Questioning ten common assumptions about peatlands

University of Leeds Peat Club: K.L. Bacon[1], A.J. Baird[1], A. Blundell[1], M-A. Bourgault[1,2],
P.J. Chapman[1], G. Dargie[1], G.P. Dooling[1,3], C. Gee[1], J. Holden[1], T. Kelly[1], K.A. McKendrick-Smith[1],
P.J. Morris[1], A. Noble[1], S.M. Palmer[1], A. Quillet[1,3], G.T. Swindles[1], E.J. Watson[1] and D.M. Young[1]

[1]water@leeds, School of Geography, University of Leeds, UK
[2]current address: Centre GEOTOP, CP 8888, Succ. Centre-Ville, Montréal, Québec, Canada
[3]current address: Geography, College of Life and Environmental Sciences, University of Exeter, UK

SUMMARY

Peatlands have been widely studied in terms of their ecohydrology, carbon dynamics, ecosystem services and palaeoenvironmental archives. However, several assumptions are frequently made about peatlands in the academic literature, practitioner reports and the popular media which are either ambiguous or in some cases incorrect. Here we discuss the following ten common assumptions about peatlands:

1. the northern peatland carbon store will shrink under a warming climate;
2. peatlands are fragile ecosystems;
3. wet peatlands have greater rates of net carbon accumulation;
4. different rules apply to tropical peatlands;
5. peat is a single soil type;
6. peatlands behave like sponges;
7. *Sphagnum* is the main ‘ecosystem engineer’ in peatlands;
8. a single core provides a representative palaeo-archive from a peatland;
9. water-table reconstructions from peatlands provide direct records of past climate change; and
10. restoration of peatlands results in the re-establishment of their carbon sink function.

In each case we consider the evidence supporting the assumption and, where appropriate, identify its shortcomings or ways in which it may be misleading.

KEY WORDS: carbon, climate, ecosystem, hydrology, peatland

INTRODUCTION

Peatlands represent globally-important carbon (C) stores (e.g. Gorham 1991, Turunen *et al.* 2002, Page *et al.* 2011, Yu 2012), potentially vulnerable habitats (e.g. van Breemen 1995, Rydin & Jeglum 2006), and archives of palaeoenvironmental information (e.g. Barber 1981, Chambers & Charman 2004). There is growing concern over the stability of peatland C stores and the provision of other peatland ecosystem services in response to climate change (e.g. Ise *et al.* 2008), wildfire (e.g. Turetsky *et al.* 2006), resource exploitation (e.g. Turunen 2008) and conversion for agriculture (e.g. Carlson *et al.* 2013). Within peatland science there have been substantial advances in conceptual frameworks and the development of interdisciplinary approaches in recent decades (e.g. Ingram 1982, Clymo 1984a, Clymo 1984b, Foster & Wright 1990, Belyea & Baird 2006, Charman *et al.* 2009, Morris *et al.* 2015b). Arguably one consequence of such rapid progress has been the proliferation of a number of ideas which, although sometimes insightful at the time, have subsequently been superseded, or shown to be oversimplified or ambiguous (*cf.* Belyea & Baird 2006). In this review we tackle ten commonly-held assumptions in peatland science; we present the evidence for and against each idea and an evaluation based on the most pertinent scientific literature. We deal with each assumption in turn and, where appropriate, identify where the assumption may be misleading and where focused research may usefully help resolve any misunderstandings or lack of understanding. This paper was written as a community effort by members of ‘Peat Club’ at the University of Leeds, UK (see AUTHOR CONTRIBUTIONS). Each assumption was researched and written about by one or two members of the author team and reviewed by another member, after which revisions, if necessary, were made before submission. The discussion of each assumption is self-contained. Given this, and the wide variety of topics that we cover, we do not

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attempt to provide a conclusion where we seek to identify more general messages from our analysis.

QUESTIONING THE TEN COMMON ASSUMPTIONS

1. Will the northern peatland carbon store shrink under a warming climate?

Northern peatlands (north of ~45° N) have acted as a C sink during the Holocene, owing to inhibited decomposition of peat in waterlogged and/or frozen conditions (Gorham 1991, Yu 2012, Charman *et al.* 2013). However, there is much concern over their future because increasing temperatures may cause a large release of the buried C stock to the atmosphere (Figure 1). Several authors argue that increased temperature and deepening water tables could cause a C release through enhanced aerobic decomposition (Ise *et al.* 2008, Dorrepaal *et al.* 2009, Fenner & Freeman 2011). This could ultimately lead to the northern peatland C store shrinking (e.g. O'Donnell *et al.* 2011, Elberling *et al.* 2013), with the potential of initiating a positive feedback mechanism within the Earth's climate system (Dorrepaal *et al.* 2009). Furthermore, thawing permafrost peatlands have the potential to become a major source of both carbon dioxide (CO_2) and methane (CH_4), the latter being a much more potent greenhouse gas (28 times more potent than CO_2 over a 100-year timeframe (Myhre *et al.* 2013)). Frolking *et al.* (2011) estimated that permafrost thaw would increase sequestration of C by 300 to 1000 kg ha^{-1} yr^{-1} during the 21st Century while CH_4 emissions of C could increase and release as much as 375 kg ha^{-1} yr^{-1}.

Peat formation and decomposition, and therefore net accumulation, are all modulated through several complex ecohydrological feedbacks (Belyea & Baird 2006, Waddington *et al.* 2015). There has been recent debate over the relative importance of plant productivity and decomposition in determining C accumulation in northern peatlands. Charman *et al.* (2006) analysed a network of well-dated peat cores from across the northern hemisphere to illustrate that

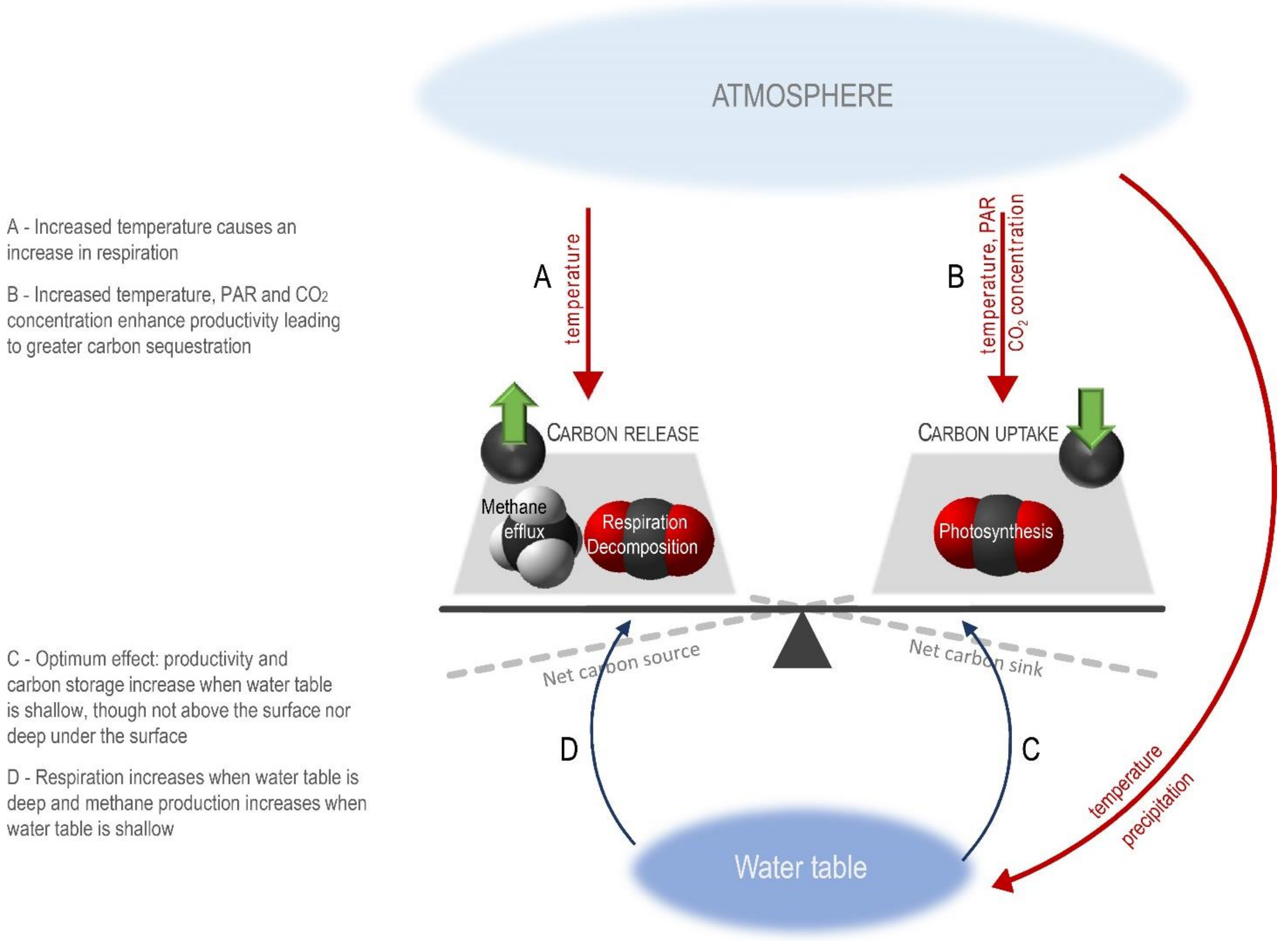

Figure 1. Dynamics and feedbacks of the carbon balance in peatlands.

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C accumulation is primarily related to growing-season length and photosynthetically active radiation (PAR). This suggests that gross ecosystem productivity (GEP) is more important than decomposition for determining peat C accumulation over millennial timescales.

Low rates of peatland C sequestration have been observed during the Little Ice Age, plausibly a result of suppressed productivity under cold conditions and/or increased cloudiness (lower PAR) (Mauquoy *et al.* 2002, Charman *et al.* 2013, T.E. Turner *et al.* 2014); while some northern peatlands have undergone increases in C accumulation in response to recent warming (Charman *et al.* 2013, Klein *et al.* 2013, Swindles *et al.* 2015). The thawing of permafrost peatlands may lead to wetter conditions that inhibit decomposition and enhance C accumulation (Swindles *et al.* 2015), although in some cases strong net C losses have been observed in the first century after thaw (O'Donnell *et al.* 2011).

It is conceivable that future warming could lead to increased C accumulation rates in some northern peatlands owing to invigorated productivity. This would potentially compensate the C released from thawing permafrost and from peatlands degrading from aerobic decomposition. However, it is currently unknown whether the effects of climate change will lead to an overall reduction of the northern peatland C store or if instead the store will remain approximately at current values or increase (e.g. Hartmann *et al.* 2013). Under warming climates, speciation of future C emissions (CO_2, CH_4) from peatlands is likely to be at least as important as the overall C budget in terms of radiative forcing. Thawed permafrost peatlands in particular seem likely to become strong sources of CH_4 owing to saturated soil conditions (e.g. Olefeldt *et al.* 2012).

2. Are peatlands fragile ecosystems?

Peatlands throughout the world have accumulated large stores of organic C (Yu *et al.* 2010) that have developed due to positive feedback mechanisms that promoted their expansion under waterlogged and favourable climatic conditions (Belyea 2009, Jones & Yu 2010). The maintenance of these anoxic conditions results from internal negative feedbacks between ecological, hydrological, and biogeochemical processes that stabilise shallow water tables for long periods of time, and promote the growth of peat-forming vegetation (Belyea 2009, Waddington *et al.* 2015). However, many peatlands have been modified by humans for agriculture, habitat management, forestry, and for fuel and horticulture (Limpens *et al.* 2008, Page & Hooijer 2016), which can combine with natural disturbances such as wildfire and erosional gullies (Tallis 1985, Turetsky *et al.* 2002). These disturbances have destabilised stores of C through the imposition of deeper water tables and a subsequent shift away from peat forming vegetation, leading to an increase in gaseous and fluvial C fluxes, and vulnerability to wildfire (S. Moore *et al.* 2013, C.D. Evans *et al.* 2014a, Kettridge *et al.* 2015, Turetsky *et al.* 2015). Furthermore, studies have proposed that climate-induced warming, or an increase in droughts and subsequent rewetting, may cause the rapid loss of peatland C (Ise *et al.* 2008, Fenner & Freeman 2011). Together, these negative consequences suggest that peatlands are fragile ecosystems. However, peatlands have persisted over millennia (e.g. Aaby & Tauber 1975), and while the loss of peat C is likely to occur in the short term, an understanding of the long-term (100–200 years) response of peatlands to these disturbances needs to take account of internal adaptive mechanisms (Laiho 2006). For example, Swindles *et al.* (2016) demonstrated that peatlands can be resilient to anthropogenic disturbance, such as repeated phases of peat cutting, by resuming peat accumulation over longer timescales.

Peatlands are complex adaptive systems (Belyea & Baird 2006) where long periods with little change (negative feedbacks dominate) are interspersed with short periods of rapid transition (positive feedbacks dominate) (Belyea 2009). Studies have shown how autogenic negative feedback mechanisms can sometimes decouple peatlands from external forcing and dampen their response to changes in climate (Swindles *et al.* 2012, Wang *et al.* 2015). However, some peatlands appear to be more vulnerable to disturbance of their hydrological regime. The tropical peat swamp forests of Sarawak were shown by Cole *et al.* (2015) to have been resilient to variations in climate and burning regimes throughout the Holocene, but, in the past 500 years, resilience has declined as anthropogenic pressure has increased. The drainage of tropical peatlands has resulted in a greater loss of older peat than from drained high latitude peatlands (S. Moore *et al.* 2013, C.D. Evans *et al.* 2014a), which has been attributed to the higher values of hydraulic conductivity found in tropical peats (Baird *et al.* 2017). It has also been reported that drainage features in degraded UK blanket peatlands have revegetated autogenically (Evans & Warburton 2005); yet, in some locations, the combined impacts of pollution, grazing, burning and gullying have resulted in large areas of persistently bare peat that show little sign of recovery without intervention (C.D. Evans *et al.* 2014b).

Complex ecohydrological and biogeochemical feedbacks provide peatlands with a degree of resilience to both climate and land-use change. These feedbacks are likely to enable short-term disturbances in peat accumulation to be counteracted over centennial timescales by processes that favour the long-term sequestration of C (Swindles *et al.* 2016). However, because of continued and increasing pressure from humans, these mechanisms can sometimes be overridden (*sensu* Scheffer *et al.* 2001). Therefore, to avoid the further mobilisation of stored C, encourage renewed C sequestration, reverse the loss of important habitat, and mitigate damage to human wellbeing (e.g. Page & Hooijer 2016), the widespread restoration of peatlands has become an international priority (Bonn *et al.* 2014).

3. Do wet peatlands have greater rates of net carbon accumulation?

Peatlands are highly valued for C accumulation and storage, so knowledge of the environmental drivers which control these ecosystem services is important. Net C accumulation is ultimately a balance between GEP and C losses *via* processes such as plant respiration, heterotrophic decomposition (together called ecosystem respiration) and, in some sites, erosion. Surface wetness, often approximated from water-table depth, is a key focus in peatland management and restoration. High water tables can support peat accumulation by maintaining anoxic conditions in the peat profile, thus slowing decomposition (e.g. Clymo 1965, Belyea 1996). Sufficient water availability may also facilitate the growth of peat-forming plants such as *Sphagnum* spp. and *Eriophorum* spp. (González *et al.* 2014). However, GEP and C loss are both influenced by several drivers besides wetness (Figure 2) and the assumption that wetter peatlands accumulate more C may be overly simple and even misleading.

Climate variability is a major driver of change in wetness, but palaeoecological studies have found reductions in net C accumulation during colder, wetter periods such as the Little Ice Age (Mauquoy *et al.* 2002) and increased net C accumulation during warmer, drier, periods such as the Medieval Warm Period (T.E. Turner *et al.* 2014). Climate related variables, including growing season length, can limit *Sphagnum* growth (Loisel *et al.* 2012) and GEP, and, when surface moisture conditions do not inhibit the growth of peatland vegetation, temperature may influence net C accumulation more strongly than the position of the water table (Charman *et al.* 2013). Additionally, events associated with wetter climates such as heavy rain or snowmelt can cause bog bursts or peat slides, causing a loss of stored C (Warburton *et al.* 2004).

Wetness influences vegetation composition, which in turn influences both GEP and the rate of peat decomposition. In managed peatlands, raising water tables which have been lowered by past drainage is frequently used as a tool to encourage recolonisation of peat forming plants such as *Sphagnum*, which can benefit from increased wetness (Campeau & Rochefort 1996, González *et al.* 2014). However, flooding associated with very wet conditions can also inhibit *Sphagnum* colonisation (Tuittila *et al.* 2003). Furthermore, there is some evidence that aquatic species such as *Sphagnum cuspidatum* decay faster than other *Sphagnum* species (Belyea 1996, Johnson & Damman 1991). On

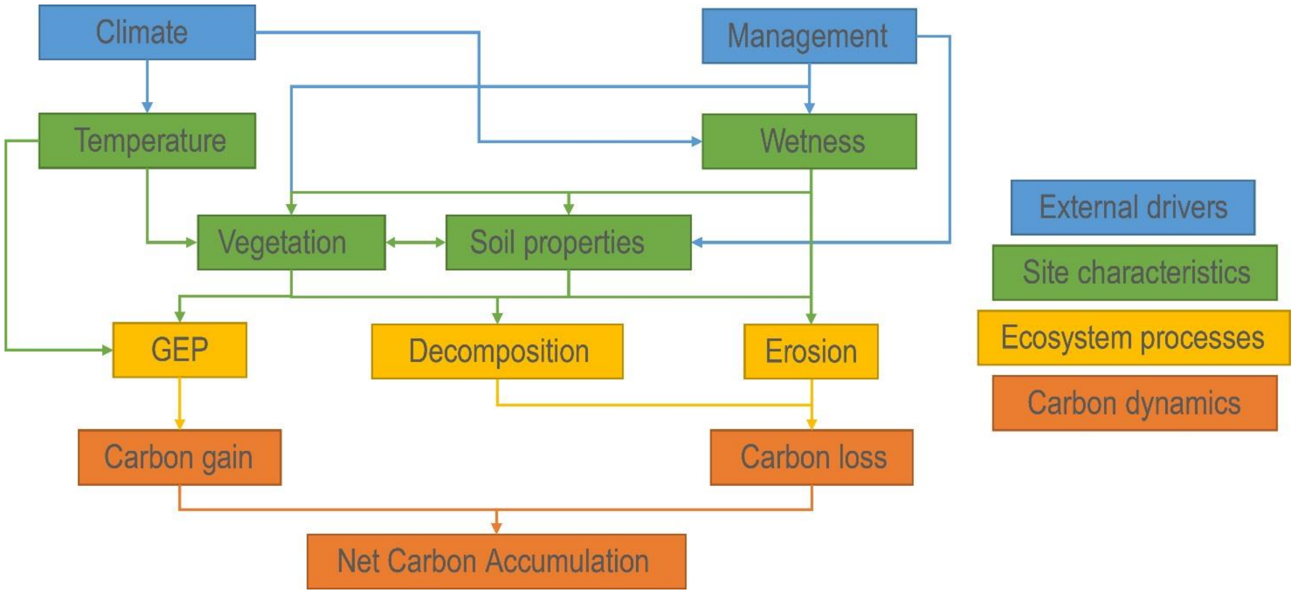

Figure 2. A conceptual diagram of variables influencing net carbon accumulation.

the other hand, the remains of woody plant species associated with drier conditions are sometimes associated with increased C accumulation, perhaps due to the low litter quality of some ligneous material (Loisel & Garneau 2010). The balance between GEP and C loss through decomposition is complex and strongly influenced by site-specific as well as external factors such as climate.

If increasing wetness can have a detrimental effect on net C accumulation in some situations, the focus on rewetting in peatland restoration may be called into question. However, it is likely that a threshold of surface wetness must be reached to limit decomposition and support peat accumulation. At sites where drainage has brought wetness below this threshold, increases in wetness (water tables nearer the ground surface) are likely to be beneficial to net C accumulation. Beyond this threshold, other factors controlling GEP (e.g. temperature) are likely to have a greater role in driving net C accumulation, and further increases in wetness may actually cause a decrease in rates of net C accumulation.

4. Do different rules apply to tropical peatlands?

The title of this section suggests that tropical peatlands differ from extra-tropical peatlands. Given their area and the size of their C store (Yu *et al*. 2010), it is tempting to think of 'extra-tropical peatlands' as being mainly northern peatlands and, in turn, to think of these as *Sphagnum* bogs. However, northern peatlands vary considerably (Rydin & Jeglum 2006), and there is, arguably, a greater difference between, for example, a northern floodplain fen and a raised bog dominated by *Sphagnum* than there is between the latter and a tropical raised bog. Nevertheless, there is interest in how tropical peatlands compare with other peatland types (e.g. Page *et al*. 2006, Page & Baird 2016). Lawson *et al*. (2014) suggested that lowland tropical peatlands[1] differ from temperate, boreal and montane peatlands in four ways: (i) biologically, especially in terms of tree dominance; (ii) hydrologically, with a more “vigorous” hydrological cycle leading to higher-amplitude water-table fluctuations; (iii) in having a lower availability of plant nutrients in the heavily-weathered lowland landscapes in which they (tropical peatlands) are mostly found; and (iv) in being exposed to higher temperatures. Below, we examine (i), (ii), and (iv).

Tree dominance

Trees dominate the vegetation in tropical peatlands, where lignin forms an important fraction of the peat (Jauhiainen *et al*. 2005, Page *et al*. 2006, Lawson *et al*. 2014). Trees are also a common feature on many extra-tropical peatlands, and woody peat occurs as distinct layers or thicker units (> ~0.5 m), especially under floodplain woodland (Lambert *et al*. 1960, Dawson & Smith 1997, Glaser *et al*. 2004). Nevertheless, closed-canopy forests are not dominant across the range of extra-tropical peatlands in the way that they are in the lowland tropics.

Lawson *et al*. (2014) noted that there is no extra-tropical analogue for pneumatophoric tropical tree species - trees with breather roots - and suggested that, even below the water table, tropical peats may be well-oxygenated (see also Ueda *et al*. (2000), Wüst & Bustin (2001), and Gandois *et al*. (2013)). However, plants from genera such as *Phragmites*, *Eriophorum*, and *Carex*, which are common in peatlands outside the tropics, have aerenchyma (spongy gas-conducting tissue) in their stems and roots which may be considered analogous to pneumatophores. Aerenchyma allows air to be transported to those parts of the plant below the water table, from which some may diffuse into the surrounding peat ('rhizospheric oxidation' – see, e.g., Armstrong (1970), Armstrong *et al*. (1992), Popp *et al*. (2000), Ström *et al*. (2005)).

High-amplitude water-table fluctuations

Lawson *et al*. (2014) suggested a high peat hydraulic conductivity, high evapotranspiration, and strong inter-seasonal and inter-annual variability in rainfall give greater water-table fluctuations in tropical peatlands than elsewhere. Currently, few data exist on either hydraulic conductivity or water-table dynamics in tropical peatlands. Kelly *et al*. (2014) and Baird *et al*. (2017) found that hydraulic conductivities in tropical peatlands may be higher than in many non-tropical peatlands. The high hydraulic conductivities are, perhaps, not surprising given the structure of tropical peats: they are reported as comprising coarse woody material - probably mostly from roots - set in a matrix of sedge and grass peat of varying degrees of humification (e.g. Dommain *et al*. 2015, Baird *et al*. 2017). More surprising is that Kelly *et al*. (2014) and Baird *et al*. (2017) found that high hydraulic conductivity did not lead to rapid or pronounced water-table fluctuations - subsurface water flow is restricted by the low hydraulic gradients that prevail in tropical peatlands. Dommain *et al*. (2010) suggested a different mechanism for low-amplitude fluctuations of water tables: surface ponding of water behind the buttress roots of some tropical peatland tree species that

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[1] Most tropical peatlands occur in lowland settings (Page & Baird 2016).

buffers against drops in water tables during dry periods and seasonal drought. Strictly, the water table is the free water surface (i.e. the surface where water is at atmospheric pressure) *within* the peat column, although Lawson *et al*. (2014) used the term more loosely to include surface inundation. To our knowledge there are no published data on inter-annual variations in water tables in tropical peatlands. Inter-seasonally, sub-surface water-table fluctuations from pristine forested tropical peatlands have been reported to vary from about 25 to 90 cm (Jauhiainen *et al*. 2005, Melling *et al*. 2007, Lawson *et al*. 2014). While these fluctuations are large, similar ranges have been reported for non-tropical peatlands (e.g. Roulet *et al*. 2007).

Higher temperatures

In all extant peatlands the addition of organic matter to the peatland has exceeded its loss over long periods of time (decades to millennia), allowing peat to accumulate. However, the details of this mass balance ‘rule’ may vary. In northern peatlands, especially bogs, it is thought that the ‘failure’ of decay in cool, acidic, generally anoxic soils is the main reason why peat accumulates; plant productivity may be low, but the rate of depth-integrated decay (i.e., the rate of decay at any moment occurring through the peat profile as a whole) is often even lower (Page & Baird 2016). Low decay rates in some northern peatlands may also arise from the dominance of *Sphagnum*, which is especially resistant to decomposition (Clymo 1983). In the tropics, the picture is less clear. Because of year-round high temperatures, GEP in domed tropical bogs may be a factor of two or three higher than in extra-tropical bogs. For the same reason, decay rates, especially of surface litter, may also be extremely high, and peat formation may be controlled by belowground dead roots and rhizomes - even though they represent a relatively small fraction of GEP (Chimner & Ewel 2005, Sjögersten *et al*. 2014, Ono *et al.* 2015, Page & Baird 2016).

It is clear that there are differences between tropical and non-tropical peatlands and that these are related to differences in climate and vegetation. However, these differences can, perhaps, be over-emphasised, and the commonalities between tropical and non-tropical peatlands understated. In addition, tropical peatlands are under-studied, and future work may show that variability between different tropical peatlands is as great as that between different types of northern peatland.

5. Is peat a single soil type?

In most soil classification systems, peats fall into a single major class or division that is defined by the percentage organic matter content and/or depth of organic layer. Although such broad classification is fit for purpose at a coarse scale - i.e. identification of land management suitability for agriculture, horticulture or as a fuel source - it is potentially limiting at the finer scale where physical and chemical characteristics can vary widely, yet are key to understanding peatland ecosystem functioning and development.

Further classification of peatlands is often based on their hydromorphic setting and chemical status (Charman 2002). The source of water and its chemical status are fundamentally linked (P.D. Moore 1995). At one extreme are peats fed solely by atmospheric inputs that typically have a low concentration of solutes and are acidic (ombrotrophic bogs), and at the other extreme are peats receiving groundwater inputs that may have relatively high solute concentrations (minerotrophic fens). Atmospheric inputs can vary considerably in their chemistry depending on proximity to the ocean (bringing sea salts: Gorham (1958)) and anthropogenic sources of acidic and solute inputs (e.g. Proctor & Maltby 1998). The chemistry of groundwater inputs varies depending on the nature of underlying geology, and peatlands may also receive water from lakes and rivers and from surface runoff. The chemistry of the source waters subsequently affects key peat properties such as the cation exchange capacity (CEC). Cation exchange capacity in peats is attributable to the negative charge caused by deprotonation of functional groups within the organic matrix. Deprotonation is pH-dependent (e.g. de Wit *et al.* 1993), such that at $pH > 3$ CEC increases with increasing pH (Sparks 2003). Peat CEC is also influenced by the availability of polyvalent metal ions - such as Fe^{3+} and Al^{3+} - which interact and compete with protons at binding sites (Tipping & Hurley 1992). For these reasons, the chemistry of incoming waters is very important in determining peat chemical properties. Even within a peatland complex the chemistry may be spatially variable depending on proximity to groundwater sources (e.g. Lembrechts & Vanstraaten 1982, Larocque *et al.* 2016) or on peatland geomorphology and proximity to the peatland margin (Langlois *et al.* 2015). Therefore, in reality, peatlands may be exposed to a broad spectrum of hydrochemical influences (Figure 3) such that a precise geochemical classification has been thought impossible (Charman 2002).

The variation in these peatland environments results in different types of peat forming, due to variation in vegetation composition and

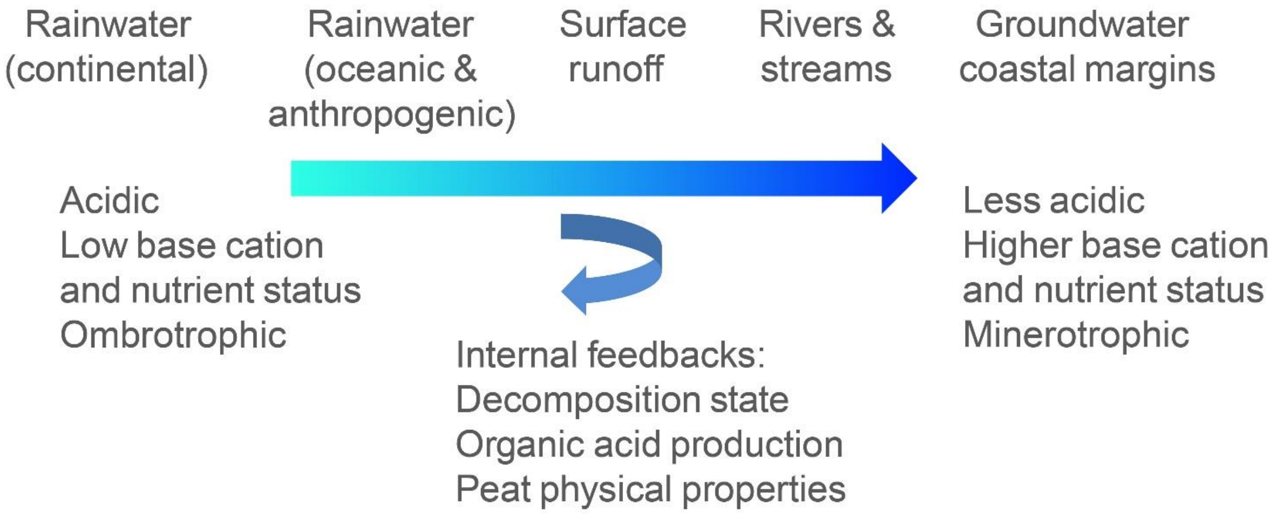

Figure 3. Schematic representation of the hydrochemical influence on peat properties and internal feedbacks, demonstrating increasing solute inputs from left to right. Note that marked gradients in solute concentrations may also occur within the peat profile when groundwater or geological influences transition to rainwater influence (e.g. Muller *et al*. 2008, Steinmann & Shotyk 1997a, b).

decomposability (Grover & Baldock 2013). The degree of decomposition (i.e. how much of the original plant structure remains) has often been used to differentiate peat soils (Rydin & Jeglum 2006). Degree of decomposition reflects the nature of past and recent vegetation composition along with the chemical and physical conditions for microbial activity. It gives rise to differences in organic chemistry which may modify the transition from bog to fen (Dasgupta *et al*. 2015), and also has a strong influence on the physical structure of the peat. This has implications for the physical properties such as hydraulic conductivity and bulk density (Gnatowski *et al*. 2010, Grover & Baldock 2013, Rezanezhad *et al*. 2016) which are important for peatland functioning. Considerable spatial variability exists in bulk density and hydraulic conductivity, both between peatlands (e.g. Branham & Strack 2014) and within single peatland complexes (e.g. Holden & Burt 2003a, Baird *et al*. 2008, Lewis *et al*. 2012). Peat that has higher content of identifiable parts of higher plants (such as roots and woody tissues) tends to yield higher hydraulic conductivity values than amorphous well humified peat (Chason & Siegel 1986). Boelter (1965) showed that undecomposed moss peats yielded hydraulic conductivity values of 3810×10^{-5} cm s^{-1}, while dense decomposed herbaceous peats had lower values of 0.75×10^{-5} cm s^{-1}.

This complexity of peats (Histosols) is partially captured in the classification of organic soils in the World Soil Reference Base (IUSS Working Group WRB 2015), through up to twelve ‘qualifying’ classes that include a mixture of observed, qualitative descriptors supported with semi-quantitative (e.g. percent identifiable plant fragments) and quantitative descriptors determined using recommended standard laboratory methods (e.g. pH, base saturation). The WRB classification thus offers an international standard with sufficient level of detail to permit comparisons at a global scale. However, the WRB is still limited in many aspects, particularly in capturing the variation in physical properties.

While there are similarities within peat soils which could lead to them being considered a single soil type - i.e. their organic matter content - considerable variation exists in other key properties important to peatland functioning. This variation both argues against broad classification and yet challenges attempts at further classification.

6. Do peatlands behave like sponges?

Peat has been described as behaving like a sponge for over 200 years (N. Turner 1757, Ingram 1983). The analogy is still commonly mentioned today, in the popular press (e.g. Shardlow 2016) as well as in scientific papers (e.*g*. Jaenicke *et al*. 2010), but may lead to misinterpretation of the hydrological functioning of peatlands. The sponge analogy comes from similarities between sponge material and peat. Sponges (natural and artificial) are highly porous with channels allowing lots of water storage and flow. Peat itself is very porous and typically has a saturated water content from 86 to 94 % of its volume (Hobbs 1986, Plyusnin 1964). However, Richardson & Siccama (2000) showed that, after 16 hours of gravitational drainage, a saturated popular brand of cellulose sponge on a 3.6 % slope lost 2.5 times more water than peat (re-packed horticultural peat), and that the peat had a greater capacity for water retention. Despite these large differences, Richardson & Siccama (2000) still concluded that, in terms of drainage properties, soils (including peat) and sponges appeared to hold water (as measured by the shape of water potential curves), and discharge water (as measured by the shape of curves of drainage under gravity over time) in “more or less the same way” (p. 917).

Sponges can be used to soak up water and then squeezed to release the water. Herein lies the problem with the analogy. Humans use sponges to perform small-scale water-based domestic tasks, principally related to soaking up water and squeezing it out at will. However, we cannot use a peatland in the same way. The sponge analogy is often applied to describe how peatlands might act as a buffer to rainfall, soaking it up and slowly releasing water later, thereby reducing downstream flood peaks. While peatlands hold a lot of water, some are not good aquifers, as water does not readily drain from them. In many settings, peatland-dominated river flows are poorly sustained between rainfall events (Baden & Eggelsmann 1964, Price 1992, M.G. Evans *et al*. 1999). In other systems, peatlands can sustain small streams throughout the year, although these are often fen systems which are largely supplied by groundwater sources. Even during dry periods peatlands can remain largely saturated with shallow water tables. During rainfall or snowmelt, most peatlands will shed incoming water quickly because they have little spare storage capacity (Bragg 2002, Holden & Burt 2003b, Quinton *et al*. 2003).

In peatlands, two ranges of the quotient P/H, where P is rainfall depth and H is water-table rise height, are observed: (i) those greater than 1 and (ii) those between 0 and 1 (McLaughlin & Cohen 2014, Bourgault *et al*. 2017). In (i), precipitation exceeds the capacity of the peatland to store water and excess rainwater will flow off site relatively quickly. In (ii), rainfall will accumulate within the pore spaces, and the hydraulic conductivity and hydraulic gradient will control the subsurface flow velocity and discharge. In (ii), most rainfall will reach the river/aquifer more slowly than in (i). However, contrary to earlier assumptions, the water table does not need to reach the surface for $P/H > 1$ (Bourgault *et al*. 2017) because the uppermost peat may contain pores which are large enough that they drain as quickly as rainwater is added (Holden 2009). Hence, a peatland’s ability to store rainwater in the uppermost peat can be much lower than the total pore space. Thus, the shift for a given peatland between a state that will store rainfall and buffer the flood peak to a state that will contribute to rapid and peaky flow occurs at a point when water tables are below the peat surface (M.G. Evans *et al*. 1999).

Artificial drainage (ditches and pipe drains) has been used to lower peatland water tables. Holden *et al*. (2004) showed that drainage may reduce downstream flood peaks by creating storage space in some cases, while in other cases flood peaks could be enhanced following peatland drainage. Peatlands which have a flood reduction function tend to be located in floodplains or depressions where the topography supports flood water storage (Jaenicke *et al*. 2010, Acreman *et al*. 2011, Acreman & Holden 2013). The perception created by the sponge analogy that peatlands can soak up most rainwater and thereby reduce downstream flood risk, is not the reality in most cases (Acreman & Holden 2013). Scientists should endeavour to explain how peatlands really function hydrologically and should recognise the problems with the sponge analogy. There also needs to be recognition that not all peatlands behave in the same way and that their topographical and geological setting, vegetation and management can influence their hydrological functioning.

7. Is *Sphagnum* the main ‘ecosystem engineer’ in peatlands?

The notion that *Sphagnum* is a genus of central importance to the functioning of peatlands - as a ‘keystone species’, a ‘bog builder’, or an ‘ecosystem engineer’ - has been in the literature for many years (Morrison 1959, van Breemen 1995, Malmer *et al.* 2003). Here, we critically examine the importance of *Sphagnum* species in the development of peatlands by addressing the following questions:

(i) To what extent does *Sphagnum* ‘engineer’ peatland environments?

(ii) To what extent are global peatlands composed of *Sphagnum* remains?

Sphagnum creates highly acidic conditions in peatlands (Clymo 1984b, Kooijman & Bakker 1994, Verhoeven & Liefveld 1997), both when alive and when decomposing, thereby aiding both organic matter preservation and peat accumulation. This acidity also decreases the availability of nutrients and limits the growth of many other species (van Breemen 1995). Additionally, there is abundant evidence that *Sphagnum* has a significant effect on soil conditions (e.g. hydraulic conductivity and surface temperature) and the microtopography of peatlands (van Breemen 1995, Eppinga *et al.* 2009). However, *Sphagnum* is not alone in shaping the environmental conditions and microtopography of a peatland. For example, vascular plants are often important in providing the architecture of peatland microforms (Malmer *et al.* 1994, Pouliot *et al.* 2011), including facilitating the formation of hummocks through the association of dwarf shrubs and *Sphagnum* (Belyea & Clymo 2001).

Sphagnum is an important genus in arctic, temperate and boreal peatlands. The living and preserved remains of *Sphagnum* may store more C than any other plant genus (Clymo & Hayward 1982, Rydin & Jeglum 2006), and *Sphagnum* cover in boreal peatlands could be as much as 1.5×10^6 km^2 (Rydin & Jeglum 2006). Studies of palaeoecological records often reveal earlier successional phases dominated by other peatland plants, such as *Eriophorum*, but the layers of peat accumulated following the transition to ombrotrophy almost always contain abundant *Sphagnum* remains (e.g. Hughes *et al.* 2000). However, there are numerous exceptions to this in the northern hemisphere (e.g. the ‘patterned’ peatlands of North America dominated by sedges and trees and the forested peatlands of Finland and Sweden (Zoltai & Martikainen 1996)).

Outside of northern temperate and boreal regions, many peatlands are composed primarily of vascular plants. In New Zealand, *Sphagnum* is not as important a peatland plant, with other plant genera, including the Restionaceae, being more widespread (McGlone & Wilmshurst 1999, Clarkson *et al.* 2004). Around 441,000 km^2 of peatland is found in lowland tropical regions - equivalent to ~11 % of global peatland area and potentially up to 25 % of peatland volume (Page *et al.* 2011) - but most is forested and does not contain any *Sphagnum* (e.g. Phillips *et al.* 1997, Lähteenoja *et al.* 2009, Householder *et al.* 2012, Morley 2013, Roucoux *et al.* 2013). Domed ombrotrophic peatlands in Central America, Amazonia and Patagonia, and Southeast Asia, despite sharing some functional similarities with *Sphagnum*-based peatlands (see Question 4), have formed without *Sphagnum* mosses (e.g. Lähteenoja *et al.* 2012, Morley 2013, Swindles *et al.* 2014). Only in rare cases has *Sphagnum* been found in lowland tropical peatland areas, such as Belize (Meerman *et al.* 2003).

There is no doubt that *Sphagnum* is an important plant genus in many peatlands, particularly in the northern hemisphere. *Sphagnum* engineers its environment in a manner that aids peat formation and affects the distribution of other plant species. However, although *Sphagnum* is an important ecosystem engineer in many peatlands, it is seldom the only one. Additionally, the extensive peatland areas where *Sphagnum* plays a limited or non-existent role in peatland development and function should not be forgotten.

8. Does a single core provide a representative palaeo-archive from a peatland?

Carbon accumulation rates and palaeoenvironmental information for individual peatlands are often inferred from analyses conducted on a single core. However, within-site differences in C accumulation and the complex responses of proxy indicators to both allogenic and autogenic changes could make this practice problematic. Studies demonstrating similar results from multiple cores taken in an individual site help provide confidence in the adoption of the single core approach.

In Western Europe, influential early peatland palaeoenvironmental studies on raised bogs involved the detailed description and analysis of peat stratigraphy and macrofossils in vertical peat cut faces, which revealed relatively continuous lateral stratigraphy. This was taken to indicate that bog surfaces reacted uniformly to, and were primarily driven by, allogenic factors (e.g. climate change) (Walker & Walker 1961, Barber 1981). Confidence derived from these studies and others (e.g. Wimble 1986, Svensson 1988), and a progression towards increasingly time intensive high-resolution reconstructions, often involving multiple environmental proxies, meant the use of a ‘well-placed single core’ has largely been adopted, especially in Holocene palaeoclimate reconstruction (Barber *et al.* 1994, Langdon *et al.* 2003, Blundell & Barber 2005). However, examination of records at ever finer temporal resolution and from systems with complex topographies such as blanket bogs (Chiverrell 2001) and patterned peatlands (Loisel & Garneau 2010) emphasises the importance of establishing the degree of autogenic influence within single-core records (see also Question 9).

Multiple core studies with varying chronological quality from ombrotrophic bogs (Barber *et al.* 1999, Charman *et al.* 1999, Chiverrell 2001, Hendon *et al.* 2001) demonstrate that major changes in reconstructed water tables derived from both macrofossils and testate amoebae are largely replicated (Table 1). Increased replicability in the last 1000 years potentially reflects diminishing autogenic effects as peatlands mature (Charman *et al.* 1999, Hendon *et al.* 2001). However, different sensitivities of coring locations at the microform scale can result in inconsistent recording of minor fluctuations across replicate cores (Loisel & Garneau 2010). With the aid of improved Bayesian age-depth modelling, Mauquoy *et al.* (2002) and Blaauw & Mauquoy (2012) identified considerable variability of reconstructed ‘climate’ signals between replicate cores. Blaauw & Mauquoy (2012) demonstrated that indices reflecting the reactions of vegetation to

Table 1. Selected paleoenvironmental or carbon accumulation studies which include more than one core from a peatland. Only studies with an independent chronology have been included. Proxy abbreviations are as follows: P = pollen; M = plant macrofossils; NPP = non-pollen palynomorphs; T = tephra; C = carbon accumulation; MC = micro-charcoal; TA = Testate amoebae; H = humification. Other abbreviations: RERCA = average recent rate of carbon accumulation.

Reference	Proxy	Site type	Chronology	Cores (*n*)	Distance between cores	Summary of results
Blaauw & Mauquoy (2012)	P, M, NPP	Raised bog	^{14}C	4	10 m to ~2 km	*“Single cores are of limited value for reconstructing centennial-scale climate change, and only by combining multiple cores and proxies can we obtain a reliable understanding of past environmental change and possible forcing factors.”*
Watson *et al*. (2015)	T, C	Raised bog	Tephrochronology, SCP (Spheroidal Carbonaceous Particles)	15	A few to hundreds of metres	*“In small, largely undisturbed, mid-latitude peatlands, the presence or absence of tephra from a given eruption can be determined, with a high degree of certainty, by analysing a single core.”*
Innes *et al*. (2004)	MC	Upland spring-head site	^{14}C	2	30 cm	*“While the record of major trends will be accurate, therefore, too precise an interpretation of micro-charcoal data at this temporal scale [1cm subsamples] may not be justified”*
Charman *et al*. (1999)	TA, M	Blanket mire	^{14}C, Pollen analysis	2	10 m	*“Differences between cores are most likely to be a function of the microscale hydrological variability of the peat system and thus it would be logical to combine records from the same technique on two or more cores from the same site”.*
Chiverrell (2001)	TA, H	Ombrotrophic blanket mire	^{14}C	6	Between 500 m and <5 m	*“Comparison of adjacent profiles identifies a broad consistency in testate amoebae and plant macrofossil stratigraphies, but there are discrepancies between adjacent humification profiles. Clearly it is prudent to base palaeohydrological interpretation of peat stratigraphy on more than one profile”.*
Hendon & Charman (2004)	TA	Ombrotrophic mire	^{210}Pb, SCP, pollen	2	10 m	*“While the general sequence of change is similar in both locations, there are differences in terms of the absolute values as well as in the detail of changes through time.”*
Hendon *et al*. (2001)	TA	Ombrotrophic mire	^{14}C, pollen	4	10 m to 450 m	*“Although the general patterns of change can be considered broadly similar in terms of species successions, there are significant differences over short distances…and between the centre and edges of the mire”*
J. Turner *et al*. (1989)	P	Blanket peatland	No chronology - comparison of pollen diagrams	2	1 m	*“Two pollen diagrams from within one metre of each other… are similar, and fully justify the usual practice of preparing only one diagram. There are however minor differences”.*
Loisel & Garneau (2010)	C, M, TA, H	Ombrotrophic surface vegetation	3 to 6 ^{14}C dates on each core	2 sites, 2 cores in each	~200 m	*“Cores taken from the wetter and more depressed sections potentially only recorded major hydroclimatic changes due to constantly high water table levels. In contrast, because of their slightly higher topographic position within the peatlands, records obtained from…(ridges) may contain the most climate-sensitive records.”* Two cores from the same peatland had different average peat accumulation rates of 0.037 cm yr^{-1} and 0.056 cm yr^{-1}.
Mauquoy *et al*. (2002)	M, H, C	Raised peat bog	Wiggle matched ^{14}C dates: ~20 dates on some cores	3	7 to 36 m	*“Wet-shifts are not all consistently recorded in the replicate peat monoliths…A single monolith from a raised peat bog may therefore not be representative and/ or record the entire palaeoclimatic signal contained in peat archive records.”*
Turunen *et al*. (2004)	C	Ombrotrophic peatlands	^{210}Pb, ^{14}C,	23 sites 3 cores in each	Not specified	*“Considerable variation in C mass accumulation was found both among and within peatlands, and differences in 150-year RERCA between hummocks and hollows were reflected in the average vertical height growth rates (4.0 and 2.8 mm yr^{-1}, respectively).”*

water-table changes are inconsistently recorded; the regionally recognised major climate change ~2.8 ka BP (van Geel *et al.* 1996, 1998) being marked in some cores and subdued or lagged in others, potentially reflecting the sensitivity of the microform to past climate variability.

In a similar fashion, pollen data from multiple cores have shown consistent major trends (J. Turner *et al.* 1989). However, studies have been inhibited by the quality of the derived chronology. Improved chronological control suggests coherence at millennial but not centennial time scales, bringing into question the single core approach to reconstructing regional changes in flora over centennial timescales (Blaauw & Mauquoy 2012). Watson *et al.* (2015) suggested that tephra layer presence, if not load, can be ascertained from the analysis of a single core in mid-latitude peatlands. Although single core palaeoclimate studies are not invalidated by these studies, most imply that multiple core analyses are preferable to successfully differentiate regional signals from local noise, especially at high temporal resolution.

Rates of calculated C accumulation vary considerably between different cores from a single site (Turunen *et al.* 2004, Loisel & Garneau 2010, Fyfe *et al.* 2013, Watson *et al.* 2015). In some instances, differences in accumulation can be explained by the choice of coring location (e.g. hummock or hollow) (Loisel & Garneau 2010). However, cores taken from the same contemporary microform type can have varied rates of C accumulation even in the relatively recent past (~350 years) (Watson *et al.* 2015). Peatlands subject to the influence of human activity may also show different amounts of damage or C loss over small spatial scales (Swindles *et al.* 2016). Such spatial differences in C accumulation within one site could lead to unrepresentative estimates of C accumulation when results from one core are extrapolated over a large area.

In terms of C accumulation estimates and palaeoenvironmental reconstruction, more than one core is undoubtedly advantageous, but this must be reconciled with the additional time and cost of analyses. If a single core is to be employed, effort to discern site stratigraphy and underlying topography (Blundell *et al.* 2016) and coring of a microform type which is climatically sensitive (e.g. lawns) and thus likely to record the most complete palaeoenvironmental record (Barber 1982) would be advised. Comparison of well dated regional single core archives also allows the assessment of local noise *versus* regional signal (e.g. Charman *et al.* 2006, Swindles *et al.* 2013).

9. Do water-table reconstructions from peatlands provide direct records of past climate change?

Down-core changes in peat proxies for bog-surface wetness (e.g. plant macro- and microfossils, testate amoeba assemblages, $\delta^{13}C$ and degree of humification) are commonly interpreted as indicators of past changes in climate, although a debate exists over the relative roles of temperature and precipitation (e.g. Charman *et al.* 2009). Evidence of large, abrupt climatic events may sometimes be identified in bogs separated by hundreds of kilometres (Barber *et al.* 2000, Charman *et al.* 2006). Examples include Medieval warming (e.g. Hendon *et al.* 2001, T.E. Turner *et al.* 2014); the Little Ice Age (Barber *et al.* 1999); and drought phases in North America (Booth *et al.* 2005, 2006, Clifford & Booth 2013) and Ireland (Swindles *et al.* 2010). However, in other cases, peat-based evidence for some suspected climatic events may be ambiguous or even absent entirely, such as the 4.2 ka BP event in Britain and Ireland (Barber *et al.* 2003, Roland *et al.* 2014). Reconstructions from multiple bogs in close proximity can sometimes be seen to drift in and out of agreement with one another, sometimes recording synchronous wet or dry shifts, and sometimes not (Charman *et al.* 2006, Swindles *et al.* 2012). Such discrepancies may be explained to some degree by chronological error (Charman *et al.* 2006, Swindles *et al.* 2013) or genuine climatic variability (Langdon & Barber 2004). However, autogenic mechanisms may diminish the degree of connection between peatland ecosystems and climate (e.g. Morris *et al.* 2015b).

In peatlands, depth to water table is not measured against a static datum, but against peat surface elevation. Changes in bog thickness due to changes in rates of peat formation, decomposition and compression therefore also affect water-table depth unless the rate of change of water table exactly matches changes in surface elevation (*cf.* Belyea & Baird 2006). Additionally, although water inputs to bogs are determined by climate, other components of the water budget such as drainage and evapotranspiration are influenced by peat hydraulic properties, and therefore the state of peat decomposition and its vegetation content (Grover & Baldock 2013, Branham & Strack 2014, Morris *et al.* 2015a). Long-term water-table manipulation studies (e.g. P.A. Moore *et al.* 2015) illustrate how quickly peat accumulation regimes and hydraulic properties may adapt to altered hydrological conditions, with reciprocal effects on water budgets. Feedbacks that affect peat mass balance, hydraulic properties and hydrological processes must therefore be thoroughly understood and accounted for before bog surface wetness can be interpreted reliably in terms of climatic change. Doing so probably requires the use of simulation models of peat accumulation and hydrology in parallel with palaeoecological techniques (*cf.* Charman 2007).

A growing body of literature explores the complexity of peatland ecohydrological processes, and the potential for autogenic changes that are unrelated to climate (Belyea & Baird 2006, Belyea 2009, Waddington *et al.* 2015). Morris *et al.* (2015b) illustrated how internal mechanisms may cause peatland water table depths to become insensitive to certain modes or rates of climatic change, particularly slow changes in rainfall; and how climatic information may be removed from peat after formation. Such filtering of climatic information from peat records is distinct from spontaneous changes in peatlands that have the potential to add non climatic information to peat records. Examples include spontaneous drying, (or pool infilling: Barber 1981, Aaby 1976); and other, more complex changes in vegetation composition not driven by climate (Belyea & Malmer 2004).

A debate exists as to whether peatland microtopographic features and plant microhabitats remain stationary over long timescales, or whether they migrate (e.g. Barber 1981, Koutaniemi 1999, Kettridge *et al.* 2012, Pedrotti *et al.* 2014). Although this issue is currently unresolved, it has the potential to add much complexity to the climatic interpretation of peat cores (Loisel & Yu 2013, Baird *et al.* 2016). In all cases, distinguishing genuine climatic information from autogenic signals and noise is aided greatly by within- (Blaauw & Mauquoy 2012) and between-site (Charman *et al.* 2006, Swindles *et al.* 2013) replication (see also Question 8).

10. Does restoration of peatlands result in the re-establishment of their carbon sink function?

Although pristine or undamaged peatlands are important C sinks, degraded peatlands can be major sources of CO_2. Therefore peatland restoration is advocated for climate change mitigation. Peatland restoration includes one or more of water management, re-vegetation, and vegetation management, and aims to restore hydrological function and active peat forming vegetation. However, studies investigating the time span required for re-establishment of the net C sink function following restoration are lacking. Despite the lack of data, restoration projects are being pursued to protect peat C stocks and prevent further loss of C to the atmosphere, in addition to protecting biodiversity and wildlife. However, assumptions have been made about how CO_2 and CH_4 emissions change following restoration. For example, while peatland rewetting commonly causes CH_4 emissions to increase (Tuittila *et al.* 2000, Waddington & Day 2007, Cooper *et al.* 2014), these larger CH_4 fluxes are assumed to be a transient phenomenon of limited duration (e.g. Augustin & Joosten 2007, Bain *et al.* 2011).

Augustin & Joosten (2007) developed a hypothesis on the succession of CO_2 and CH_4 emissions following restoration, expressed as CO_2 equivalents (CO_2-e), and therefore related to global warming potential (GWP), for peatlands in Belarus following restoration (Figure 4). In this hypothesis, immediately following restoration, the GWP of a peatland rises as a result of high CH_4 emissions and low CO_2 sequestration (phase 1). The rise is followed by a sharp decline caused by lowered CH_4 emissions and increased CO_2 sequestration (phase 2) and ends with an equilibrium state of low rates of CH_4 emissions and CO_2 sequestration, similar to that observed in pristine peatlands. Augustin & Joosten (2007) calculated three scenarios for how long each phase might last, although no information is provided on how the scenarios were derived. The best-case scenario has phase 1 lasting for only 5 years, phase 2 for 15 years and phase 3 for 50 years. In the worst-case scenario phase 1 extends to 50 years, phase 2 lasts for only 1 year and phase 3 for 49 years.

Owing to the lack of long-term post-restoration greenhouse gas (GHG) data, Augustin & Joosten (2007) used data from studies of undisturbed peatlands as a proxy for the C balance of a 'long-term' restored peatland. However, Strack *et al.* (2016) found that, while restoration greatly alters CO_2 and CH_4 dynamics compared to unrestored areas, fluxes were, on average, significantly different from those from undisturbed peatlands, in both the magnitude of mean growing-season fluxes and the controls on variations in these fluxes. These differences probably reflect the fact that the hydrological function and vegetation of a restored degraded peatland may not quickly return to that of an undisturbed peatland (Price 1997, Schlotzhauer & Price 1999, Gorham & Rochefort 2003, Poulin *et al*. 2013, Strack *et al*. 2016).

Bain *et al*. (2011) presented a similar hypothesis to Augustin & Joosten (2007) for UK blanket bog (Figure 4). They suggested that phase 1 lasted for between 1 and 10 years and phase 2 >10–20 years. Thus a restored UK blanket bog could switch from a source to a net C sink within ten years of restoration. This faster re-establishment of the C sink function could be because Bain *et al*. (2011) included non-gaseous C fluxes in their calculations unlike Augustin & Joosten (2007).

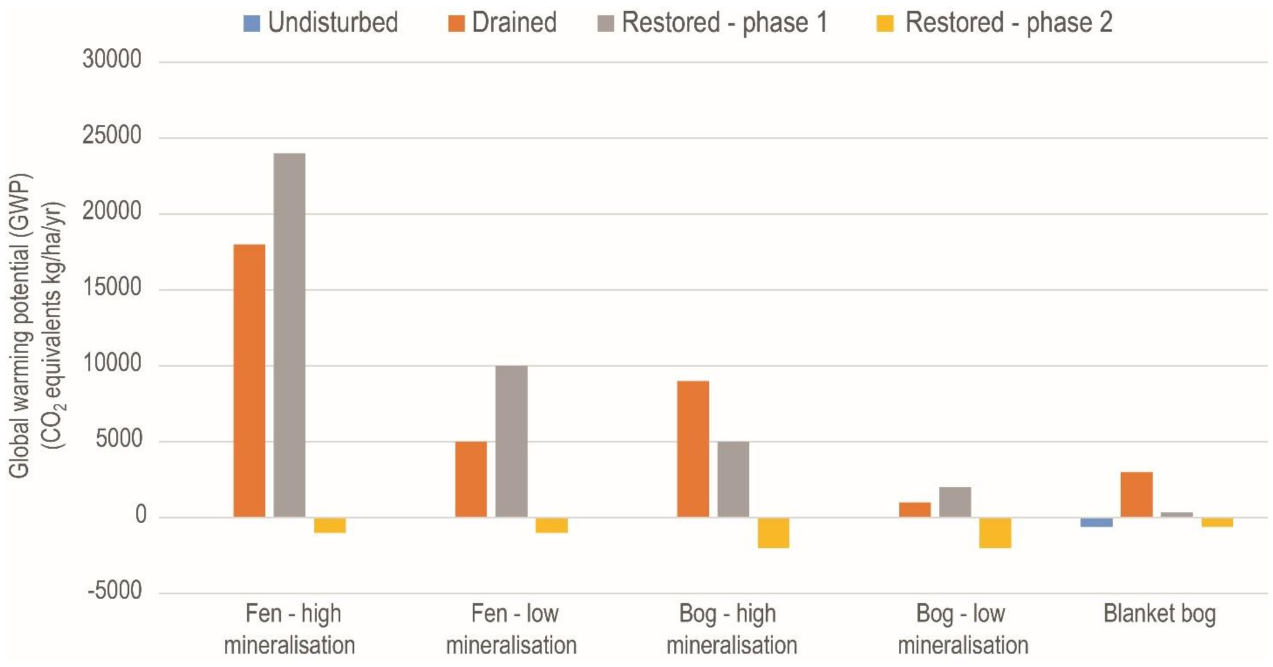

Figure 4. Modelled changes in global warming potential (GWP) of peatlands following restoration (negative numbers represent global cooling). The first three peatland types are adapted from Augustin & Joosten (2007); the blanket bog from Bain et al. (2011), who included additional assumptions about non-gaseous fluxes. Values for the undisturbed state are available for the blanket bog, but not for the other three cases.

Vanselow-Algan *et al.* (2015) monitored the annual GHG balance of three different vegetation types on a peatland, previously used for peat harvesting, 30 years after rewetting. They found all three vegetation types (*Sphagnum*, heath and *Molinia caerulea*) were still net CO_2 sources. In addition, they reported that the GHG balance of all three sites was dominated by CH_4 emissions (up to 98 %), which were particularly high from the *M. caerulea* site. Thus they suggest that high CH_4 fluxes may be a permanent feature of severely damaged rewetted peatlands, as it is difficult to re-establish ecosystem functions on these sites. They suggested high CH_4 fluxes were due to a combination of land-use history, restoration method, large water-level fluctuations and the coverage of plants containing aerenchymatous (gas-conducting) tissue (see Section 4). Samaritani *et al.* (2011) also observed that a *Sphagnum*-dominated European cut-over peatland was still a net source of CO_2 29 years after re-wetting, but sites restored 42 and 51 years ago had become net sinks for CO_2.

Overall, there are still limited data available on CO_2 and CH_4 fluxes from restored peatlands and our understanding of how these fluxes change over space and time is still quite basic. While peatland restoration can reduce the rate of net C loss to the atmosphere, the time required to restore the C sink function remains uncertain. Therefore, more research focusing on gaseous fluxes, particularly CH_4, from restored peatlands is needed to better understand the long-term effects of restoration on these fluxes. Particular attention would be beneficial on areas restored in excess of ten years, because data on gaseous fluxes on these longer timescales is the area most lacking in the literature (Strack *et al.* 2016). Without more data on fluxes from more sites, more peat types and over longer time periods post-restoration, the prediction of future GHG emissions, and therefore the GWP, from restored peatlands will be hard to calculate. A lack of accurate predictions of future peatland GHG emissions will also make it harder to quantify the impact that peatlands could have on the ability of a country to meet Kyoto Protocol targets.

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AUTHOR CONTRIBUTIONS

This is a contribution by the University of Leeds 'Peat Club' - an informal group composed of researchers from different career stages (postgraduate student to senior professor) who are interested in at least one aspect of peatland science. Research interests of Peat Club members include peatland ecology, palaeoecology, geochronology, archaeology, C stocks, greenhouse gas emissions, hydrology, hydraulics, geochemistry, modelling, management and restoration. Our work spans arctic, temperate and tropical peatlands. GTS and AJB conceived and led the project. GTS, AJB and PJM wrote the introduction and edited the final paper. GTS, PJM, AJB and TK compiled and formatted the references. All other authors contributed equally to writing the manuscript. All authors discussed the overall content and were given the opportunity to comment on the complete manuscript.

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Author for correspondence: Dr Graeme T. Swindles, water@leeds, School of Geography, University of Leeds, Woodhouse Lane, Leeds, LS2 9JT, UK.   Email: g.t.swindles@leeds.ac.uk;   Telephone: +44 (0)1133 439127