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Brown, LE, Holden, J, Palmer, SM et al. (3 more authors) (2015) Effects of fire on the hydrology, biogeochemistry, and ecology of peatland river systems. Freshwater Science, 34 (4). 1406 - 1425. ISSN 2161-9565

https://doi.org/10.1086/683426

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LRH: Fire and peatland river systems L. E. Brown et al. RRH: Volume 34 December 2015

Effects of fire on the hydrology, biogeochemistry, and ecology of peatland river systems

Lee E. Brown^{1,5}, Joseph Holden^{1,6}, Sheila M. Palmer^{1,7}, Kerrylyn Johnston^{2,3,8}, Sorain J. Ramchunder^{4,9}, Richard Grayson^{1,10}

- ¹water@leeds, School of Geography, University of Leeds, Woodhouse Lane, Leeds LS2 9JT UK
- ²Marine and Freshwater Research Laboratory (MAFRL), Murdoch University, 90 South Street, Murdoch 6150 Western Australia, Australia.
- ³Environmental and Conservation Sciences, Murdoch University, 90 South Street, Murdoch 6150 Western Australia, Australia
- ⁴Tropical Marine Science Institute, National University of Singapore, S2S, 18 Kent Ridge Road, Singapore 119227

E-mail addresses: ⁵l.brown@leeds.ac.uk; ⁶j.holden@leeds.ac.uk; ⁷s.m.palmer@leeds.ac.uk; ⁸kerrylyn.johnston@murdoch.edu.au; ⁹tmssjr@nus.edu.sg; ¹⁰r.grayson@leeds.ac.uk

Received 7 October 2014; Accepted 31 March 2015; Published online XX Month 2015.

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Abstract: Peatlands are found around the world and cover ~3.4% of the Earth's surface. In the UK, peatlands cover 17.2% or ~1.58 Mha of the land surface and occur mainly in upland areas covering the headwaters of most major British rivers. However, large areas are now subject to prescribed vegetation burning despite policy guidance that recommends a strong presumption against burning deep blanket peat. Wildfires occur sporadically but are forecast to increase in frequency in the future. This paper provides a synthesis of current knowledge about how UK peatland-dominated river catchments respond to fires caused by prescribed vegetation burning and uncontrolled wildfire. We provide insight into the effects of fire on the hydrology, biogeochemistry, and biota of peatland river ecosystems, and the peatlandsoil-driven controls on these effects at the catchment-scale. Burning increases the depth to water table and water-table variability, although some small-scale studies indicate shallower water table in some places. More work is needed on fire effects on peatland river flow, but recent results suggest a complex response with smaller flow peaks for burned systems associated with most rainfall events, but enhanced peaks compared to unburned systems for the top quintile of rainfall events with the largest total rain. Evidence from biogeochemical studies suggests that fire leads to increased dissolved organic C concentrations in rivers. River biota responses primarily include significant reductions in the density of grazing mayflies but increases among detritivores including Chironomidae and Baetis mayflies. We provide a conceptual synthesis that links the main responses of terrestrial and aquatic systems to fire, and we summarize some major research gaps that should be prioritized to inform future policy around peatland management.

Key words: DOC; land-use; macroinvertebrate; moorland; prescribed-fire; wildfire;

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Catchment-scale changes to land cover following urbanization or land development for agriculture and forestry (Paul and Meyer 2001, Allan 2004) pose a major threat to river ecosystems (Vörösmarty et al. 2010). When fire is used as a tool in landuse management to produce substantial changes in catchment vegetation cover (or if wildfire occurs), significant responses also are usually evident in river flow and thermal regimes, sediment loading, and biogeochemistry (Knapp et al. 2009, Russell-Smith and Thornton 2014). In turn, clear changes in the abundance and diversity of many aquatic and riparian organisms and functional processes, such as primary production, respiration, decomposition, and nutrient cycling, often occur (Minshall 2003, Betts and Jones 2009, Ramchunder et al. 2009). Prescribed burning of vegetation is practiced worldwide (Yibarbuk et al. 2001, Freckleton 2004, Verble and Yanoviak 2013) to mitigate wildfire effects by producing fire breaks and reduce available natural fuel sources, to promote changes in catchment vegetation structure for food and game-bird production, and to manage biodiversity. Concerns about the environmental impacts of these burning regimes have been expressed, but few integrated studies have addressed how river catchments respond to prescribed vegetation burning (e.g., Britton 1991, Bêche et al. 2005, Arkle and Pilliod 2010) in comparison to wildfires, which have received much more attention (e.g., Dwire and Kauffman 2003, Minshall 2003, Beganyi and Batzer 2011, Verkaik et al. 2013).

Peatlands are found around the world and cover ~3.4% of the Earth's surface (Buytaert et al. 2006) from the tropics to the high latitudes. In the UK ~1.58 Mha of peatland covers 17.2% of the land surface (Bather and Miller 1991). These systems are predominantly rain-fed (ombrotrophic) blanket peatlands, which occur over rolling terrain and where a water surplus has led to the build-up of organic matter over time because of slow decomposition rates. Blanket peatlands in the UK cover many important headwater catchments, but in some upland regions (typically >300 m altitude and areas above the upper limits of enclosed

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farmland), large areas of bog are subject to prescribed vegetation burning. For example, an estimated >40% of burns now occur on peatland (Yallop et al. 2012, Thacker et al. 2014) despite policy guidance in parts of the UK that states "there should be a strong presumption against burning sensitive areas" (DEFRA 2007, p. 6), with 'sensitive areas' defined to include peat bogs. Instances of burning on designated conservation areas have led to alleged breaches of some EU directives (RSPB 2012).

Fire has been used to control upland vegetation in the UK since ~7700-6300 BC (Goodfellow 1998), but over the last 100 to 150 y, many upland landscapes have been subjected to intensive and regular prescribed rotational burning regimes (Simmons 2003). For example, $>\frac{1}{3}$ of the upland peat cover in the Peak District of northern England now undergoes regular prescribed burning geared at encouraging Red Grouse (Lagopus lagopus scotica) production (WCA Environment Limited 2010). Red Grouse are ground/shrubnesting game birds, keenly targeted in sports shooting, which constitutes a source of income for some estates in the UK uplands. Vegetation removal, predominantly the heather shrubs Calluna vulgaris and Erica spp., and some grass/sedge species, is undertaken in a controlled manner by burning relatively small patches that are typically $\leq 2000 \text{ m}^2$, on rotations of 7 to 25 y depending on local conditions (Fig. 1A). Over time, a characteristic mosaic of Callunadominated patches develops, with older stands providing nesting sites for grouse, and recently burned patches with exposed soils and Calluna shoots providing food for young birds. Burning is undertaken each year from 1 October to 15 April (30 April in Scotland), which corresponds to the northern hemisphere late autumn to late spring. Patches of vegetation typically are burned within tens of minutes and extinguished by hand before the underlying soils can ignite. However, serious concerns have been raised regarding the effects of this practice on upland biodiversity, C storage, and water quality (Yallop et al. 2006, Glaves et al. 2013, Thacker et al. 2014). As a consequence, stakeholders have made

vociferous calls for more evidence to underpin evidence-based policy development (Sutherland et al. 2006, Grant et al. 2012, Glaves et al. 2013).

In contrast to prescribed burning, uncontrolled wildfires on peatlands generally burn hotter, for longer (Radley 1965), and over much larger areas (Fig. 1B), although they tend to be infrequent in the UK. However, wildfires can lead to smouldering of peat for periods of weeks to months after the surface fire has occurred, often resulting in major losses of peat (Rein et al. 2008, Benscoter et al. 2011a, Turetsky et al. 2015). Burn severity during wildfire can be strongly affected by land management, such as artificial drainage, which dries out upper peat layers, and antecedent conditions, with deeper water tables at the time of fire being associated strongly with deeper burns and more C loss (Turetsky et al. 2002, Turetsky et al. 2011a). In the UK uplands, wildfires have caused substantial damage and vegetation loss (Radley 1965, Gilchrist et al. 2004), and such damage can be difficult to restore on sloping blanket peatlands because once the vegetation cover is removed from large areas, the peat surface becomes exposed to desiccation, and subsequent rainfall events may cause rapid erosion (Maltby et al. 1990). Climate-change modeling suggests that summer wildfire risk will increase in many blanket-peat-covered parts of the UK (Albertson et al. 2010), and the wider environmental consequences of such fires will have to be considered as part of future management planning.

We provide a synthesis of current knowledge about how UK peatland-dominated river catchments respond to fires that result from prescribed vegetation burning and from uncontrolled wildfire, in the context of relevant studies of fire effects on peatland from across the world. We examine the effects of fire on the hydrology, biogeochemistry, and biota of peatland river ecosystems, and the peatland-soil driven-controls on these systems at the catchment-scale. We do not detail effects on terrestrial biota, land–atmosphere gaseous exchange, total peat C losses, or the biogeochemistry of smoke. Information on these effects

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can be found elsewhere (e.g., Page et al. 2002, Turetsky et al. 2011b, Grant et al. 2012, Glaves et al. 2013). We provide a short contextual section to outline the key features of peatland terrestrial and aquatic systems that are unburned and not subjected to other significant management pressures, but more detailed reviews can be found elsewhere (e.g., Ramchunder et al. 2009). An overview of the effects of fire on peatland river catchments then provides a background for a critical evaluation of current understanding about how prescribed burning and wildfire impact peatland river system hydrology, biogeochemistry, and ecology. Last, we provide a conceptual summary of the main linkages and responses between hydrological, chemical, sedimentary, and river ecological properties and processes after removal of peatland vegetation with fire, and outline some of the major research gaps that ought to be filled to inform future policy around peatland management.

PEATLAND ECOSYSTEMS

Much of the UK's uplands were covered historically by woodland. However, anthropogenic deforestation in the early to mid-Holocene, subsequent grazing of domestic livestock to minimize tree regrowth, and a wet climate promoted the development of peat (Simmons 2003). Several management interventions that have occurred mainly within the last 2 centuries have reduced the extent of undisturbed blanket peatland in the UK uplands. For example, ditch drainage on open peatlands and on those with coniferous plantations have caused deeper water tables, enhanced Al release, lower pH, and changes to river flow with both increases and decreases in baseflows and flood peaks reported, at least at the local scale (Heal 2001, Holden et al. 2004, 2006, Ramchunder et al. 2012). Near industrial regions, such as Sheffield and Manchester, erosion related to overgrazing and atmospheric pollution has been extensive (Rothwell et al. 2005, Haigh 2006). Herein, we use the term unburned to refer to systems that have no recent (i.e., within the last ≥3 decades) history of prescribed or

wildfire and, other than light grazing by livestock, no additional management stressors, such as plantation forestry, artificial drainage, mining, or erosion.

Terrestrial vegetation

Peat builds up when climatic conditions prevent or slow the decomposition of plant remains. Typically in the UK, peat is derived from the partly decomposed and compacted litter of Sphagnum moss and the sedge Eriophorum. These 2 plant genera are slow to decompose but are not necessarily the dominant living components of upland peatlands (Table 1). The UK National Vegetation Classification (NVC) recognizes 5 main vegetation complexes associated with peatlands, composed of, to a greater or lesser extent, dwarf shrubs, bryophytes, and sedges, depending on whether the peatland is ombrotrophic or minerotrophic (Averis et al. 2004). Some upland peatlands have been afforested to provide commercial conifer plantations (Brown et al. 2010), but most are dominated by low shrub (<1 m), sedge, and grass cover, so peatland rivers lack extensive shading (Evans and Warburton 2007).

Soil hydrology and biogeochemistry

Blanket peatlands are characterized by shallow water tables, often at or within a few centimeters of the surface. Full saturation occurs rapidly during rainfall, leading to generation of saturation-excess overland flow or near-surface throughflow (Ingram 1983, Price 1992, Holden and Burt 2003b, c). During rainfall-free periods in winter, when plant growth is restricted by low temperature and short day-length, water tables are kept high by the very low hydraulic conductivity of the deeper peat, which means that free soil drainage is restricted (Holden and Burt 2003a). Thus, water-table fluctuations are controlled primarily by summer evapotranspiration in undisturbed sites (Gilman 1994, Holden et al. 2011). In mid-summer, on the rare occasions when no rain falls for prolonged periods (i.e., weeks), water tables often

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do not drop to >30–40 cm depth (Evans et al. 1999). Therefore, runoff production to generate river flow is dominated by processes within the uppermost peat where the hydraulic conductivity is several orders of magnitude greater than deeper within the peat. Macropores within the upper layers of peat can dominate the flowpaths for water (Baird 1997, Holden et al. 2001, Holden 2009). However, larger forms of macropores, known as soil pipes, also are common in peatlands (Jones 1981, Norrstrom and Jacks 1996, Holden et al. 2009), often occur at depth, and can contribute 10–14% of river flow (Holden and Burt 2002, Smart et al. 2013). Most pipeflow tends to be fresh rainwater that has rapidly percolated through macropore and pipe networks, although some appears to be derived from older, deeper sources (Billett et al. 2012).

Blanket peatlands are nutrient poor and fed by rainfall and receive very little chemical input from underlying mineral soils. Hence, in the UK, their chemistry is influenced strongly by inputs of sea-salts and air-borne pollution delivered by rainfall. The highly organic soils also have very high capacity to retain exchangeable cations, and concentrations of Ca and Mg, in particular, are often much higher in surface peats than in the underlying mineral soils (Billett and Cresser 1996). As a consequence of their waterlogged nature and slow decomposition, the cycling of other major plant nutrients, especially N, P, and K, is slow and typically depends on internal recycling within the living plants or top few cm of peat (Rydin and Jeglum 2006). Runoff from peat catchments is usually acidic and characterized by high concentrations of dissolved organic C (DOC) from partial oxidation of soil organic matter (Freeman et al. 2004).

River hydrology and sediments

Many UK peatlands are found in the headwaters of large river systems, with discharge from the headwaters progressively moving downstream through areas of enhanced grassland,

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farmland, and urban areas. However, in some systems, the peatland may cover almost the entire catchment to its outlet at the sea, e.g., systems in parts of the Flow Country in northern Scotland. Peatland river flow is dominated by saturation-excess overland flow, and when it rains, water can travel rapidly to the river channel because water tables are close to the surface for most of the year in blanket peat systems. Therefore, the flow regime in blanket peat catchments is very flashy with rapid rising and falling limbs to storm hydrographs (Price 1992). Upland peatlands are unable to buffer the river system from flooding because of a lack of additional rainwater storage capacity (Acreman and Holden 2013). However, the surface vegetation cover and its roughness can play a large part in controlling the velocity of water across the peat. Holden et al. (2008) showed that overland flow velocities were typically an order of magnitude greater across bare peat than across dense Sphagnum-covered peat, with flow velocities across Eriophorum-dominated peat being in between. Thus, the lag time and size of the river hydrograph peak may be affected by peatland vegetation cover. Less vegetation and less Sphagnum would typically equate to a shorter lag time and higher peak, although the exact effects will depend on river network connectivity and synchronicity of flows from tributaries into the main river channel (Holden 2005b). The effects of peatland vegetation cover on flood peaks have been demonstrated in recent field and modeling studies (Grayson et al. 2010, Gao et al. 2015). Thus, changes to the composition of the surface vegetation cover may be an important consideration for land managers who are concerned about downstream flood risk. The low hydraulic conductivity of the deeper peat layers means that river discharge can decrease very quickly once overland flow ceases, and some peatland streams may be ephemeral, with no flow following rain-free periods of a few days (Holden 2005b).

River biogeochemistry

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The chemistry of rivers draining upland peat-dominated catchments depends strongly on the extent to which water flows through the surface peat or through the underlying mineral soil. Cresser et al. (1997) showed that the base cation chemistry of peatland rivers strongly resembles precipitation chemistry during storm events as a direct effect of rainwater inputs on the peat exchange complex. Flow that originates in the upper peat layers also delivers DOC to rivers (Clark et al. 2008), and the extent of organic soils, such as peat, in upland catchments has long been associated with high outputs of DOC in river waters (Hope et al. 1997, Aitkenhead et al. 1999). Clark et al. (2008) demonstrated that river-water DOC concentration in a catchment dominated by peats was negatively correlated with river flow and attributed this phenomenon to dilution by rainfall. In other catchments with shallower peat or a mixture of soil types, river-water DOC concentrations can increase with increasing discharge (Hope et al. 1994, Soulsby et al. 2003) as flow through the upper organic horizons becomes dominant.

As river catchment size increases in peat-dominated headwater systems, scope increases for mineral and organo-mineral soil influences to impart effects on river chemistry. For example, a study of 11 rivers ($1^{st}-4^{th}$ order; 0.14–26.6 km²) at Moor House, northern England, found that electrical conductivity, SO₄^{2–} concentration, and pH increased with stream size, whereas Al concentrations decreased (Ramchunder et al. 2011). In this instance, water-chemistry changes were attributed to weathering of limestone bedrock, thus increasing the ionic strength and pH and decreasing Al. Higher SO₄^{2–} was linked to increasing organomineral soil cover and less saturated conditions, and thus, less retention by SO₄^{2–}-reducing bacteria (Daniels et al. 2008). In addition, Ramchunder et al. (2011) observed strong seasonal variability regardless of river size in water temperature, benthic particulate organic matter, NO₃[–], and Cl[–] concentrations. DOC also typically shows a pronounced seasonal increase in peat-dominated catchments during mid-summer to late autumn because of flushing of soils

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after warmer, drier summer conditions have favored enhanced decomposition of organic matter (Chapman et al. 2010). Despite the importance of C in UK upland river systems, the fates of DOC and particulate organic C (POC) in peatland river systems are poorly understood. Studies from the UK and elsewhere have shown that peat-derived DOC and POC do contain a biodegradable component (Fellman et al. 2008, Dawson et al. 2012, Stutter et al. 2013), and results of some studies suggest that DOC removal can occur as water flows along peatland rivers because of processes, such as microbial breakdown and photo-oxidation (Dawson et al. 2001, Aspray 2012, Moody et al. 2013). Interest in the fate of peat-derived POC and DOC is increasing because of a need to understand: 1) their contribution to peatland C budgets (Billett et al. 2010); 2) their role in the delivery of Fe and, therefore, in biogeochemical cycling in estuaries (Krachler et al. 2010); and 3) whether they contribute to downstream CO₂ efflux and, therefore, to C budgets at larger scales (Wallin et al. 2013), or whether they are delivered and buried in ocean sediments. Disentangling these multiple roles of DOC/POC on C cycling requires more detail on the relative importance of the different processes influencing peatland-river C cycling across a range of spatial and temporal scales.

River biota

Ecological research on upland rivers has a long history (Butcher et al. 1937), and for UK peatland environments, the literature is dominated by work undertaken in Upper Teesdale, north Pennines, and in particular at Moor House National Nature Reserve (Brown et al. 1964, Armitage et al. 1974, 1975, Crisp et al. 1974, 1975, Wotton 1976, Ramchunder et al. 2011). Algal community richness (~50%) and cell density (~70%) in Trout Beck at Moor House is dominated by diatoms, with green algae accounting for 30% of the richness and 12% of density (Burns 2000). How algal communities vary more generally throughout these peatland river systems is not known. The macroinvertebrate fauna of these rivers is not

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particularly unique in terms of specialist species, but spatial gradients are notably strong over short distances (i.e., linked to high habitat heterogeneity), and assemblages of acid-tolerant taxa are particularly notable. For example, Eyre et al. (2005) briefly highlighted how small acidic rivers in north Pennine peatland areas had distinct macroinvertebrate assemblages compared with the rest of the River Tyne and Tees system. These unique assemblages are dominated by several Coleopteran species, and low abundances of Gammarus pulex and Plectrocnemia conspersa. Earlier, investigators identified >120 macroinvertebrate taxa from several rivers in and around the Cow Green Reservoir basin, Upper Teesdale (Armitage et al. 1975). In other peatland river systems, Hynes (1961) recorded >90 taxa from the Afon Hirnant, Wales, whereas Minshall and Kuehne (1969) recorded 62 taxa along the length of the 16-km-long River Duddon, Cumbria.

More recent studies by Ramchunder et al. (2011) at Moor House showed that macroinvertebrate community abundance and diversity typically were similar across peatland rivers of different sizes, but turnover of macroinvertebrate assemblages with increases in river order was significant. In particular, 1^{st} - and 2^{nd} -order rivers hosted small-sized acidic and fine-sediment tolerant stoneflies, such as Amphinemura standfussi and Nemoura cambrica (Fig. 2A), whereas circumneutral 3^{rd} - and 4^{th} -order rivers with larger bed-sediment clasts supported more mayflies and larger predatory stoneflies (e.g., Dinocras cephalotes and Perla bipunctata; Fig. 2B). Johnston (2012) examined catchment management influences on macroinvertebrate assemblages in 30 rivers throughout the Pennine hills and found that unburned sites had higher macroinvertebrate richness as catchment size increased. Production of the top invertebrate predators is low in these rivers (up to only 0.16 g C m⁻² y⁻¹ at Moor House; Burns 2000). Predatory Plecoptera and Trichoptera can supplement their diets with algal consumption, and some predators display dietary shifts from carnivory to algivory as they develop in peatland influenced rivers (Lancaster et al. 2005)

Fish populations in headwater peatland rivers have been studied very little, perhaps because these environments are considered particularly harsh environments unsuitable for fish because of their low baseflows, wide thermal range resulting from the lack of shading from riparian vegetation (Brown et al. 2010), and relatively low pH and high Al concentrations. However, populations of small Brown Trout (Salmo trutta) and Bullhead (Cottus gobio) often occur in the larger rivers where pH is close to neutral, or where rivers cross exposed outcrops of base-rich rocks. Crisp et al. (1975) found that S. trutta densities were lower in 3 populations in the north Pennines than in rivers at lower altitude and ranged from 0.1–0.22 individuals (ind)/m² although some fish were up to age VIII. Cottus gobio were found in densities of 2.5–8 ind/m². Trout production ranged from 1.02–3.50 g m⁻² y⁻¹ and Bullhead from 0.48–7.43 g m⁻² y⁻¹. These values are low compared to nonpeatland rivers. The influence of fish on the wider aquatic food web of peatland rivers has yet to be studied.

PEATLAND RESPONSES TO FIRE

Fire is prescribed to control vegetation on UK peatlands, overwhelmingly for the creation of conditions conducive to supporting enhanced Red Grouse abundance, but also for improving grazing habitat for cattle and reducing fuel loads to prevent wildfire. Wildfires occur infrequently in the UK, with the main causes being loss of control of prescribed burns, human-induced fires (accidental or arson), and lightning strikes (Worrall et al. 2010). A conservation status assessment made by Natural England (2010) suggested that <1% of peat in England has been mapped as undamaged, with 70% having visible evidence of damage on-the-ground. An estimated 16% of all peats and 30% of blanket bog are subjected to prescribed burning. Both research effort and the number of publications/y on the subject of prescribed vegetation burning in the UK uplands have increased notably in parallel with the

global increase in research on fire and peatlands (Fig. 3A, B). Studies of wildfire effects on UK peatlands remain rare (Fig. 3C), although this type of fire disturbance poses a considerable future threat to the biodiversity of the UK because of climate change and projected increases in tourist numbers (McMorrow et al. 2009). The following section is predominantly a review of the catchment-wide effects of prescribed burning, with wildfire-related knowledge integrated where it is available and relevant.

Terrestrial vegetation

Vegetation burning cycles depend on productivity, habitat type, grazing level, traditional burning schedules, or government-instigated management prescriptions (Glaves et al. 2013). An individual river catchment can have many patches of vegetation that are of different ages and at different stages of recovery from fire because the primary reason for prescribed burning of vegetation is to remove the older, woody shrubs and encourage regeneration of young shrub shoots for grazing of game-birds and livestock. Burning typically takes place within the catchment most years, but each year a different set of patches is burned so that, on average, an individual patch will be burned once every 7–25 y. Therefore, patches that have been very recently burned (i.e., within the last 12 mo) and those that have not been burned for many years can be found across burned peatland, thereby creating a mosaic.

Burning is considered particularly detrimental to peat-forming Sphagnum species (Grant et al. 2012), although some results from a small number of experimental burning plots have contradicted this suggestion (Lee et al. 2013). Thus, the processes for changes in Sphagnum cover require study in further detail. One proposed reason for the difference found between experimental-plot studies and wider studies is that burning in the field is subject to less stringent controls than in experimental plots. Government guidelines (DEFRA 2007)

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recommend against burning into living moss layers, but this level of control is not always achievable. Moss removal exposes the soil, and subsequent rapid surface erosion of bare peat makes conditions detrimental to the reestablishment of seedlings and Sphagnum diaspores, so vegetation recovery can often be very slow (Radley 1965, Anderson 1997). Fire return times may be $>20\times$ more frequent than is necessary for full recovery to occur (Thacker et al. 2014). Some fires, such as wildfire that often burns hotter and penetrates into the peat mass, also may destroy the local seed bank. Thus, recovery of blanket peat often involves intensive and expensive management techniques, such as the use of geotextiles to protect the peat surface from erosion, plug planting (Parry et al. 2014), or the spreading of Sphagnum beads (Hinde et al. 2010).

Soil hydrology

In some environments, such as swamp peatlands in Indonesia, burning can lead to enhanced inundation from water and impeded revegetation (Wösten et al. 2006). In other environments, drying of peat (resulting from management actions or meteorological conditions) can increase the impact of fire (Benscoter et al. 2011b, Turetsky et al. 2011a, 2015), but relatively little is known about fire effects on peatland hydrology. Intense fire can result in the development of hydrophobic compounds in surface peat (Clymo 1983). Thompson and Waddington (2013) showed that water-table response to rainfall in an ombrotrophic forested peatland in northern Alberta was significantly more variable over time and was more responsive to smaller rain events after wildfire than for unburned peat. Enhanced surface drying, combined with increased bulk density and associated water retention in the near-surface peat, made conditions less conducive for Sphagnum colonization after the fire because pore-water tensions, which place moss under stress, were more quickly reached. Compared with unburned soil plots, Holden et al. (2014) also found smaller near-

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surface hydraulic conductivity and less macropore flow associated with a greater peat bulk density where prescribed burning of UK blanket peat had occurred recently. However, this study also showed that as time since burning increased (2–>15 y), near-surface bulk density decreased and the near-surface hydrological conditions became more similar to those in undisturbed peatlands.

Data from small experimental plots on blanket peatland at Moor House in the north Pennines, UK, that were set up in 1954 (Rawes and Williams 1973) and burned on 10- and 20-y cycles suggest that shallower water tables are more strongly associated with burned (and more frequent burned) plots than with unburned plots (Worrall et al. 2007, Clay et al. 2009a). However, these plots may not be typical of managed burns elsewhere given their extremely controlled nature (Lindsay 2010). Moreover, the studies were based on single monthly samples, so data were not available to investigate finer temporal-scale water-table dynamics. Holden et al. (in press) identified water-table responses to prescribed fire in 10 catchments across the Pennine region (Brown et al. 2014) that are inconsistent with wildfire responses in North American peatlands (Thompson and Waddington 2013). Holden et al. (in press) showed that plots subjected to prescribed vegetation burning had significantly deeper water tables and greater water-table variability than plots on unburned peat. Water-table depths differed significantly among burn age classes, and the most recently burned plots had the deepest water tables. Overland flow was less common on burned than on unburned peat. Water tables would be expected to be deeper after fire for several reasons, including enhanced evaporation caused by warmer summer surface temperatures in the years immediately after the burn (Kettridge et al. 2012, Brown et al. 2015), compression of peat resulting in larger water-table declines for the same volume of evaporation, and enhanced transpiration by new plant growth (Ward et al. 2012). However, results of water repellency tests showed that hydrological effects may differ with peat type. Sphagnum peatlands were

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subject to deep water tables after fire because the water repellency effect was limited, whereas feather moss peat underwent severe water repellency after fire, which would restrict the upward supply of water to the peat surface and evaporation (Kettridge et al. 2014).

Piping is enhanced in peatlands disturbed by drainage (Holden 2005a), but whether piping and pipeflow are affect by wildfire or prescribed burning is not known. Overall, the effect of prescribed patch fires on UK blanket peatland hydrology is poorly understood, and both direct hydrological studies and indirect investigations using ecological indicators (Turner and Swindles 2012, Blundell and Holden 2015) are required urgently.

Soil biogeochemistry

Holden et al. (2012) conducted a critical synthesis of the effect of vegetation burning on the discoloration of surface waters by DOC, for both organic peats and organo-mineral soils. Much of the early work was conducted on organo-mineral soils rather than peat. Authors of 2 experiments conducted on peat soil and solution chemistry reported an increase in water color in leachates from peat cores extracted from beneath burned heather compared to leachates from cores beneath unburned peat (McDonald et al. 1991, Miller 2008). In contrast, Clay et al. (2009) found no evidence of a lasting burn effect on soil solution DOC collected from 0 to 90 cm depth in the Moor House long-term experiment. However, Clay et al. (2009b) did report a transient DOC peak 1 mo after a burn at Moor House. More recently, Clay et al. (2012) reported on soil solution DOC in surface runoff and in solutions in a chronosequence of plots burned at 1- to 2-y intervals during a 10-y period. This chronosequence yielded 8 burn 'ages' since last burned. The most recently burned plots had soil solutions (collected from 40–70 cm depth) that were more colored (measured by ultraviolet [UV] absorbance at 400 nm) than solutions from older burned plots, but had lower DOC concentrations, suggesting an influence of burning on DOC composition rather than

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concentration. No effect on DOC and water color was discernible in surface runoff (Clay et al. 2012).

Most upland peatlands are inherently nutrient poor, and a consequence of vegetation burning may be a release of nutrients via ash or root decomposition, or even volatilization. However, surprisingly few data are available on the effects of fire on peat chemistry other than DOC. Rosenburgh et al. (2013) measured a suite of surface peat chemical properties in a chronosequence of plots burned 2 to 20 and >40 y previously at 3 separate Peak District sites. All plots were situated on a mixture of deep peats and organo-mineral soils with a surface peat horizon of \geq 50 cm. No burn effects were consistent across all 3 sites except a slight decrease in C:N between plots burned <20 y and those burned >40 y ago. The authors attributed this result to enrichment from atmospheric N deposition or losses incurred during burning of younger plots. Trends in other variables, notably available P, exchangeable Ca, and total K, varied among sites; e.g., available Ca decreased at one site and increased at another (Rosenburgh et al. 2013).

Several investigators have reported the effects of wildfire on C losses from peat soils (Page et al. 2002, Benscoter et al. 2011b, Turetsky et al. 2011a, 2015) attributable to volatilization. However, these data must be interpreted cautiously, particularly in afforested peatlands on shallow peaty horizons that are variable in depth, because combustion during fire is spatially variable (Benscoter and Wieder 2003). Studies of the effects of fire on other aspects of peat biogeochemistry are still rare, in part because of the challenge of interpreting soil chemistry and other ecological indicators in the absence of baseline prefire data. In one study of wildfire in the Florida Everglades where prefire data existed, Smith et al. (2001) observed markedly different effects on soil C, N, and P concentrations in areas where only above-ground vegetation had burned (surface fire) compared to areas where the fire had burned into the peat (peat fire). Peat fire caused a physical concentration of total Ca and P in

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the top 2 cm of soil that was attributed to their resistance to volatilization relative to the bulk of organic matter, particularly C and N. In addition, the form of P changed significantly from organic P to an inorganic and more bioavailable form after peat fire. This result suggests that wildfire may fundamentally alter the conditions for plant growth postfire. Smith et al. (2001) observed only minor changes in soil constituents in areas where only the surface vegetation had burned, a situation that could be regarded as similar to prescribed vegetation burning.

Even if C is not completely volatilized by fire, experimental evidence suggests that C, and more importantly N, may be transformed from a relatively labile form to increasingly recalcitrant forms with increasing severity of burn (Almendros et al. 2003, Clay and Worrall 2011). Mild heating conditions (350°C for 60 s) caused the release of relatively reactive, low-molecular-weight compounds from the breakdown of large complex molecules, but with successive heating stages lasting for up to 180 s, aromatic compounds and new N-containing heterocyclic structures formed that were not present in the original peat (Almendros et al. 2003). Other studies have reported increased polycyclic aromatic hydrocarbon content of soils after burning (Vane et al. 2013).

Overall, the evidence suggests that effects of fire on soil biogeochemistry are likely to be minor when surface vegetation is burned and much more profound when peat burns. Increasing severity of peat fire may result in increased bioavailability of P and decreased bioavailability of N. Fire also may cause a change in the characteristics of dissolved and peatmatrix C toward more aromatic and colored compounds. However, firm conclusions are difficult to draw because of the paucity of available evidence.

River hydrology and sediments

Despite significant effects of burning on soil hydrology and concerns among some residents of flood-affected areas below peatlands that are routinely managed by prescribed

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burning, only one study has examined the effects of burning on river flows. Holden et al. (in press) showed that storm lag times and hydrograph recession limb periods were significantly greater in burned than unburned catchments overall, probably because of deeper water tables and a reduction in overland flow occurrence in burned than in unburned peatlands. Thus, the potential effect of reduced vegetation cover on overland flow velocity described earlier may be minimized because the propensity for saturation is reduced in burned catchments. However, the storms that had rainfall totals in the top 20% of those analysed were associated with significantly greater hydrograph intensity (peak discharge divided by total storm discharge) in burned than in unburned catchments. Thus, for the larger-volume rainfall events, when full saturation of the peat occurs even in burned systems, overland flow velocities may be increased by reduced moss cover and reduced vegetation density. Further studies are needed of the effects of peatland burning on river flow, but evidence to date suggests a complex, nonlinear response.

Our knowledge of responses of river sediments to fire is derived from studies of pollutant release after peatland wildfires, and mainly as contextual information from studies of benthic biota. Wildfires strongly affect sediment loads in peatland rivers because removal of vegetation exposes large expanses of soil to erosion, particularly during intense rainfall events (Rothwell et al. 2007, Page et al. 2009). River reaches in burned catchments often have substrates composed of more deposited fine organic sediments than river reaches in unburned catchments. For example, Ramchunder et al. (2011) and Brown et al. (2013) both found higher mean concentrations of fine particulate organic matter (FPOM; up to $4\times$ higher), and coarse POM (CPOM; up to $3\times$ higher) in burned than in unburned rivers. Elevated amounts of organic matter (predominantly peat particles) in headwater reaches of burned UK peatland rivers are likely because many 1^{st} -order river reaches are small and incised into the peat, and heather burning is undertaken relatively close by. Thus, the

resulting fines eroded from exposed soils are easily transported to and deposited in these rivers. Sediment mobilization and deposition in rivers after prescribed burning on UK peatlands appears to be a low-intensity, semicontinuous process that contrasts markedly with higher and more acute sediment inputs to rivers that occurs during rainfall events that follow wildfires on peatland (Rothwell et al. 2007) and in other environments (Ryan et al. 2011).

River biogeochemistry

Despite significant interest in the effects of prescribed burning on surface runoff and soil water chemistry, very few investigators have examined its effects on DOC in rivers. Many headwater rivers draining peatland in the UK are used for abstraction by water-utility companies, but DOC concentrations that exceed certain levels can cause problems in the treatment process by producing carcinogenic disinfection by-products (Gough et al. 2014). Several investigators have identified causal relationships between historic water-quality records or limited field samples and catchment burning intensity and coverage (Grayson et al. 2008, Yallop et al. 2008, 2010, Yallop and Clutterbuck 2009, Clutterbuck and Yallop 2010). Holden et al. (2012) carried out a critical synthesis of the effects of prescribed burning on DOC at the catchment scale from these and other studies and suggested that, based on the available evidence, prescribed burning increases river water color and DOC.

In contrast to the results gleaned from the larger-scale and historic approaches described above, O'Brien et al. (2008) found no statistically significant difference in riverwater DOC between a catchment where burning continued and one where it had been discontinued for <3 y, a period that probably is too short for detection of a clear signal because of the relatively slow (re-)growth rates of vegetation in these environments. Chapman et al. (2010) also failed to find a link between burning and DOC, but their study was limited to several adjacent subcatchments and was not undertaken to examine the effects

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of burning. Despite apparent links between rotational burning and increased river-water DOC, Holden et al. (2012) suggested that increases in prescribed burning are difficult to reconcile with increases in river-water color and DOC (Roulet and Moore 2006), and disentangling the effects of burning from those of changes in vegetation is difficult with currently available data sets.

Most studies of peatland river biogeochemistry were focused on DOC, and data on other chemical changes in rivers are fewer and predominantly contextual, e.g., data collected in studies of changes in river biodiversity. For example, Ramchunder et al. (2013) found higher concentrations of Al, Fe, and DOC but lower concentrations of major anions in 3 burned than in 3 unburned catchments studied approximately quarterly over an 18-mo period. Brown et al. (2013) also found higher Al and Fe concentrations in 5 burned than in 5 unburned catchments over a study of similar length. Elevated concentrations of Mn can be characteristic of burned river systems (Brown et al. 2013), an effect hypothesized to be a consequence of increased soil temperatures after removal of vegetation by fire and subsequent stimulation of microbial Mn production (Heal 2001). These studies point to an effect of burning on river-water chemical species other than C, but research at higher temporal resolution is needed to test this hypothesis.

River biota

Rotational burning of peatlands and resulting alterations to the environmental properties of burned catchments have been associated with changes in the structure and composition of northern UK river macroinvertebrate communities. Four common findings in rivers in burned catchments are reduced taxonomic richness and diversity and increased dominance of Chironomidae and Baetis spp. (Brown et al. 2013, Ramchunder et al. 2013), probably because these taxa tolerant of a wide range of environmental conditions and feed on

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FPOM, which is generally present in higher amounts in rivers draining burned than unburned catchments (Brown et al. 2013). Increases in Chironomidae relative abundance (27% in burned vs 9% in unburned) parallel the findings of studies of wildfire in nonpeatland systems. For example, in Yellowstone National Park, USA, collector–gatherers (predominantly Chironomidae and baetid mayflies) typically composed 40 to 60% of the macroinvertebrate assemblages in burned rivers but only 15 to 18% in an unburned reference site (Minshall et al. 2001). Richards and Minshall (1992) consistently found chironomids among the top 3 most abundant macroinvertebrate groups present in rivers affected by wildfire in Idaho, USA. Baetis spp. also occur in higher abundance in rivers subject to prescribed burning similar to wildfire-affected North American rivers than in unburned peatland rivers (Minshall et al. 2001, Minshall 2003). Thus, common geographically independent effects of fire on freshwater ecosystems and their macroinvertebrate assemblages seem to exist across the globe.

Another common effect of burning on macroinvertebrate assemblages in UK rivers is reduced abundance of some pollution-sensitive Ephemeroptera, Plecoptera, and Trichoptera taxa in rivers in catchments subjected to prescribed burning. An amalgamated data set assembled from 10 sites (5 burned vs 5 unburned) sampled in autumn 2008 (Ramchunder et al. 2013) and 10 sites (5 burned vs 5 unburned) sampled in autumn 2010/2011 (Brown et al. 2013) illustrates some comparable responses of macroinvertebrate communities to burning (Fig. 4). Brown et al. (2013) found higher relative abundance of Plecoptera at their study sites than Ramchunder et al. (2013) did at their sites, but relative abundance of Ephemeroptera was lower and Chironomidae were more abundant in burned than unburned sites in both studies. Furthermore, in a separate study comparing the macroinvertebrate assemblages of 30 northern Pennine peatland rivers, burned sites had lower proportions of Ephemeroptera, Plecoptera, and Trichoptera taxa than either unburned or eroded sites (Johnston 2012).

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Burned sites appear to have lower proportions of these sensitive taxa typically, with experimental manipulations hinting at strong effects of sediment and peat deposition on the river bed (Aspray 2012). Lower river pH and higher Al concentrations resulting from burning also are likely to be significant drivers of change (Ormerod et al. 1989, Brown et al. 2013).

Recent increases in our understanding of peatland river ecosystems provide an opportunity to evaluate earlier predictions about burn-related changes in the resource base and benthic macroinvertebrate functional feeding groups (Ramchunder et al. 2009; Fig. 5A– F). The lack of ecological studies in relation to peatland management prior to the late 2000s meant that Ramchunder et al. (2009) hypothesised responses based on general freshwater biological knowledge, and findings from studies of forest fires. The predictions of increased benthic detritus linked to removal of vegetation cover (Fig. 5A, D) and enhanced soil erosion, lower herbivore relative abundance caused by smothering of algal resources by deposits of fine sediment, and higher relative abundance of gatherers feeding on fine particulates, have since been largely upheld. Evidence is now available of significant increases in river bed particulate organic matter in burned catchment rivers (Brown et al. 2013, Ramchunder et al. 2013). However, contrary to predictions, some evidence indicates that benthic primary producers (measured as chlorophyll a) may be invariant or slightly elevated (Aspray 2012) in some burned rivers (Fig. 5B, C, D, F).

Hypothesised algal resource increases (biomass) may be a result of the observed loss of grazing invertebrates from burned rivers (Fig. 6), whereas decreases might be observed where the bed is affected by significant deposition of fines. Rivers draining burned catchments can exhibit low or 0 relative abundance of invertebrate herbivores, predominantly linked to the loss of sensitive grazing Ephemeroptera taxa. However, relative abundances of shredders typically are higher than expected (Fig. 5B, C, D, F), mainly because small stonefly species, such as Leuctrids and Nemourids, increase in burned systems. However, some

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authors have suggested that some of these taxa might not feed strictly on detritus in low-pH rivers, such as those found draining peatlands, because they have the ability to switch diets to include algae (Ledger and Hildrew 2000). Nemouridae in burned systems appear to benefit from the significant increase in the availability of benthic POM and lower pH because of their dietary flexibility, univoltine life history, small-body size. and ability to live in fine sediment burrows under conditions of relatively low pH (Brown et al. 2013). Increased Nemouridae abundances in peatland rivers draining catchments with prescribed vegetation burning are similar to responses seen in some burned forest systems (Vieira et al. 2011).

Predicted higher relative abundances of predominantly Chironomidae collectorgatherers in burned systems also have been seen across some of our studies (Aspray 2012, Johnston 2012, Ramchunder et al. 2013). Last, Ramchunder et al. (2009) expected that elevated concentrations of organic particles would increase collector-filterer populations. This effect has been observed in some of our studies (Ramchunder 2010, Ramchunder et al. 2013) but not others (Brown et al. 2013) and requires further examination (Fig. 6). To date, we have observed no fish in rivers draining burned catchments, and very few in unburned systems, results that might reflect low pH and overall community production. However, our efforts have been restricted to single deployments of baited traps, hand searches of netted-off river sections at the sites studied by Brown et al. (2013), and observations from incidental catches of C. gobio or unidentified juvenile fish in Surber samples. In summary, a body of recent evidence shows that prescribed burning of vegetation on blanket peatland leads to significant changes in the detrital resource base of peatland rivers which, coupled with changes in physicochemical stressors, leads to changes across the entire macroinvertebrate community.

SUMMARY AND FUTURE RESEARCH DIRECTIONS

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A growing body of evidence shows significant negative effects of prescribed burning and wildfire on peatland ecosystems (Worrall et al. 2010, Holden et al. 2012, Glaves et al. 2013). From our synthesis, we developed a conceptual schematic model of the interactions between fire and river-basin hydrology, chemistry, sediments, and river ecology (Fig. 7). Vegetation removal is central to observed hydrological changes in soils, which scale to influence river runoff through drying of the upper peat layers. For smaller rainfall events, the deeper water table associated with more recent prescribed burning results in less frequent occurrence of overland flow, longer streamflow lag times, and longer hydrograph recession limbs. However, for larger rainfall events where peat saturation is more widespread, river streamflow peaks are increased in burned catchments, probably because of removal of the rough understory of dense mosses and compaction of the peat. Thus, lateral flow through the near-surface zone is reduced in favor of overland flow. We expect these effects to have a larger effect on river flow as catchment coverage of recent burning plots increases (Holden et al. in press).

Our knowledge of how peatlands respond to fire has increased significantly in the last decade, but the effect of prescribed fires on hydrology remains poorly understood. Direct hydrological studies (Clay et al. 2009a, Holden et al. 2014), and studies using ecological indicators, such as soil dwelling testate amoebae (Turner and Swindles 2012), are required. A specific field of the hydrological sciences, for which we have knowledge from only 1 study, is how peatland river flows respond to fire. In particular, peak flows require examination because of their potential to influence downstream flood magnitude. Extrapolating flow from plot-scale run-off studies, where most studies of the effects of burning have been done, to the catchment-scale is difficult (Pattison and Lane 2012), and more catchment-scale studies are needed.

Evidence is emerging of indirect effects of prescribed vegetation burning on soil

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hydrology via changes in soil thermal regime (Brown et al. 2015) and generation of ash, which can block soil macropores (Holden et al. 2014). Hydrological alterations may interact with chemical and sediment erosion and transport processes (Fig. 7). Surface desiccation enhanced by deeper water tables during dry weather is a key mechanism for sediment production in blanket peatlands (Evans and Warburton 2007). Therefore, fire is likely to lead to enhanced sediment production, and although overland flow occurrence might be reduced on burnt peat, it still occurs during heavy rainfall events, thereby transporting the additional sediment across the peat surface. Without a dense vegetation cover to trap the sediment, enhanced sediment connectivity between slopes and streams may occur in burned peat systems.

The most consistent reported effect of burning on peat biogeochemisty is a change in the C quality of surface peat or DOM in peat pore waters. Coupled with the evidence of a change in peat thermal properties, this effect on C quality has important consequences for microbial cycling in the terrestrial–aquatic continuum and C budgets at the wider scale, and practical consequences for water-treatment companies for whom removal of DOC is a necessary and costly process. The efficiency of DOC removal treatments depends heavily on DOM quality, with hydrophobic components of humic and fulvic acids more readily removed than hydrophilic components, characteristics that are not readily ascertained by routine monitoring of DOC concentrations and color (Sharp et al. 2006). Changes in the quality of DOM also may have wider implications for the transport of metals in river systems and onward to the ocean, particularly of Fe and Al that are strongly reactive with hydrophobic DOM (hence they are used in water treatment to remove DOC). However, more work needs to be done to determine whether changes to C quality attributable to burning are long-lasting and to differentiate between burn effects and confounding environmental drivers, particularly increases in anthropogenic N deposition.

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The combined changes to river hydrology, chemistry, and sediment transport/deposition following vegetation burning, lead to altered river ecosystem structure and potentially to altered functioning (Fig. 7). These effects have become far better understood in recent years, particularly for benthic macroinvertebrate communities (Brown et al. 2013, Ramchunder et al. 2013). Despite suggestions that burning is associated with changes to river dissolved organic matter (Holden et al. 2012), we do not understand the effects of these changes on river microbial communities, or their processing of C (Fig. 7). Moreover, we have no information on responses of organisms, such as benthic algae or fungi. At the opposite end of aquatic food webs, the implications of changes in benthic macroinvertebrate communities for fish, birds, or amphibians have not been examined, and to date, no studies on the effects of peatland vegetation burning or wildfire on whole river functional responses have been published.

Most studies of responses of peatlands fire have been focused on relatively small headwater systems (i.e., <3 km²) because of their importance for water supply, C sequestration, tourism/recreation, and biodiversity (Bonn et al. 2010). However, we lack a clear understanding of the extent to which changes to these headwaters propagate downstream. A large proportion of upland rivers used as biomonitoring reference sites in the UK are downstream of managed peatlands (Ramchunder et al. 2009), but we do not know the extent to which these sites are affected by burning of vegetation. In addition, most studies have been undertaken in different catchments, over different timescales, and with different methods. As a result, direct comparisons and development of process understanding are hindered, and the policy-making process is beset with uncertainties (Glaves et al. 2013). With the limited resources available to researchers, more rapid progress could be made by establishing a network of field sites where researchers from different institutes work alongside each other toward a common goal.

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Prescribed fires are sometimes used to reduce the potential effects of wildfire or to remove vegetation ahead of peatland restoration efforts (Glaves et al. 2013). Little research has been done on the responses of peatland river basins to these approaches, but the effects are likely to be similar to those of burns undertaken for grouse moor management. Little evidence exists that prescribed removal of peatland vegetation actually does reduce wildfire risk because post-burning drying renders the peat more susceptible to wildfire (Glaves et al. 2013, Holden et al. 2014, Holden et al. in press). The limited number of studies of the effect of wildfire probably reflects a general lack of prewildfire data sets with which to compare impacts. Therefore, studies ought to be undertaken using spatial comparisons of wildfire vs unburned systems, especially given predicted increases in future wildfire occurrence (McMorrow et al. 2009).

Despite significant recent improvements in our knowledge of peatland river basin responses to fire, significant research gaps remain to be addressed. As the effects of burning become more evident, moorland owners, businesses such as water utilities, and government agencies, are increasingly requesting clearer information on which to base decision making. Therefore, addressing these research gaps is urgent and of great importance.

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ACKNOWLEDGEMENTS

This work was funded primarily via a grant to LEB, JH, and SMP as part of the EMBER (Effects of Moorland Burning on the Ecohydrology of River basins) project (UK Natural Environment Research Council [NERC] grant NE/G00224X/1, with additional support from Yorkshire Water [YW]). YW also funded several additional projects (to LEB, JH, SMP, and RG) on peatland river basin processes and management. Moors for the Future grant MRF0610 to KJ and LEB supported multisite studies of river ecosystems throughout the Peak District. Other studies related to fire and referred to herein were conducted as part of a NERC studentship quota award (NER/S/A/2006/14151) with CASE support from YW to SR, LEB, and JH, the North Pennines AONB Peatscapes project (ED1113347) to LEB and JH, Natural England (NE; SAE03-02-051) to LEB, and a NERC open CASE studentship award (NE/F/013663/1) with NE to LEB and JH with work undertaken by Katie Aspray.

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FIGURE CAPTIONS

- Fig. 1. River catchments in the South Pennines region of England showing fresh areas of prescribed burning (black patches) with charred and ashed vegetation, and patches of unburned vegetation (orange/red patches of heather) (A), and the aftermath of a wildfire, with a large area of burned vegetation across the entire foreground (B).
- Fig. 2. Changes in the density of Nemoura cambrica (A) and Perla bipunctata (B) along a continuum of peatland river sizes (1st-4th order). Data were collected from 3 reaches/river order over an 18-mo period (Ramchunder et al. 2011).
- Fig. 3. The number of publications/y (1950–2013) on the subjects of prescribed and wildfire on peatlands worldwide (A), prescribed vegetation burning in the UK uplands (B), and wildfire in the UK uplands (C). Searches for panel A were undertaken in Web of Knowledge on 30 January 2015 using the search term "PEAT* and FIRE not PALAEO". Data sources for Panels B and C were detailed by Glaves et al. (2013). Two references to work on Hard Hill burning plots, Moor House, had date ranges spanning multiple years and were omitted.
- Fig. 4. Relative abundance of major macroinvertebrate orders in Pennine rivers of northern England that drain burned (B) and unburned (U) peatland catchments (Ramchunder et al. 2013, Brown et al. 2013).
- Fig. 5. Comparison of river ecosystems in unburned (A–C) and burned (B–E) peatland river systems in the UK based on aerial photographs showing the difference in catchment vegetation cover of 2 similar rivers that flow northeast (A, D), the hypotheses of Ramchunder et al. (2009) (B, E), and updated versions based on the findings of recent studies of unburned and burned river systems (C, F). Det = detritus, PP = primary producers, G = grazers, S = shredders, CF = collector-filterers, CG = collector gatherers, IP = invertebrate predators.

- Fig. 6. Relative abundance of macroinvertebrate functional feeding groups in Pennine rivers of northern England that drain burned (B) and unburned (U) peatland catchments (Ramchunder et al. 2013, Brown et al. 2013).
- Fig. 7. Schematic summary of the main linkages and responses between hydrological, chemical, sedimentary, and river ecological properties and processes following removal of peatland vegetation with fire. ? denotes a hypothesized change (little or no current literature).

Table 1. Main vegetation complexes that are typical of upland blanket peatlands (Averis et al.

2004). NVC = National Vegetation Classification.

NVC	Dominant species	Bog type	Also often present
M15a	Tricophorum cespitosum–Erica tetralix	Flushed channels in blanket	Molinia caerulea, Eriophorum angustifolium,
		bogs and wet heaths	Carex spp.
M18	E. tetralix–Sphagnum papillosum	Blanket and raised bog	S. capillifolium, Sphagnum magellanicum, open
			canopy of Eriophorum spp., T. cespitosum, or
			Calluna vulgaris
M17	T. cespitosum–Eriophorum vaginatum	Blanket bog	Molinia caerulea, C. vulgaris, E. tetralix, Myrica
			gale, Sphagnum spp.
M19	C. vulgaris–E. vaginatum	Blanket bog	Vaccinium spp, Empetrum nigrum, abundant
			mosses including S. capillifolium and
			Pleurocarpus mosses
M20	E. vaginatum	Blanket and raised bog	Scattering of Vaccinium spp., E. nigrum, C.
			vulgaris, sparse mosses

Α













