03.010>.
- Ingram, H.A.P., 1978. Soil layers in mires: function and terminology. *J. Soil Sci.* 29, 224–227. <https://doi.org/10.1111/j.1365-2389.1978.tb02053.x>.
- Jassey, V.E.J., Lamentowicz, L., Robroek, B.J.M., Gabka, M., Rusińska, A., Lamentowicz, M., 2014. Plant functional diversity drives niche-size-structure of dominant microbial consumers along a poor to extremely rich fen gradient. *J. Ecol.* 102, 1150–1162. <https://doi.org/10.1111/1365-2745.12288>.
- Jassey, V.E.J., Signarbieux, C., Hättenschwiler, S., Bragazza, L., Buttler, A., Delarue, F., Fournier, B., Gilbert, D., Laggoun-Déferge, F., Lara, E., T. E. Mills, R., Mitchell, E.A.D., Payne, R.J., Robroek, B.J.M., 2015. An unexpected role for mixotrophs in the response of peatland carbon cycling to climate warming. *Sci. Rep.* 5, 1–10. <https://doi.org/10.1038/srep16931>.
- Jassey, V.E.J., Reczuga, M.K., Zielińska, M., Słowińska, S., Robroek, B.J.M., Mariotte, P., Seppey, C.V.W., Lara, E., Barabach, J., Słowiński, M., Bragazza, L., Chojnicki, B.H., Lamentowicz, M., Mitchell, E.A.D., Buttler, A., 2018. Tipping point in plant–fungal interactions under severe drought causes abrupt rise in peatland ecosystem respiration. *Glob. Chang. Biol.* 24, 972–986. <https://doi.org/10.1111/gcb.13928>.
- Joosten, H., Sirin, A., Couwenberg, J., Laine, J., Smith, P., 2016. The role of peatlands in climate regulation. In: Bonn, A., Allot, T., Evans, M., Joosten, H., Stoneman, R. (Eds.), *Peatland Restoration and Ecosystem Services: Science, Policy and Practice*. Cambridge University Press/British Ecological Society, Cambridge, pp. 19–43.
- Jousset, A., Bienhold, C., Chatzinotas, A., Gallien, L., Gobet, A., Kurm, V., Küsel, K., Rillig, M.C., Rivett, D.W., Salles, J.F., Van Der Heijden, M.G.A., Youssef, N.H., Zhang, X., Wei, Z., Hol, G.W.H., 2017. Where less may be more: how the rare biosphere pulls ecosystems strings. *ISME J.* 11, 853–862. <https://doi.org/10.1038/ismej.2016.174>.
- Juottonen, H., Hynninen, A., Nieminen, M., Tuomivirta, T.T., Tuittila, E.S., Nousiainen, H., Kell, D.K., Yrjölä, K., Tervahauta, A., Fritze, H., 2012. Methane-cycling microbial communities and methane emission in natural and restored peatlands. *Appl. Environ. Microbiol.* 78, 6386–6389. <https://doi.org/10.1128/AEM.00261-12>.
- Kalaska, M., Lalonde, M., Moore, T.R., 2015. Estimation of foliar chlorophyll and nitrogen content in an ombrotrophic bog from hyperspectral data: scaling from leaf to image. *Remote Sens. Environ.* 169, 270–279. <https://doi.org/10.1016/j.rse.2015.08.012>.
- Kuiper, J.N., Mooij, W.M., Bragazza, L., Robroek, B.J.M., 2014. Plant functional types define magnitude of drought response in peatland CO₂ exchange. *Ecology* 95, 123–131.
- Largeron, C., Krinner, G., Ciais, P., Brutel-Vuilmet, C., 2018. Implementing northern peatlands in a global land surface model: description and evaluation in the ORCHIDEE high-latitude version model (ORC-HL-PEAT). *Geosci. Model Dev.* 11, 3279–3297. <https://doi.org/10.5194/gmd-11-3279-2018>.
- Lees, K.J., Quaife, T., Artz, R.R.E., Khomik, M., Clark, J.M., 2018. Potential for using remote sensing to estimate carbon fluxes across northern peatlands – a review. *Sci. Total Environ.* 615, 857–874. <https://doi.org/10.1016/j.scitotenv.2017.09.103>.
- Lees, K.J., Artz, R.R.E., Khomik, M., Clark, J.M., Ritson, J., Hancock, M.H., Cowie, N.R., Quaife, T., 2020. Using spectral indices to estimate water content and GPP in Sphagnum moss and other peatland vegetation. *IEEE Trans. Geosci. Remote Sens.* 58, 4547–4557. <https://doi.org/10.1109/tgrs.2019.2961479>.
- Lehmann, J.R.K., Münchberger, W., Knoth, C., Blodau, C., Nieberding, F., Prinz, T., Pancotto, V.A., Kleinebecker, T., 2016. High-resolution classification of south patagonian peat bog microforms reveals potential gaps in up-scaled CH₄ fluxes by use of Unmanned Aerial System (UAS) and CIR imagery. *Remote Sens.* 8. <https://doi.org/10.3390/rs8030173>.
- Lembrechts, J.J., Broeders, L., De Gruyter, J., Radujković, D., Ramirez-Rojas, I., Lenoir, J., Verbruggen, E., 2020. A framework to bridge scales in distribution modeling of soil microbiota. *FEMS Microbiol. Ecol.* 96 (5), fnaa051. <https://doi.org/10.1093/femsec/fnaa051>.
- Limpens, J., Berendse, F., Blodau, C., Canadell, J.G., Freeman, C., Holden, J., Roulet, N., Rydin, H., Schaapman-Strub, G., 2008. Peatlands and the carbon cycle: from local processes to global implications – a synthesis. *Biogeosciences* 5, 1475–1491. <https://doi.org/10.5194/bgd-5-1379-2008>.
- Lindahl, B.D., Tunlid, A., 2015. Ectomycorrhizal fungi – potential organic matter decomposers, yet not saprotrophs. *New Phytol.* 205, 1443–1447. <https://doi.org/10.1111/nph.13201>.
- Logue, J.B., Findlay, S.E.G., Comte, J., 2015. Editorial: microbial responses to environmental changes. *Front. Microbiol.* 6, 1–4. <https://doi.org/10.3389/fmicb.2015.01364>.
- Lopatín, J., Kattenborn, T., Galleguillos, M., Perez-Quezada, J.F., Schmidtlein, S., 2019. Using aboveground vegetation attributes as proxies for mapping peatland belowground carbon stocks. *Remote Sens. Environ.* 231. <https://doi.org/10.1016/j.rse.2019.111217>.
- Lunt, P., Allott, T., Anderson, P., Buckler, M., Coupár, A., Jones, P., Labadz, J., Worrall, P., Evans, M. (Eds.), 2010. *Peatland Restoration. IUCN UK Peatland Programme's Commission of Inquiry on Peatlands*.
- Madritch, M.D., Kingdon, C.C., Singh, A., Mock, K.E., Lindroth, R.L., Townsend, P.A., Madritch, M.D., 2014. Imaging spectroscopy links aspen genotype with belowground processes at landscape scales. *Philos. Trans. R. Soc. B* 369.
- Madritch, M., Cavender-Bares, J., Hobbie, S.E., Townsend, P.A., 2020. Linking foliar traits to belowground processes. In: Cavender-Bares, J., Gamon, J.A., Townsend, P.A. (Eds.), *Remote Sensing of Plant Biodiversity*. Springer International Publishing, Cham, pp. 173–197. https://doi.org/10.1007/978-3-030-33157-3_8.
- Malik, A.A., Puissant, J., Buckeridge, K.M., Goodall, T., Jehmlich, N., Chowdhury, S., Gweon, H.S., Peyton, J.M., Mason, K.E., van Aghmaal, M., Blaud, A., Clark, I.M., Whitaker, J., Pywell, R.F., Ostle, N., Gleixner, G., Griffiths, R.I., 2018. Land use driven change in soil pH affects microbial carbon cycling processes. *Nat. Commun.* 9, 1–10. <https://doi.org/10.1038/s41467-018-05980-1>.
- Malik, A.A., Martiny, J.B.H., Brodie, E.L., Martiny, A.C., Treseder, K.K., Allison, S.D., 2020. Defining trait-based microbial strategies with consequences for soil carbon cycling under climate change. *ISME J.* 14, 1–9. <https://doi.org/10.1038/s41396-019-0510-0>.
- McMorrow, J.M., Cutler, M.E.J., Evans, M.G., Al-Roichdi, A., 2004. Hyperspectral indices for characterizing upland peat composition. *Int. J. Remote Sens.* 25, 313–325. <https://doi.org/10.1080/0143116031000117065>.
- McPartland, M.Y., Falkowski, M.J., Reinhardt, J.R., Kane, E.S., Kolka, R., Turetsky, M.R., Douglas, T.A., Anderson, J., Edwards, J.D., Palik, B., Montgomery, R.A., 2019. Characterizing boreal peatland plant composition and species diversity with hyperspectral remote sensing. *Remote Sens.* 11. <https://doi.org/10.3390/rs11141685>.
- Megonigal, J.P., Rabenhorst, M., 2013. Reduction–oxidation potential and oxygen. In: DeLaune, R., Reddy, K., Richardson, C., Megonigal, J. (Eds.), *Methods in Biogeochemistry of Wetlands* <https://doi.org/10.2136/sssabookser10.c5>.

- Millin-Chalabi, G., McMorrow, J., Agnew, C., 2014. Detecting a moorland wildfire scar in the Peak District, UK, using synthetic aperture radar from ERS-2 and Envisat ASAR. *Int. J. Remote Sens.* 35, 54–69. <https://doi.org/10.1080/01431161.2013.860658>.
- Moxey, A., 2011. *Illustrative economics of peatland restoration. Report to IUCN UK Peatland Program*, pp. 1–3.
- Oh, Y., Zhuang, Q., Liu, L., Welp, L.R., Lau, M.C.Y., Onstott, T.C., Medvigy, D., Bruhwiler, L., Dlugokencky, E.J., Hugelius, G., D'Imperio, L., Elberling, B., 2020. Reduced net methane emissions due to microbial methane oxidation in a warmer Arctic. *Nat. Clim. Chang.* 10, 317–321. <https://doi.org/10.1038/s41558-020-0734-z>.
- Parry, L.E., Holden, J., Chapman, P.J., 2014. Restoration of blanket peatlands. *J. Environ. Manag.* 133, 193–205. <https://doi.org/10.1016/j.jenvman.2013.11.033>.
- Peacock, M., Jones, T.G., Fitter, M.N., Freeman, C., Gough, R., Baird, A.J., Green, S.M., Chapman, P.J., Holden, J., Evans, C.D., 2018. Peatland ditch blocking has no effect on dissolved organic matter (DOM) quality. *Hydrol. Process.* 32, 3891–3906. <https://doi.org/10.1002/hyp.13297>.
- Poindexter, C.M., Baldocchi, D.D., Matthes, J.H., Knox, S.H., Variano, E.A., 2016. The contribution of an overlooked transport process to a wetland's methane emissions. *Geophys. Res. Lett.* 43, 6276–6284. <https://doi.org/10.1002/2016GL068782>.
- Potter, C., Freeman, C., Golyshin, P.N., Ackermann, G., Fenner, N., McDonald, J.E., Ehbair, A., Jones, T.G., Murphy, L.M., Creer, S., 2017. Subtle shifts in microbial communities occur alongside the release of carbon induced by drought and rewetting in contrasting peatland ecosystems. *Sci. Rep.* 7, 1–14. <https://doi.org/10.1038/s41598-017-11546-w>.
- Putkinen, A., Juottonen, H., Juutinen, S., Tuittila, E.S., Fritze, H., Yrjälä, K., 2009. Archaeal rRNA diversity and methane production in deep boreal peat. *FEMS Microbiol. Ecol.* 70, 87–98. <https://doi.org/10.1111/j.1574-6941.2009.00738.x>.
- Putkinen, A., Tuittila, E.S., Siljanen, H.M.P., Bodrossy, L., Fritze, H., 2018. Recovery of methane turnover and the associated microbial communities in restored cutover peatlands is strongly linked with increasing Sphagnum abundance. *Soil Biol. Biochem.* 116, 110–119. <https://doi.org/10.1016/j.soilbio.2017.10.005>.
- Räsänen, A., Aurela, M., Juutinen, S., Kumpula, T., Lohila, A., Penttilä, T., Virtanen, T., 2019. Detecting northern peatland vegetation patterns at ultra-high spatial resolution. *Remote Sens. Ecol. Conserv.*, 1–15. <https://doi.org/10.1002/rse2.140>.
- Read, D.J., 1991. Mycorrhizas in ecosystems. *Experientia* 47, 376–391. [https://doi.org/10.1016/0006-2952\(93\)90100-B](https://doi.org/10.1016/0006-2952(93)90100-B).
- Reczuga, M.K., Seppey, C.V.W., Mulot, M., Jassey, V.E.J., Buttler, A., Słowińska, S., Słowiński, M., Lara, E., Lamentowicz, M., Mitchell, E.A.D., 2020. Assessing the responses of Sphagnum micro-eukaryotes to climate changes using high throughput sequencing. *PeerJ* 8, e9821. <https://doi.org/10.7717/peerj.9821>.
- Reumer, M., Harnisz, M., Lee, H.J., Reim, A., Grunert, O., Putkinen, A., Fritze, H., Bodelier, P.L.E., Ho, A., 2018. Impact of peat mining and restoration on methane turnover potential and methane-cycling microorganisms in a northern bog. *Appl. Environ. Microbiol.* 84, 1–17. <https://doi.org/10.1128/AEM.02218-17>.
- Rivett, D.W., Bell, T., 2018. Abundance determines the functional role of bacterial phylotypes in complex communities. *Nat. Microbiol.* 3, 767–772. <https://doi.org/10.1038/s41564-018-0180-0>.
- Robroek, Bjorn J.M., Albrecht, R.J.H., Hamard, S., Pulgarin, A., Bragazza, L., Buttler, A., Jassey, V.E., 2015a. Peatland vascular plant functional types affect dissolved organic matter chemistry. *Plant Soil* <https://doi.org/10.1007/s11104-015-2710-3>.
- Robroek, Bjorn J.M., Jassey, V.E.J., Kox, M.A.R., Berendsen, R.L., Mills, R.T.E., Cécillon, L., Poissant, J., Meima-Franke, M., Bakker, P.A.H.M., Bodelier, P.L.E., 2015b. Peatland vascular plant functional types affect methane dynamics by altering microbial community structure. *J. Ecol.* 103, 925–934. <https://doi.org/10.1111/1365-2745.12413>.
- Robroek, B.J.M., Jassey, V.E.J., Payne, R.J., Marti, M., Bragazza, L., Bleeker, A., Buttler, A., Caporn, S.J.M., Dise, N.B., Kattge, J., Zajac, K., Svensson, B.H., Van Ruijven, J., Verhoeven, J.T.A., 2017. Taxonomic and functional turnover are decoupled in European peat bogs. *Nat. Commun.* 8. <https://doi.org/10.1038/s41467-017-01350-5>.
- Robroek, B.J.M., Marti, M., Svensson, B.H., Dumont, M.G., Veraart, A.J., Vincent, E.J., 2020. Rewiring of peatland plant-microbe networks outpaces species turnover. *BioRxiv* <https://doi.org/10.1101/2020.05.12.090274>.
- Rydin, H., Barber, K.E., 2001. Long-term and fine-scale coexistence of closely related species. *Folia Geobot.* 36, 53–61.
- Scheffer, M., Hosper, S.H., Meijer, M.-L., Moss, B., Jeppesen, E., 1993. *Alternative equilibria in shallow lakes*. *Trends Ecol. Evol.* 8, 275–279.
- Schmidtlein, S., Feilhauer, H., Bruehlheide, H., 2012. Mapping plant strategy types using remote sensing. *J. Veg. Sci.* 23, 395–405. <https://doi.org/10.1111/j.1654-1103.2011.01370.x>.
- Schweiger, A.K., Cavender-Bares, J., Townsend, P.A., Hobbie, S.E., Madritch, M.D., Wang, R., Tilman, D., Gamon, J.A., 2018. Plant spectral diversity integrates functional and phylogenetic components of biodiversity and predicts ecosystem function. *Nat. Ecol. Evol.* 2, 976–982. <https://doi.org/10.1038/s41559-018-0551-1>.
- Singer, D., Metz, S., Unrein, F., Shimano, S., Mazei, Y., Mitchell, E.A.D., Lara, E., 2019. Contrasted micro-eukaryotic diversity associated with Sphagnum mosses in tropical, subtropical and temperate climatic zones. *Microb. Ecol.* 78, 714–724. <https://doi.org/10.1007/s00248-019-01325-7>.
- Stocker, B.D., Spahni, R., Joos, F., 2014. DYP TOP: a cost-efficient TOPMODEL implementation to simulate sub-grid spatio-temporal dynamics of global wetlands and peatlands. *Geosci. Model Dev.* 7, 3089–3110. <https://doi.org/10.5194/gmd-7-3089-2014>.
- Strack, M., Waddington, J.M., 2007. Response of peatland carbon dioxide and methane fluxes to a water table drawdown experiment. *Glob. Biogeochem. Cycles* 21, 1–13. <https://doi.org/10.1029/2006GB002715>.
- Tedersoo, L., Bahram, M., 2019. Mycorrhizal types differ in ecophysiology and alter plant nutrition and soil processes. *Biol. Rev.* 94, 1857–1880. <https://doi.org/10.1111/brev.12538>.
- Waddington, J.M., Morris, P.J., Kettridge, N., Granath, G., Thompson, D.K., Moore, P.A., 2015. Hydrological feedbacks in northern peatlands. *Ecohydrology* 8, 113–127. <https://doi.org/10.1002/eco.1493>.
- Walker, B., Holling, C.S., Carpenter, S.R., Kinzig, A., 2004. Resilience, adaptability and transformability in social-ecological systems. *Ecol. Soc.* 9. <https://doi.org/10.1103/PhysRevLett.95.258101>.
- Ward, S.E., Ostle, N.J., Oakley, S., Quirk, H., Henrys, P.A., Bardgett, R.D., 2013. Warming effects on greenhouse gas fluxes in peatlands are modulated by vegetation composition. *Ecol. Lett.* 16, 1285–1293. <https://doi.org/10.1111/ele.12167>.
- Ward, S.E., Orwin, K.H., Ostle, N.J., Briones, M.J.I., Thomson, B.C., Griffiths, R.I., Oakley, S., Quirk, H., Bardgett, R.D., 2015. Vegetation exerts a greater control on litter decomposition than climate warming in peatlands. *Ecology* 96, 113–123. <https://doi.org/10.1890/14-0292.1>.
- Wilson, L., Wilson, J., Holden, J., Johnstone, I., Armstrong, A., Morris, M., 2011. Ditch blocking, water chemistry and organic carbon flux: evidence that blanket bog restoration reduces erosion and fluvial carbon loss. *Sci. Total Environ.* 409, 2010–2018. <https://doi.org/10.1016/j.scitotenv.2011.02.036>.
- Worrall, F., Burt, T.P., Rowson, J.G., Warburton, J., Adamson, J.K., 2009. The multi-annual carbon budget of a peat-covered catchment. *Sci. Total Environ.* 407, 4084–4094. <https://doi.org/10.1016/j.scitotenv.2009.03.008>.