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Organic sediment pulses impact rivers across multiple levels of ecological organization

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Abstract

Sedimentation is a pervasive environmental pressure affecting rivers globally. Headwaters draining catchments rich in organic soils (i.e., peat) are particularly vulnerable to enhanced sedimentation caused by land management and environmental change, yet many of the ecological consequences of peat deposition are poorly understood. We conducted a before-after-control-impact experiment in two rivers draining blanket peatland in Northern England to test the effect of sediment inputs on water quality, macroinvertebrate drift, macroinvertebrate community structure, and ecosystem metabolism. Sediment addition increased concentrations of dissolved organic carbon, total oxidised nitrogen and suspended sediment concentration in rivers, and intensified the total drift of macroinvertebrates particularly at night. By contrast, the abundance and richness of benthic macroinvertebrates were unaffected, except for declines in Coleoptera abundance in one river. The gross primary production of both rivers was strongly suppressed as the benthos was smothered by sediment. Community respiration also declined, albeit by different extents in the two rivers. Our experiment revealed that short-term pulses of organic sediment in rivers can have broad effects on water quality and biota, from influences on the dispersal of individual organisms to the modification of ecosystem processes. Organic sediments therefore warrant further examination, to include longer observation periods and more sites. It is particularly important to clarify the extent to which impacts extend from peatland streams into larger rivers downstream. Such studies are necessary to inform global management efforts to restore the integrity of river ecosystems under a range of water and biodiversity policy mechanisms.

KEYWORDS

drift, macroinvertebrate, metabolism, peat, primary production, respiration

1 | INTRODUCTION

Sedimentation is a major cause of ecological degradation in freshwater ecosystems, with artificially enhanced delivery and retention of fine sediments in rivers and lakes now a significant global problem (Dudgeon et al., 2006; Larsen & Ormerod, 2010; Piggott, Townsend, & Matthaei, 2015; Wood & Armitage, 1997). A range of policy mechanisms related to the protection of the water environment and wildlife require a better understanding of the scale, nature, and mechanisms of impact so that informed management strategies can be developed and implemented. European legislation provides a major impetus in the form of the Water Framework Directive and the Habitats and Species Directive. At a domestic level, riverine Sites of Special Scientific Interest add further motivation in the catchments within which they occur, whereas the UK's biodiversity strategy (Defra, 2011) requires restoration action for a range of priority habitats and species, including rivers and many riverine species affected by enhanced sedimentation.

Fine sediment impacts in rivers arise primarily as a result of local changes to catchment land use, intensification of land management, and external pressures such as climate change, all of which contribute to

erosion of soils and enhanced delivery to receiving freshwaters (Jones et al., 2012a; Wood & Armitage, 1997). Elevated fine sediment inputs can have profound, deleterious impacts on river ecosystems, via modification of channel geomorphology, substrate smothering, increased abrasive suspended loads, water quality, and, consequently, biodiversity (Kemp, Sear, Collins, Naden, & Jones, 2011; Wood & Armitage, 1997). Sedimentation has impacts that manifest across multiple levels of biological organisation, from individual organisms to whole-ecosystem processes. Impacts on individuals arise through altered physiology (oxygen concentrations) and behaviour (foraging efficiency and locomotion) that may promote emigration from degraded habitat. Alternatively, mortality and local extinction of sensitive species (Kemp et al., 2011; Wood & Armitage, 1997) can occur, with the remaining sediment-tolerant biota becoming unusually dominant (Larsen & Ormerod, 2010). Such marked shifts in community structure can impair key ecosystem processes for a variety of groups, including benthic algae and macrophytes (Izagirre, Serra, Guasch, & Elosegi, 2009; Jones, Duerdoth, Collins, Naden, & Sear, 2014), macroinvertebrates (Culp, Wrona, & Davies, 1986; Extence et al., 2013; Larsen, Pace, & Ormerod, 2010), and fish, especially salmonids (e.g., Greig, Sear, & Carling, 2005). As well as these direct pressures, sedimentation can elevate concentrations of metals, nutrients, and dissolved organic carbon (Bilotta & Brazier, 2008; Jones, Collins, Naden, & Sear, 2012b), which can further stress river ecosystems (Ramchunder, Brown, Holden, & Langton, 2011). An improved understanding of the interactions and linkages among sediments, water quality, and biological responses is needed to disentangle fully the mechanistic basis of river ecosystem changes caused by sedimentation and to improve management of the multiple stressors underlying ecological degradation (Mainstone, Hall, & Diack, 2016).

Impacts of sedimentation on ecosystem functioning are less well understood than those on individuals, populations, and communities. Nevertheless, sedimentation has the potential to profoundly alter ecosystem processes such as gross primary production (GPP), because increased turbidity and sediment deposition can smother benthic biofilms, thereby altering river metabolism (Gücker et al., 2008; Von Schiller et al., 2008). However, results of previous studies of river ecosystem function response to sedimentation are equivocal (Feio et al., 2010; Matthaei, Weller, Kelly, & Townsend, 2006; Nogaro, Datry, & Mermillod-Blondi, 2010), and further studies are needed to reconcile observed differences. Many studies of sediment effects on river ecosystem processes have been observational and conducted at the whole-catchment scale, where confounding environmental variability can limit the establishment of causation. Experiments addressing responses of ecosystem processes to sedimentation are still scarce (Feio, Alves, Boavida, Medeiros, & Graca, 2010; Gessner & Chauvet, 2002), although some have suggested that sediment deposition can suppress algal production (Suren & Jowett, 2001) but not detrital decomposition rates (Fairchild, Boyle, English, & Rabeni, 1987). To complement the many studies undertaken in experimental mesocosms (e.g., Jones et al., 2012a; Piggott et al., 2015; Suren & Jowett, 2001), manipulation at the scale of river reaches can provide further mechanistic understanding of ecological responses to sediment inputs, and thus better define relationships between sediment, river communities, and ecosystem processes.

Peatlands are areas of significant organic soil accumulation, but the low-bulk density of peat makes it extremely susceptible to erosion following catchment disturbances. Peatlands cover around 4 million km^2

of the Earth's surface, but their soils have been disturbed and exposed to erosional processes due to the removal of vegetation by fire or forest activity, permafrost degradation, overgrazing, peat cutting, and/or vehicle tracks (Brown et al., 2015; Campbell, Lavoie, & Rochefort, 2002; Kokelj et al., 2013). Frequent overland flows erode peat once it has been exposed and carry it to rivers during storms (Ellis & Tallis, 2001). In addition, peat can be added directly to river channels in significant quantities over short time periods by bank erosion and detachment of peat blocks or during slumping events (Evans & Warburton, 2005). Fine particulate organic sediment accumulations in peatland rivers have recently been associated with significant changes in macroinvertebrate biodiversity (Ramchunder, Brown, & Holden, 2012, 2013) and algal community change (O'Driscoll et al., 2013). However, these studies were correlational in design, and therefore, experimental studies are vital to properly attribute cause and effect. The only study of how peatland management affects river ecosystem functioning has focused on forest harvesting, with multiple environmental changes (solar radiation receipt, water temperature, and flow) linked to increased community respiration (CR; O'Driscoll et al., 2016). Controlled experimental manipulations of organic particulate supply are needed to understand the wider ecological effects of erosion, because in contrast to inert inorganic sands and silts, organic sediment has the potential to fuel heterotrophic metabolism by acting as both a substrate and by releasing nutrients as it decomposes (e.g., Mayer, Schick, Skorko, & Boss, 2006).

This paper reports the results of a manipulative experiment to quantify the short-term impacts of organic sediment inputs on the water quality and ecology of two peatland rivers in Northern England, scaling from populations and communities to ecosystem processes. A reach-scale approach was adopted with organic sediment addition used to simulate sediment influx events. Monitoring of water quality responses focused on nutrients (N,P) and dissolved organic carbon (DOC). At the community level, sediment impacts on macroinvertebrate behavioural drift and benthic assemblages were assessed. At the ecosystem scale, whole river metabolisms (net daily metabolism [NDM], GPP, and CR) were quantified to establish wider effects of sedimentation on functioning. We hypothesised (H_1) that organic sediment inputs would lead to the release of organic forms of carbon and nitrogen thus increasing river water concentration. Furthermore, we expected that (H_2) sediment deposition would trigger significantly increased macroinvertebrate drift as an avoidance behaviour (Larsen & Ormerod, 2010; Suren & Jowett, 2001) that would lead to (H_3) reduced benthic macroinvertebrate abundance and species richness (Matthaei et al., 2006). Finally, we hypothesised that (H_4) sediment smothering of algal biofilms would suppress GPP but stimulate CR via enhanced consumption of available particulate and dissolved organic matter by heterotrophs (Izagirre, Bermejo, Pozo, & Elosegi, 2007; Roberts, Mulholland, & Hill, 2007).

2 | METHODS

2.1 | Study site

Sediment addition experiments were conducted in two second-order tributaries (Moss Burn and Netherhearth Sike) of Trout Beck, North Pennines, UK (54°41′19.7″N; 2°23′01.7″W). The study area is located

TABLE 1 Mean contextual data for each reach and experimental period from Moss Burn and Netherhearth Sike

	Moss Burn				Netherhearth Sike			
	Control before	Control after	Impact before	Impact after	Control before	Control after	Impact before	Impact after
Air temperature (°C)	15.4	16.0	15.4	16.0	13.7	7.2	13.7	7.2
PAR (μmol·m^{-2}·s^{-1})	653.1	624.0	653.4	624.2	510.1	196.6	510.2	196.3
Velocity (m s^{-1})	0.10	0.10	0.08	0.07	0.11	0.13	0.11	0.12
pH	7.0	7.0	7.0	7.0	7.1	7.1	7.1	7.1
EC (μS cm^{-1})	79.9	79.9	89.1	89.1	72.7	72.8	85.3	86.3
DO (mg L^{-1})	8.2	7.9	8.1	7.5	8.6	9.3	8.4	8.9
Temp (°C)	16.2	16.9	16.2	16.8	14.1	10.7	14.2	10.7
Travel time (s)	280	270	190	150	260	260	225	225
Discharge (m^3 s^{-1})	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02

Note. DO = dissolved oxygen, EC = electrical conductivity.

at an altitude of 560 m in the Moor House National Nature Reserve, an area of open moorland characterised predominantly by *Calluna vulgaris*, *Vaccinium myrtillus*, *Eriophorum* spp., and *Sphagnum* mosses. Moor House has served as a major centre for upland research since the 1930s (Heal & Perkins, 1978), with the site being designated a nature reserve in 1952 and a World Biosphere Reserve in 1991. The underlying geology is a mix of limestone, shale, and sandstone with overlaying deep blanket-peat soils (Johnson & Dunham, 1963). The climate of Moor House is subarctic oceanic with a mean annual temperature of 5.3 °C between 1931 and 2006 (Holden & Rose, 2011) and mean annual precipitation of 2,012 mm (using full year records of 1951–1980 and 1991–2006).

The two rivers were chosen as they are typical of those on peatlands, with shallow stony beds dominated by boulders, cobbles, and gravel. The two rivers have similar water quality characteristics (Table 1) as they drain adjacent areas of blanket peatland. Both rivers were unshaded with riparian vegetation typical of many other upland headwater river systems. Some rivers within the wider nature reserve have been affected by fine sediment influx from peat erosion linked to vegetation loss (Evans & Warburton, 2005), but the two rivers chosen for experimentation were not receiving major inputs of fine sediment from upstream prior to the manipulation. The rivers also had no confounding effects of forestry activity, mining spoil, land drainage, or vegetation burning, and so they were chosen as examples of unimpacted "reference" rivers that would potentially respond to sedimentation.

2.2 | Experimental design

We used a before-after-control-impact (BACI) experimental design to test for the effect of sediment inputs in both rivers independently. Each experiment was conducted over 2 days in May 2010. Consistent with Larsen and Ormerod (2010), two 20-m reaches were identified in each river: an upstream "control" reach and a downstream "impact" reach, separated by 6 m of untreated river channel. Sampling for macroinvertebrates and metabolism was conducted in the control and impact reaches of each river before (Day 1) and after (Day 2) the sediment addition. Following pretreatment sampling on Day 1, ~0.5 kg m^{-2} of disaggregated organic sediment (peat) was applied evenly across the impact reaches, mimicking a relatively heavy influx of sediment covering ~55% of the bed. The treatment was consistent with ~75th percentile of

fine sediment cover reported in surveys of upland rivers in the UK (Aspray, 2012; Larsen et al., 2010). The inorganic content of the added peat was not quantified but typically is <10% (Green et al., 2011).

2.3 | Water quality and sediment processes

Water samples were collected in triplicate from the control and impact reaches before and after the sediment addition (total six samples per reach, 12 samples per river) to determine the extent of any release of nutrients or carbon and which might underpin changes in ecosystem metabolism. Each water sample was passed through a 0.45-μm Whatman cellulose nitrate filter and later analysed in the laboratory for nutrients (total N, total oxidised N [TON; i.e., NO_2^- and NO_3^-], and total P) and DOC. Additionally, 500 ml of unfiltered river water was collected to determine suspended sediment concentrations (SSCs) using vacuum manifold filtration (Jones, Duck, Reed, & Weyers, 1999). Contextual measurements of water temperature, electrical conductivity (EC), and pH were made on site to ensure that there were no major differences between reaches (Table 1). Water measurements were collected using an HQ40d portable multiparameter meter (Hach Lange, Düsseldorf, Germany). River flow velocity was measured throughout the experiment, with eight measurements taken randomly across each reach before and after sediment addition using a SENSA RC2 electromagnetic velocity sensor (OTT, Kempten, Germany). Measurements were taken from the bank to minimise disturbance to the substratum.

2.4 | Macroinvertebrates: behavioural drift and benthic biodiversity

Macroinvertebrate densities drifting in the water column were quantified at the downstream end of the control and impact river reaches before and after sediment addition. Samples were collected using two contiguous drift nets (dimensions 400 mm × 250 mm; 250-μm mesh) held by steel rods fixed in the riverbed. Drift nets were positioned at constrictions such that they filtered all river water flowing through the cross section of these small river channels (baseflow discharge was ~0.02m^3 s^{-1} in each river). This meant that there was no requirement to correct drift densities by the amount of water filtered through each net. Macroinvertebrates were retrieved from each net every 3 hr over the 48-hr period of monitoring each river. Drift

densities were presented as total numbers drifting per sampling period (Brittain & Eikeland, 1988).

Three benthic macroinvertebrate samples were collected from both control and impact reaches at the end of the before and after experimental periods using a modified Surber sampler (0.05 m^2 area, 250-µm mesh) and preserved immediately in 70% ethanol. Although three Surber samples are a minimal level of replication for characterising the benthos of headwater streams, the experimental design meant that it was necessary not to disturb these small stream reaches excessively by collecting larger numbers of replicates. Macroinvertebrates were sorted from debris, identified to the lowest practicable taxonomic unit—usually species, excepting Diptera and Oligochaeta; using Pawley, Dobson, and Fletcher (2011) and references therein—and counted.

2.5 | Whole river metabolism

Metabolism measurements were made using the open system dual station technique, which estimates a mass balance of dissolved oxygen (DO) along a river reach from the change in DO between two oxygen sensors, after accounting for reaeration (Demars, Thompson, & Manson, 2015; Demars et al., 2011). Measurements were taken simultaneously in the control and impacted river reaches for 24-hr periods before and after the addition of peat. DO and water temperature were sampled every 5 s and averaged every 15 min using Campbell CS512 Oxyguard Type III Dissolved Oxygen Sensors and Campbell 107-Thermistor temperature probes wired to Campbell CR1000 data loggers (all Campbell Scientific Inc., Loughborough, UK). Prior to deployment, the oxygen probes were calibrated in air at a known temperature and atmospheric pressure, and cross-calibrated in oxygen-saturated water (Campbell Scientific Inc., 2008). Contextual measurements of atmospheric pressure and photosynthetically active radiation (PAR) were measured over the same period, using a CS106 barometric pressure sensor (Campbell Scientific Inc., Loughborough, UK) and a Skye PAR sensor (Skye, Powys, Wales), respectively. Meteorological conditions were highly similar between experimental periods, with the exception of the after impact period for Netherhearth Sike (Table 1). This period experienced a decline in both mean air temperature (6.5 °C) and PAR (314 µmol·m^{-2}·s^{-1}).

Reaeration was estimated using the energy dissipation method (EDM; Grace & Imberger, 2006; Marzolf, Molholland, & Steinman, 1994). Although we were unable to compare the performance of the EDM to other reaeration methods in our study streams, the reaeration parameter serves only as a multiplier. Thus, the relative changes in metabolism can still be assessed using the BACI design. Whole-reach velocity (V) and slope (S) measurements taken at the site were multiplied by a discharge-dependant coefficient (K') to give an estimate of reaeration, EDM = $V \times S \times K'$ (Bott, 2006). Bankfull width was measured at 10 evenly spaced cross sections along the reach length and water depth measured at five intervals at each cross section. Discharge (Q) was estimated at the lower cross-sectional areas of each reach using the velocity–area method (Hauer & Lamberti, 2006). In addition, whole-reach velocity and time of travel of water were measured after the completion of the experiment using a dilute NaCl tracer, which was discharged upriver of the upper reach boundary. EC was logged concurrently every 10 s at the upriver and downriver reach boundaries,

then time of travel calculated from the time between the two peaks, and divided by reach length to give an average velocity and travel time (Grace & Imberger, 2006). The velocity–area method was used to calculate discharge at the downstream boundary of each reach.

Metabolism parameters were estimated from DO change along each reach, corrected for reaeration on the basis of the methods of Bott (2006) and modified subsequently by Demars et al. (2011). Whole-reach CR was estimated from nighttime changes in DO and extrapolated throughout the day. GPP and NDM were calculated from the change in DO and temperature between the downriver and upriver stations at time (t) and time plus travel time (tt). DO change was corrected for reaeration and multiplied by reach depth and sample interval to give areal estimates of GPP per time of travel. NDM was calculated as GPP-CR. GPP:CR was calculated to determine the trophic status of the river, with values <1 indicating net heterotrophic status. These estimates were made for each 15-min sampling interval and summed to provide daily GPP, CR, NDM, and an overall CR:GPP.

2.6 | Data analysis

Generalized linear models (GLMs) were used to compare BACI data (treatment, time period, and treatment × time period) for physicochemical variables using replicate sample data. Gaussian error distributions were specified for most tests, following examination of Q-Q plots, residual versus fitted plots, and histograms of residuals. For GLMs of count data, negative binomial error distributions were specified (O'Hara & Kotze, 2010). The differential for significant interactions was calculated from means of (Control After—Control Before)—(Impact After—Impact Before). Percent change was calculated by expressing the differential relative to the before × impact mean values of each parameter.

For macroinvertebrate drift, the samples formed a continuous time series; therefore, analyses focused specifically on differences calculated between control and impact reaches for paired time periods (e.g., control at 3 a.m.—impact at 3 a.m.), thus avoiding issues with temporal autocorrelation and pseudoreplication (James, Dewson, & Death, 2008; Larsen & Ormerod, 2010). Therefore, the GLM analyses compared control–impact (before) versus control–impact (after). If there were no impacts of peat addition, differences calculated between the two reaches would remain the same. Analyses compared (a) all sample data and (b) a subset of the samples collected over four sampling periods (19:00–04:00) corresponding with the nocturnal period when behavioural drift is typically highest (Brittain & Eikeland, 1988). Six macroinvertebrate drift composition metrics were calculated: (a) density (abundance per square metre); (b) taxonomic richness; (c) the abundance of the four most common macroinvertebrate orders in the benthos of these study rivers (Ramchunder et al., 2011): Ephemeroptera, Plecoptera, Diptera (Chironomidae), and Coleoptera.

To visualise changes in drifting macroinvertebrate community composition, non-metric multi Dimensional scaling (NMDS) was used to ordinate sample data. Macroinvertebrate densities were square root transformed, and the analysis was based on Bray–Curtis dissimilarities. To compare the composition of drifting macroinvertebrate samples, Bray–Curtis dissimilarities were calculated between control and impact
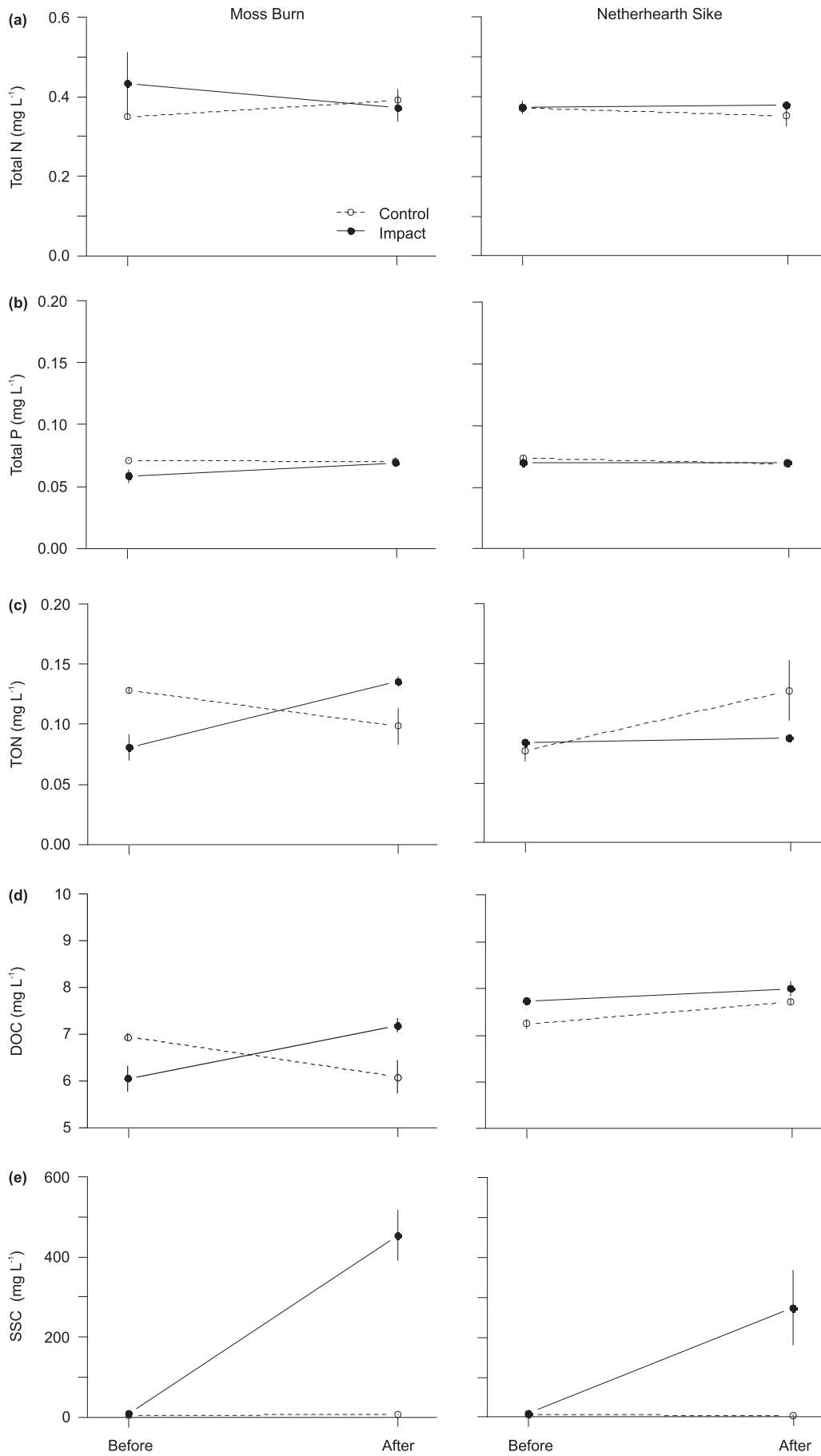
FIGURE 1 BACI interaction plots (Mean ± 1 *SE*) for water quality variables in Moss Burn and Netherhearth Sike. BACI = before-after-control-impact

reaches for paired time periods and GLM analyses used to compare control–impact (before) versus control–impact (after). The six macroinvertebrate community metrics used to describe drift samples were also calculated for the benthic community Surber samples and analysed using the same GLM approach as water quality parameters. Metabolism data were single estimates for each treatment and period; therefore, change between before and after periods in the two rivers was assessed only with interaction plots and calculation of differential values.

3 | RESULTS

3.1 | Water quality and sediment processes

The addition of fine sediment to Moss Burn led to significant increases in DOC, TON, and SSC (Figure 1; Table 2). In comparison, the addition of peat to Netherhearth Sike only led to a significant increase in SSC, the magnitude of which was lower than that in Moss Burn (Figure 1; Table 2).

3.2 | Macroinvertebrate behavioural drift

Forty-six macroinvertebrate taxa were found in the drift samples. *Leuctra inermis* (Plecoptera) were particularly dominant whereas, from the Ephemeroptera, *Baetis rhodani*, *Rhithrogena semicolorata*, and *Electrogena lateralis* were found in relatively high densities. *Oulimnius* spp. dominated from the Coleoptera, with *Esolus parallelepipedus*, *Oreodytes sanmarkii*, and *Elmis aenea* also prevalent.

Drift patterns exhibited diurnal variations over the 24-hr periods, with increases in total density and taxonomic richness at night (01:00–04:00), in both control and impacted reaches, both before and after treatment (Figure 2). Maximum drift abundance in any one 3-hr sampling period was 39 individuals (density = 1,950/m^3) and 12 taxa before the addition of peat but reached 125 individuals (6,250/m^3) and 19 taxa after the addition of peat (Figure 2). Drift density and richness increased immediately after the addition of sediment and continued to increase over subsequent nighttime samples (Figure 2). There

was a significant increase in the difference between control and impact drift abundance after sediment addition in Moss Burn but not Netherhearth Sike (Table 3; Figure 3). In contrast, analyses conducted on the nocturnal drift densities showed significant effects of peat addition in both rivers (Table 3).

The density of Plecoptera in the drift was significantly elevated across all samples following the addition of organic sediment to both rivers (Table 3; Figure 3). The analysis of nocturnal samples also revealed significant effects of sediment addition on the density of Coleoptera in Moss Burn and the density of Ephemeroptera in Netherhearth Sike (Table 3; Figure 3). The dissimilarity of drift composition between paired control and impact samples showed a change after sediment addition only for the full Moss Burn data set (Moss Burn: $t = 2.42$, $p = .03$). No changes were evident after sediment addition for the full data set in Netherhearth Sike ($t = 1.54$, $p = .15$) or the nocturnal sample periods after sediment addition in both rivers (Moss Burn: $t = 1.20$, $p = .28$; Netherhearth Sike: $t = 1.32$, $p = .24$). The NMDS analysis illustrated that the after sediment addition impact reach samples for Moss Burn were discrete from the control reach samples, plotting in the negative regions of Axis 1 (Figure 4b). These samples were characterised by elevated densities of *L. inermis*, *Polycentropus flavomaculatus*, and *Oulimnius* spp.

3.3 | Benthic macroinvertebrates

Benthic macroinvertebrate samples contained 47 taxa. Before the addition of peat, mean benthic densities were higher in impact reaches compared to the controls (Figure 5). The input of sediment reduced mean macroinvertebrate density in impact reaches, but control reaches were also reduced in the after period, and the time period × treatment interactions were not significant for either river (Table 2; Figure 5). There were no significant time period × treatment interactions for either river for all of the other five benthic macroinvertebrate community composition summary metrics with the exception of Coleoptera abundance in Netherhearth Sike, which declined by 66% (Table 2; Figure 5).

TABLE 2 Results of GLM analyses comparing water quality and benthic macroinvertebrate data sets for time period × treatment interactions

	Moss Burn			Netherhearth Sike		
	t	*p*	Differential	*t*	*p*	Differential
Water quality						
Total N (mgL^{-1})	−1.18	.27		0.68	.52	
Total P (mgL^{-1})	1.89	.096		1.40	.20	
TON (mgL^{-1})	4.52	.002	0.085 [+106%]	−1.80	.11	
DOC (mgL^{-1})	4.16	.003	1.99 [+33%]	−1.14	.29	
SSC (mgL^{-1})	7.21	.00009	443 [+4,643%]	2.84	.021	265 [+2,739%]
Benthic macroinvertebrates						
Density (per m^2)	−0.269	.79		−1.60	.15	
Richness	0.836	.43		−1.82	.11	
Ephemeroptera (per m^2)	−0.64	.54		−1.90	.09	
Plecoptera (per m^2)	1.64	.14		0.32	.76	
Chironomidae (per m^2)	0.88	.41		−1.21	.26	
Coleoptera (per m^2)	0.49	.64		−2.55	.034	−67 [−67%]

Note. Differentials are presented where interaction terms were significant at $p < .05$, with percent change calculated relative to before × impact values. GLM = generalized linear model, SSC = suspended sediment concentration, TON = total oxidised N.
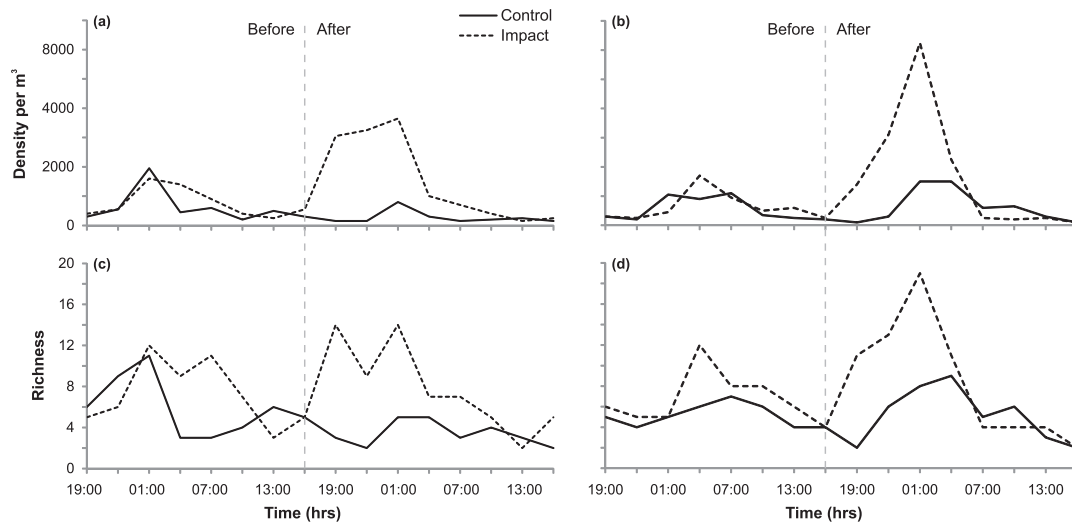
FIGURE 2 Time series of drift in control and impact reaches for 24 hr before and after sediment addition (denoted by dashed vertical line) for macroinvertebrate density in (a) Moss Burn and (b) Netherhearth Sike, and macroinvertebrate richness in (c) Moss Burn and (d) Netherhearth Sike

TABLE 3 Results of generalized linear model analyses comparing differences in drifting benthic macroinvertebrates for all data and for samples collected in the four sampling periods period after sediment addition (19:00–04:00)

	Moss Burn			Netherhearth Sike		
	t	*p*	Differential	*t*	*p*	Differential
All data						
Density (per m³)	2.21	.044	23 [+152%]	1.53	.15	
Richness	1.53	.15		0.94	.37	
Ephemeroptera (per m³)	0.97	.35		0.83	.42	
Plecoptera (per m³)	2.42	.029	11 [+326%]	2.79	.014	22 [2,200%]
Chironomidae (per m³)	−0.82	.43		1.71	.11	
Coleoptera (per m³)	2.08	.056		0.94	.36	
19:00–04:00						
Density (per m³)	3.52	.012	44 [+223%]	2.49	.047	47 [+348%]
Richness	2.38	.054		2.23	.07	
Ephemeroptera (per m³)	0.45	.67		2.53	.044	8 [+320%]
Plecoptera (per m³)	5.27	.0018	22 [+463%]	1.70	.014	16 [+1,067%]
Chironomidae (per m³)	1.80	.12		1.57	.17	
Coleoptera (per m³)	2.73	.034	14 [+144%]	1.38	.22	

Note. Differentials are presented where *p* < .05 and percent change calculated relative to before × impact values.

## 3.4 | Whole-river metabolism

All river reaches before and after sediment addition were strongly net heterotrophic (Table 4). GPP in both impact reaches was higher than control reaches before the addition of peat (+12% in Moss Burn and +3% in Netherhearth Sike; Table 4), but the input of sediment caused relatively rapid declines in both impact reaches (Figure 6 and 7). GPP was lower than that of the two control reaches throughout the subsequent 24-hr monitoring period (Figure 6) with a 54% mean decline in impact reaches compared to control reaches after the sediment influx (Figure 6; Table 4).

Before the addition of peat, CR was +64% higher in the Moss Burn impact reach compared to the control, but this difference declined considerably to only +6.5% after sediment addition (Table 4). For Netherhearth Sike, CR between the impact and control reach were similar before (−33%) and after (−35%) the addition of peat. Thus, the magnitude of the effect was considerably different between the two rivers (Figure 7). Overall, the changes in NPP and CR resulted in slightly reduced NDM in impact reaches after the addition of peat compared to before.

4 | DISCUSSION

Many headwater rivers are increasingly affected by sedimentation, including those draining peatland catchments, yet experimental studies
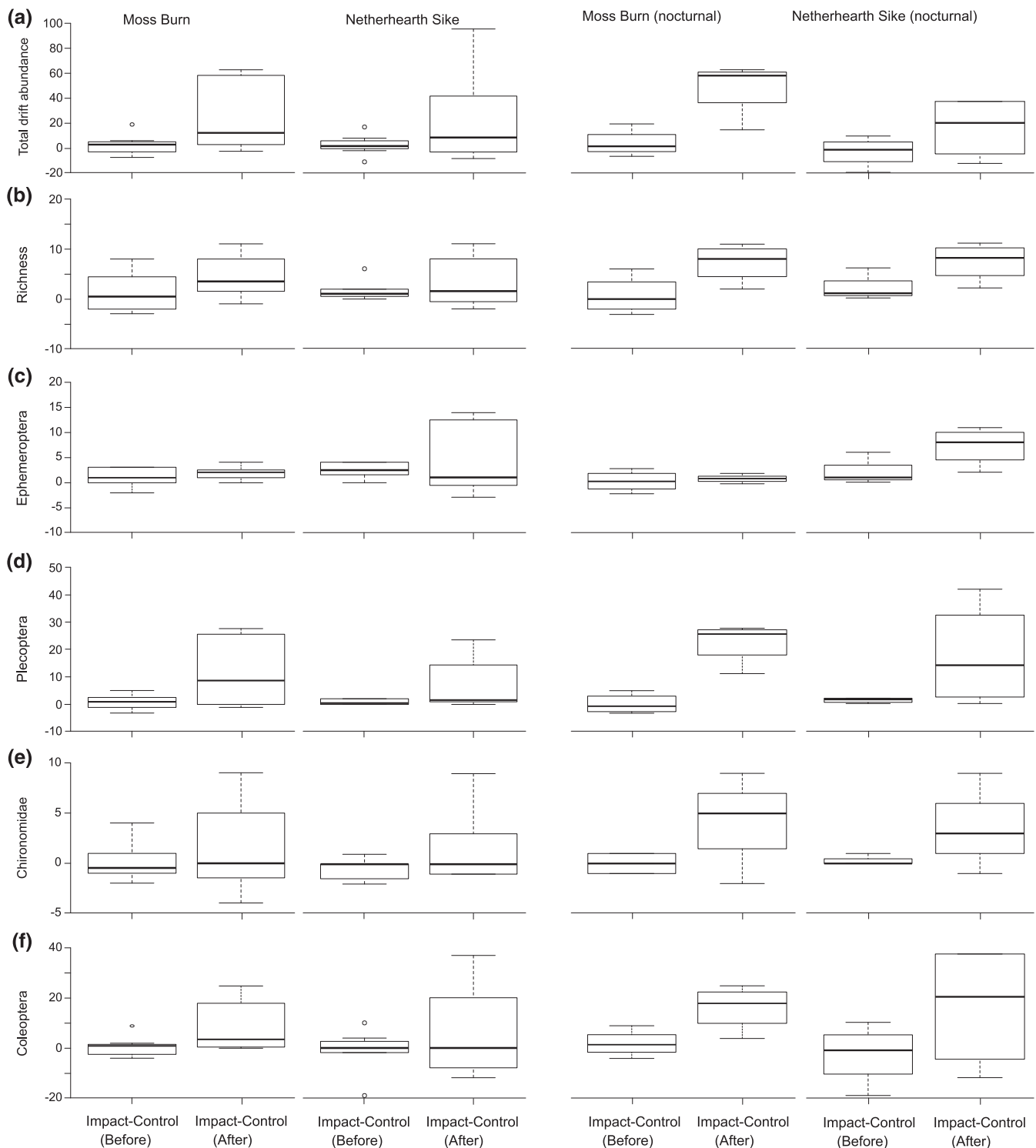
FIGURE 3 Boxplots showing differences (impact–control) in drifting macroinvertebrates, for all data and nocturnal samples only

examining the effect of organic sediment influx on populations, community structure, and functional processes in these river ecosystems remain scarce (Piggott, Lange, Townsend, & Matthaei, 2012; Piggott et al., 2015). Our experiment in two peatland rivers revealed that organic sediment influx can have immediate impacts on river water quality and across different levels of biological organisation (macroinvertebrate behavioural drift and whole river metabolism). Our results show how organic sediment influx impacts macroinvertebrate drift rates, benthic

macroinvertebrate communities, and whole-river metabolism, furthering general understanding of sediment impacts in river ecosystems.

4.1 | Water quality and sediment processes

Increased sediment loads can alter water quality in rivers, typically increasing nutrient and dissolved metal concentrations (Bilotta & Brazier, 2008). In our experiment, peat addition increased
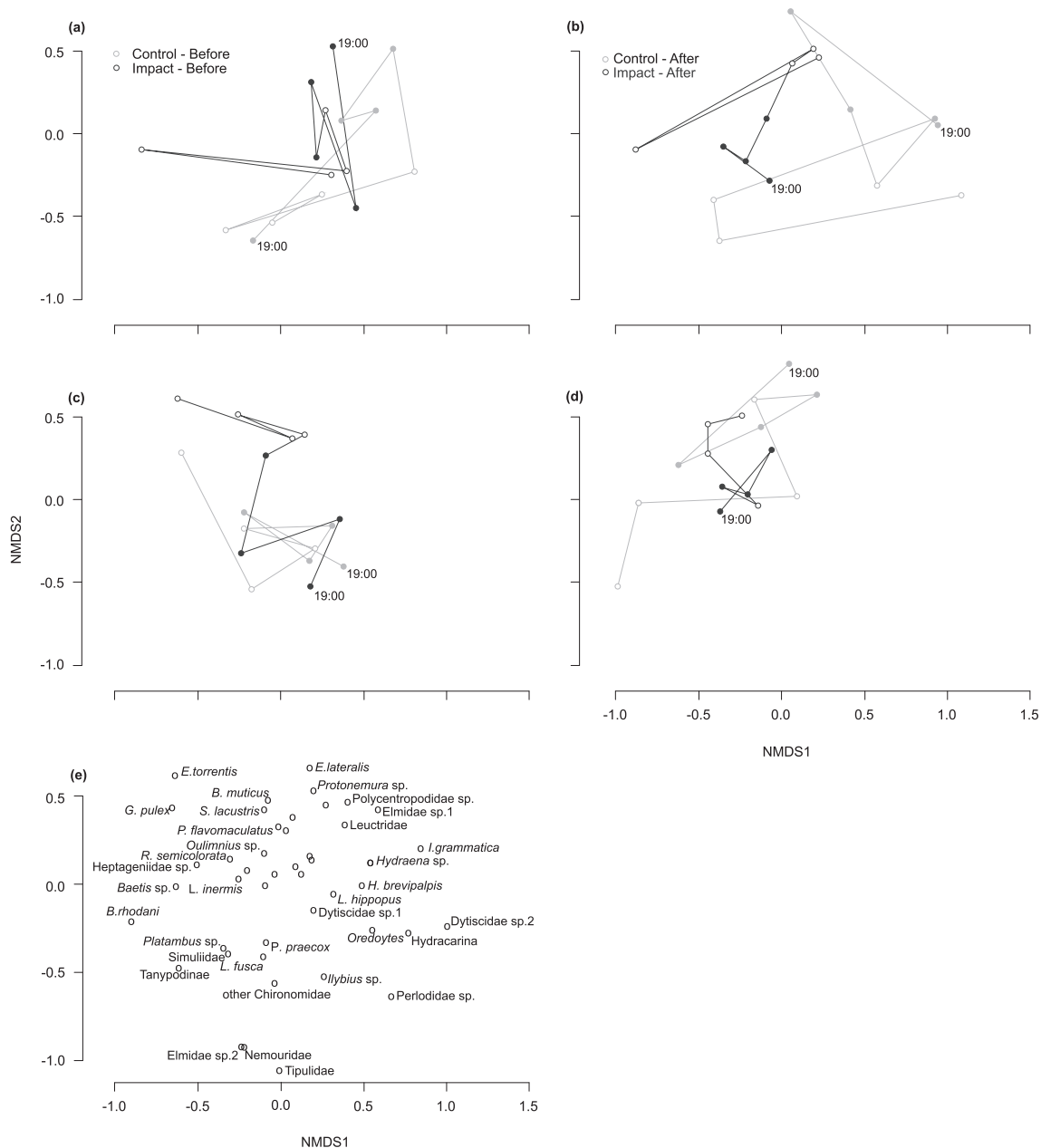
FIGURE 4 Nonmetric multidimensional scaling analysis of control and impact drift samples in Moss Burn (a) before sediment addition and (b) after sediment addition and in Netherhearth Sike (c) before sediment addition and (d) after sediment addition. Samples labelled with 19:00 denote the first sample collected in each 24-hr period. Nocturnal samples are denoted by filled circles. (e) The taxonomic biplot. Overall test stress = 0.13

concentrations of suspended sediment in both rivers, and DOC and TON in Moss Burn, consistent with H_1. Because the input of low-density peat to fast flowing upland rivers can lead to immediate downstream transport in suspension as well as significant localised sedimentation, we anticipate that these effects would likely occur throughout peatland river networks. Concentrations of river DOC have increased markedly in many regions over recent decades, including in freshwaters draining peatlands (Roulet & Moore, 2006). These increases have been linked to many drivers of change in the terrestrial landscape, including environmental warming, declining nitrogen deposition and acidity, altered vegetation cover, or management regimes such as prescribed vegetation burning and artificial drainage (Evans, Chapman, Clark, Monteith, & Cresser, 2006; Holden et al., 2007; Ramchunder, Brown, & Holden,

2009). Our finding in Moss Burn suggests that DOC increases could also be attributed to instream processing of eroded particulates (Palmer et al., 2015). Our observations also suggest that eroding peatlands could serve as a source of NO_3 (the dominant component of TON). This finding is supported by observations in other peatlands that have suggested that NH_4 released from eroding peatlands can be nitrified rapidly to NO_3 (Daniels, Evans, Agnew, & Allott, 2012).

4.2 | Macroinvertebrates: behavioural drift and benthic biodiversity

Our study revealed a typical diurnal pattern in macroinvertebrate drift abundance and density, which peaked at night. These drift patterns
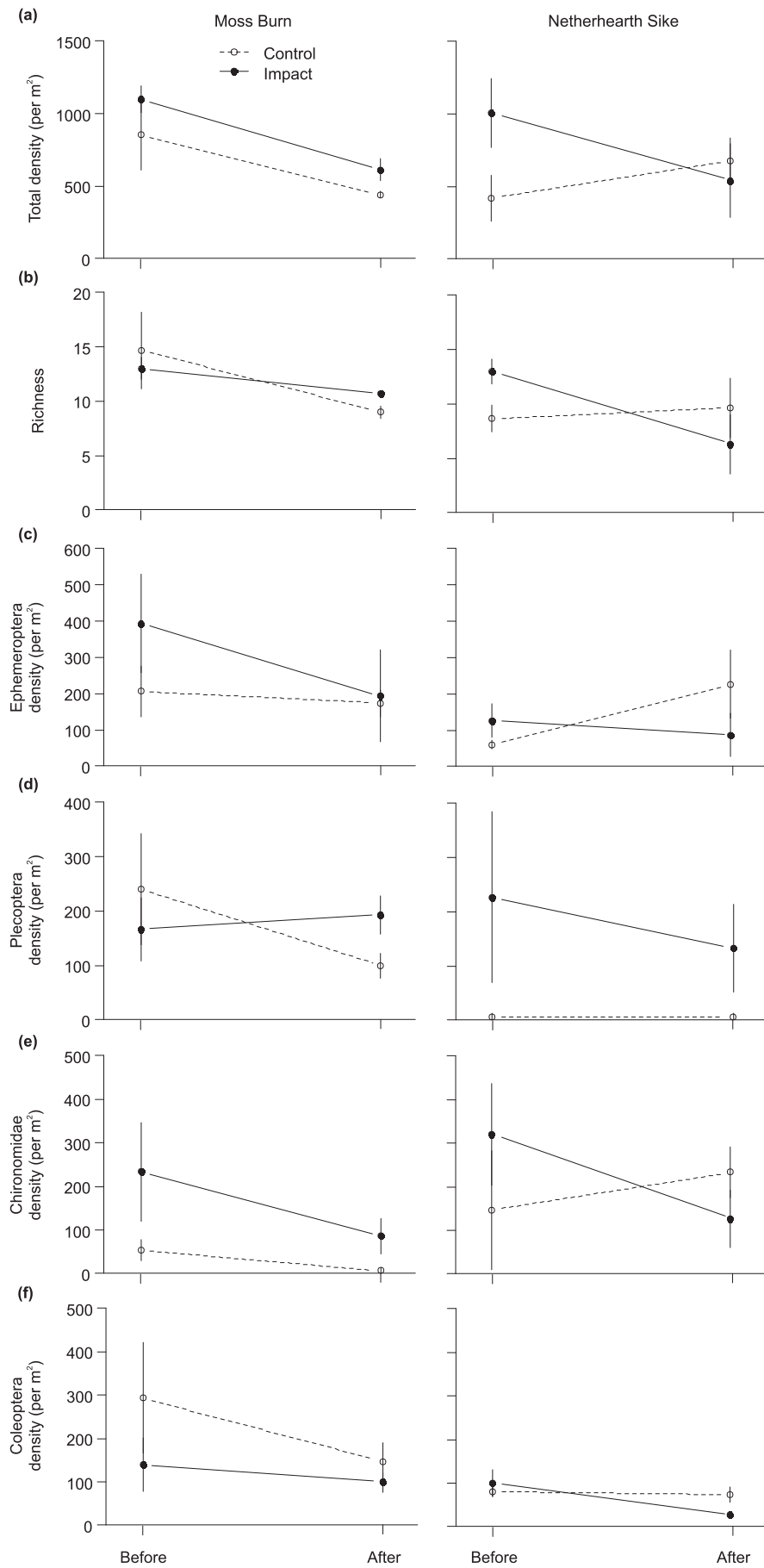
FIGURE 5 BACI interaction plots (mean ± 1 *SE*) for benthic macroinvertebrate community variables in Moss Burn and Netherhearth Sike. BACI = before-after-control-impact

TABLE 4 Gross primary production (GPP), community respiration (CR), and net daily metabolism (NDM) values for control and impacted reaches, before and after sediment additions

	GPP (gO^2·m^{-2}·d^{-1})	% difference	CR (gO^2·m^{-2}·day^{-1})	% difference	NDM (gO^2·m^{-2}·day^{-1})	% change	GPP:CR
Moss Burn							
Control before	2.4		11.4		−9.0		0.2
Impact before	2.7	+12.5%	18.7	+64%	−16.0	+77.0%	0.1
Control after	2.4		15.5		−13.3		0.2
Impact after	1.2	−50.0%	16.5	+6.5%	−15.1	+13.5%	0.1
Netherhearth Sike							
Control before	2.9		19.3		−16.0		0.2
Impact before	3.1	+7.0%	12.9	−33.0%	−9.7	+39.0%	0.2
Control after	2.6		18.4		−15.3		0.1
Impact after	1.1	−58.0%	11.9	−35.0%	−10.9	+28.0%	0.1

Note. Percent differences values are for impact relative to control reaches in the before and after periods.
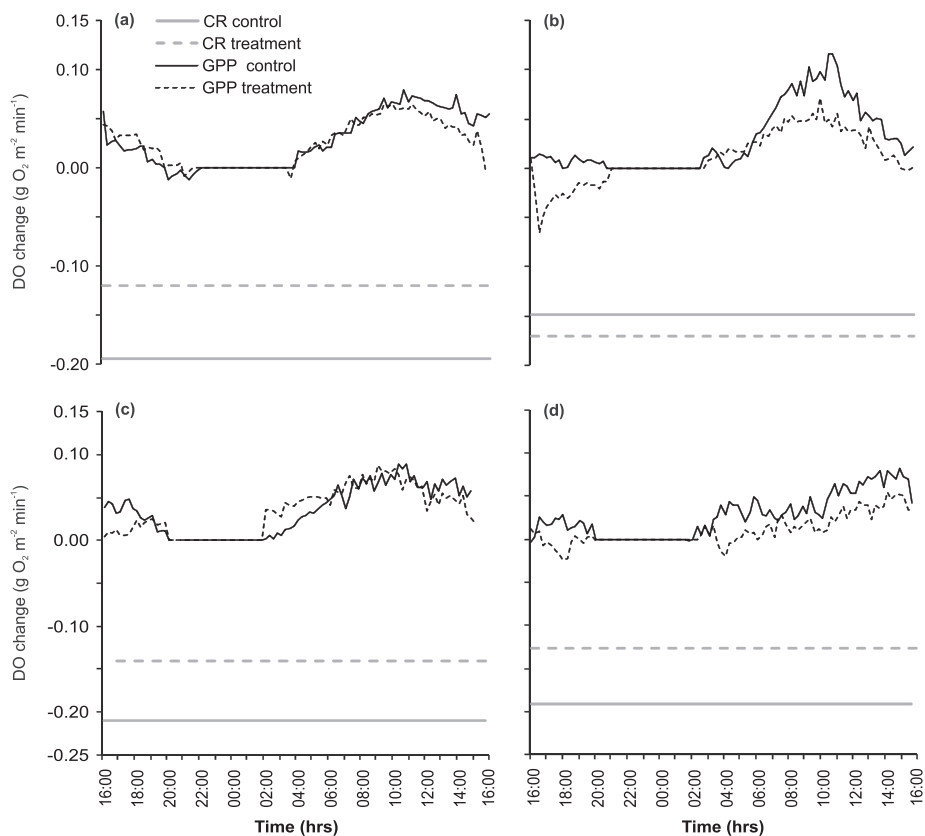
FIGURE 6 Diurnal variations in dissolved oxygen change between upstream and downstream monitoring stations in (a) Moss Burn before sediment addition, (b) Moss Burn after sediment addition, (c) Netherhearth Sike before sediment addition, and (d) Netherhearth Sike after sediment addition. The dual station oxygen method for calculating metabolism parameters assumes CR is invariable during the 24-hr periods and is averaged from overnight changes in DO. CR = community respiration; DO = dissolved oxygen

arise as a product of the behaviour of larvae in running water and includes active entry into the drift when foraging or to avoid competition (e.g., Brittain & Eikeland, 1988; Hildrew & Townsend, 1980). Consistent with H$_2$, we found that sediment addition significantly increased the density of drifting animals in Moss Burn for up to 24 hr and in both rivers at night when the effect was especially pronounced. Increased drift in response to sedimentation is a commonly reported phenomenon (Culp et al., 1986; Larsen & Ormerod, 2010; Suren & Jowett, 2001).

Observed increases in drift within 3 hr of peat addition may be indicative of avoidance behaviour by macroinvertebrates in response to the smothering effect of sediment settling onto the predominantly stony surface of the riverbed and the abrasive action of suspended sediment particles (Culp et al., 1986; Jones et al., 2012a; Piggott et al., 2015). However, the greatest and most significant increases in drift in this experiment were delayed for several hours following sedimentation, consistent with other experiments in mesocosms (Fairchild et al., 1987) and river reaches (Larsen & Ormerod, 2010). These
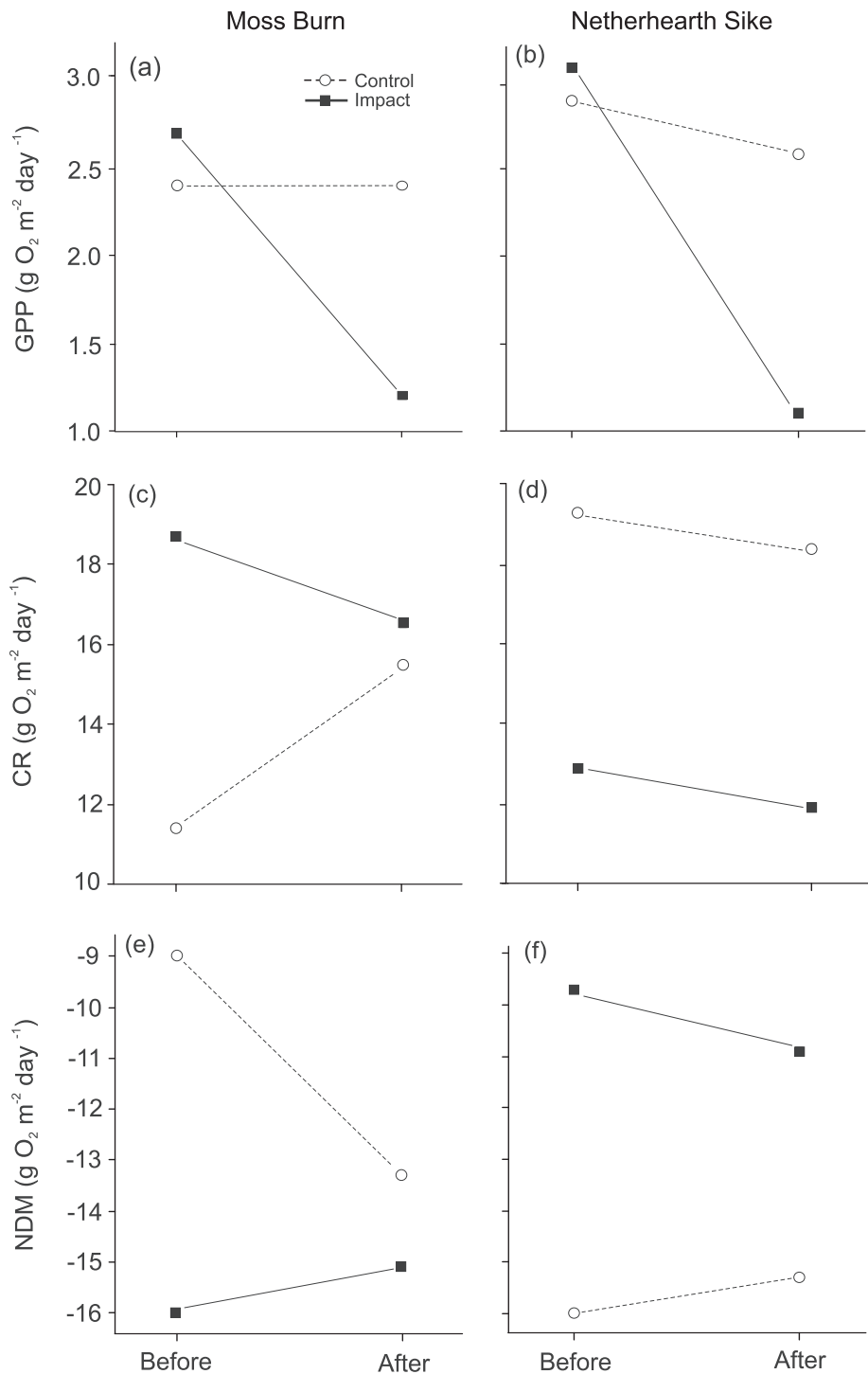
FIGURE 7 BACI interaction plots for (a and b) GPP, (c and d) CR, and (e and f) NDM before and after the addition of peat in Moss Burn and Netherhearth Sike. BACI = before-after-control-impact; CR = community respiration; GPP = gross primary production; NDM = net daily metabolism

delayed drifting behaviours following sedimentation likely reflect enhanced nocturnal active entrance into the drift, prompted by declines in habitat quality associated with the loss of interstitial habitat (Fairchild et al., 1987; Larsen & Ormerod, 2010; Suren & Jowett, 2001). Responses to sediments may also be lagged for macroinvertebrate taxa that move into surficial sediments at night (Culp et al., 1986).

Drift composition changed markedly after peat addition, driven by entrainment of Plecoptera, principally *L. inermis*. Plecoptera are intolerant of degradation in water and habitat quality and suffer increased

drift and/or decreased benthic abundance where sediment concentrations are high (e.g., Jones et al., 2012a; Larsen et al., 2010; Wood, Toone, Greenwood, & Armitage, 2005). Sand has been shown to affect Plecoptera species through feeding inhibition (Hornig & Brusven, 1986), as well as abrasion and changes in benthic habitat. However, this is the first time such immediate responses have been recorded following organic sediment influx. Where organic sediments decompose and consume DO, *Leuctra* often emigrate and show reduced abundance (Turley et al., 2016) due to their high-oxygen requirement.

Although water column DO concentrations did not fall significantly after organic sediment treatments were applied, smothering of the benthos could have led to significant reductions in interstitial flow rates, preventing the delivery of oxygenated water into these habitats. Previous work by Ramchunder et al. (2011, 2012, 2013) in peatland river networks has suggested a negative association between particulate organic sediments in the benthos and macroinvertebrate community composition, in river systems affected by artificial drainage and prescribed burning. Our study provides insights into the mechanisms by which fine sediment accumulation might have contributed to the alteration of aquatic biodiversity seen in these previous surveys.

With reference to our third hypothesis of reduced benthic macroinvertebrate abundance and richness and despite significant increases in drift following sediment addition, effects were limited to decreases of Coleoptera abundance in Netherhearth Sike. These results contrast with other experiments that reported significant declines in abundances of several benthic macroinvertebrate groups after the addition of sand to headwater rivers (Larsen & Ormerod, 2010). However, our results are more consistent with those of Fairchild et al. (1987) who found no effects of predominantly silt on benthic macroinvertebrate abundance and diversity in mesocosm channels, although Coleoptera were not considered in those experiments. The general lack of effect on benthic macroinvertebrate densities was probably due to a combination of the low number of replicate Surber samples collected (thus any "effects" being obscured by patch-scale spatial variability) and the duration of our experiments being short and missing drifting behaviour eroding benthic densities over several days. Alternatively, the results could indicate a degree of resistance to short-term sediment influx among some constituent taxa, or sediment deposition may have caused rapid mortality of some macroinvertebrates (Wood et al., 2005), which were then sampled, preserved, and counted from benthic samples. Organic sediments are lower in density than inorganic sediments, meaning that macroinvertebrates can typically avoid complete smothering, and some particles will also serve as a food resource for detritivores. Extended observational periods after the addition of sediment would provide a clearer picture of sediment influx effects on benthic communities and thus help to link experimental observations to long-term effect in rivers draining peatland catchments impacted by relatively continuous soil erosion and riverbed sedimentation (e.g., Ramchunder et al., 2012, 2013).

4.3 | Whole-river metabolism

GPP declined in impact reaches after the addition of peat, partially supporting H_4, despite increases in PAR between the before and after period in Moss Burn. This suggests that in-river processes linked to sediment addition were the primary drivers of change. The changes in meteorological conditions between the before and after period at Neatherhearth Sike were unlikely to have contributed to the lowered GPP rate in the impact reach because the dramatic decline was not replicated in the control reach. The decline in GPP in both rivers after the addition of peat provides supports for findings elsewhere in whole-catchment surveys (Izagirre et al., 2007; Roberts et al., 2007). Roberts et al. (2007) found GPP declined after storm events in a headwater river and attributed these changes to increased turbidity and abrasion.

Similar results were also found by Izagirre et al. (2007), with turbidity suggested as the main controller of GPP across rivers in northern Spain. Thus, declines in GPP seen in our study after the addition of peat could be due to a combination of abrasive sediment action, smothering of biofilm, and/or increased turbidity (linked to the significant increases in SSC) reducing light penetration and thus photosynthesis.

Contrary to H_4, increases in CR were not observed after the addition of peat. In fact, small declines in CR were quantified in impact reaches after the addition of peat to both rivers, consistent with Roberts et al. (2007) who reported declines in CR after storm events, attributable to a near complete reduction in autotrophic activity (estimated to contribute 20–50% of CR in their study) and a reduced respiration of stressed heterotrophs. It is possible that the decline in CR seen in the 24-hr period after the addition of peat was a result of the decreased activity of autotrophs, as shown by declines in GPP. Lagged increases in CR were observed by Roberts et al. (2007), attributed to delayed decomposition of organic matter delivered from the catchment. Increased CR has been reported following peatland deforestation in some Irish rivers (O'Driscoll et al., 2016); thus, it is likely that the short duration of our experiment was insufficient to capture such an effect. To test this hypothesis experimentally in peatland rivers will require longer periods of ecosystem function monitoring after the addition of organic sediments.

5 | CONCLUSION

Short-term sediment addition experiments have provided novel insights into the implications of sediment influx for headwater river ecosystems, showing notable changes to water quality, which may be different to inorganic sediments (e.g., release of organic forms of C and N with impacts on metabolism) and across different levels of ecological organisations (i.e., macroinvertebrate behaviour and functional processes). The functional processes that we examined have rarely been studied in peatland rivers, and so the effects seen on primary production point towards a need to increase our understanding of stressor effects with further experimental work and observational surveys (O'Driscoll et al., 2016). Furthermore, it is possible that the sediment influx would have longer term effects across different levels of ecological organisation. For example, if GPP remained low for prolonged periods after sediment addition, this may induce bottom-up effects through the benthic macroinvertebrate community and thus drive further emigration from affected study reaches. The delivery of organic sediments is also likely to benefit some detritivorous invertebrates, altering the relative role of "green" and "brown" energy pathways in aquatic food webs. The significance of the disturbances to the river mean that repeated and/or long-term exposure to sediment influx could lead to long-term impairment of rivers draining impacted peatland catchments (e.g., Brown et al., 2015). The prevalence of green energy pathways in upland rivers of the UK is itself a product of historic riparian tree removal though. Restoring the balance of tree cover and open reaches throughout upland river networks is a key conservation goal (Mainstone et al., 2016), and so further evidence is needed to understand the effects of organic sediment delivery from peatlands to

rivers where food web structure is reliant more on detrital energy pathways.

This experiment contributes to the growing body of knowledge regarding the impacts of sediment influxes on river ecosystems. The effects have the potential to be profound, manifesting themselves as changes to water chemistry, aquatic biodiversity, and ecosystem functioning. Changes to land use, management regimes, and impacts from acidification and climate change in river catchments have contributed to a continuing elevation in sediment delivery rates to river networks worldwide (Piggott et al., 2015; Wood & Armitage, 1997). Gaining an improved understanding of sediment effects on rivers is necessary for the conservation and restoration river habitats impaired by erosion and is becoming more imperative due to the widespread occurrence of catchment degradation and soil erosion. Our findings show that where significant quantities of fine organic sediments are delivered to river systems, effects can be expected throughout the whole aquatic ecosystem. Land managers should therefore take steps to limit organic sediment erosion and delivery to aquatic systems to prevent ecological impairment and thus increase resilience of aquatic communities throughout entire river networks.

REFERENCES

Aspray, K. (2012). Macroinvertebrate communities and ecosystem functioning in peatland streams. Unpublished PhD thesis. University of Leeds.

Bilotta, G. S., & Brazier, R. E. (2008). Understanding the influence of suspended solids on water quality and aquatic biota. *Water Research*, *42*, 2849–2861.

Bott, T. L. (2006). Primary productivity and community respiration. In G. Lamberti, & F. R. Hauer (Eds.), *Methods in stream ecology*). New York: Academic Press.

Brittain, J. E., & Eikeland, T. J. (1988). Invertebrate drift—A review. *Hydrobiologia*, *166*, 77–93.

Brown, L. E., Johnson, K. L., Palmer, S., Holden, J., Ramchunder, S. J., & Grayson, R. (2015). Effects of fire on the hydrology, biogeochemistry and ecology of peatland river systems. *Freshwater Science*, *34*, 1406–1425.

Campbell Scientific Inc. (2008). *CS512 Oxyguard type III dissolved oxygen sensor*. Loughborough: Campbell Scientific Ltd.

Campbell, D. R., Lavoie, C., & Rochefort, L. (2002). Wind erosion and surface stability in abandoned milled peatlands. *Canadian Journal of Soil Science*, *82*, 85–95.

Culp, J. M., Wrona, F. J., & Davies, R. W. (1986). Response of stream benthos and drift to fine sediment deposition versus transport. *Canadian Journal of Zoology*, *64*, 1345–1351.

Daniels, S. M., Evans, M. G., Agnew, C. T., & Allott, T. E. H. (2012). Ammonium release from a blanket peatland into headwater stream systems. *Environmental Pollution*, *163*, 261–272.

Defra (2011). *Biodiversity 2020: A strategy for England's wildlife and ecosystem services*. London: Department of the Environment, Food and Rural Affairs.

Demars, B. O. L., Manson, J. R., Ólafsson, J. S., Gíslason, J. M., Gudmundsdóttir, R., Woodward, G., … Friberg, N. (2011). Temperature and the metabolic balance of streams. *Freshwater Biology*, *56*, 1106–1121.

Demars, B. O. L., Thompson, J., & Manson, J. R. (2015). Stream metabolism and the open diel oxygen method: Principles, practice, and perspectives. *Limnology and Oceanography: Methods*, *13*, 356–374.

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z., Knowler, D. J., Lévêque, C., … Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, *81*, 163–182.

Ellis, C. J., & Tallis, J. H. (2001). Climatic control of peat erosion in a North Wales blanket mire. *New Phytologist*, *152*, 313–324.

Evans, M., & Warburton, J. (2005). Sediment budget for an eroding peat-moorland catchment in Northern England. *Earth Surface Processes and Landforms*, *30*, 557–577.

Evans, C. D., Chapman, P. J., Clark, J. M., Monteith, D., & Cresser, M. (2006). Alternative explanations for rising dissolved organic carbon export from organic soils. *Global Change Biology*, *12*, 2044–2053.

Extence, C. A., Chadd, R. P., England, J., Dunbar, M. J., Wood, P. J., & Taylor, E. D. (2013). The assessment of fine sediment accumulation in rivers using macro-invertebrate community response. *River Research and Applications*, *29*, 17–55.

Fairchild, J. F., Boyle, T., English, W. R., & Rabeni, C. (1987). Effects of sediment and contaminated sediment on structural and functional components of experimental stream ecosystems. *Water, Air, and Soil Pollution*, *36*, 271–293.

Feio, M. J., Alves, T., Boavida, M., Medeiros, A., & Graca, M. A. S. (2010). Functional indicators of stream health: A river-basin approach. *Freshwater Biology*, *55*, 1050–1063.

Gessner, M. O., & Chauvet, E. (2002). A case for using litter breakdown to assess functional stream integrity. *Ecological Applications*, *12*, 498–510.

Grace, M, & Imberger, S. (2006) Stream metabolism: Performing and interpreting measurements. Water Studies Centre Monash University, *Murray Darling Basin Commission and New South Wales Department of Environment and Climate Change*. Accessed at http://www.sci.monash.edu.au/wsc/docs/tech-manual-v3.pdf

Green, S., Baird, A., Evans, C., Ostle, N., Holden, J., Chapman, P. & McNamara, N. (2011) Investigation of peatland restoration (grip blocking) techniques to achieve best outcomes for methane and greenhouse gas emissions/balance. SP1202. Defra. London.

Greig, S. M., Sear, D. A., & Carling, P. A. (2005). The impact of fine sediment accumulation on the survival of incubating salmon progeny: Implications for sediment management. *Science of the Total Environment*, *344*, 241–258.

Hauer, R. F., & Lamberti, G. A. (2006). *Methods in stream ecology*. London: Academic Press.

Heal, O. W., & Perkins, D. F. (1978). *Production ecology of British moors and montane grasslands. Ecological Studies 27* (pp.428). Berlin Heidelberg: Springer-Verlag.

Hildrew, A. G., & Townsend, C. R. (1980). Aggregation, interference and foraging by larvae of *Plectrocnemia conspersa* (Trichoptera: Polycentropidae). *Animal Behaviour*, *28*, 553–560.

Holden, J., & Rose, R. (2011). Temperature and surface lapse rate change: A study of the UK's longest upland instrumental record. *International Journal of Climatology*, *31*, 907–919.

Holden, J., Shotbolt, L., Burt, T. P., Chapman, P. J., Dougill, A. J., Fraser, E. D. G., … Worrall, F. (2007). Environmental change in moorland landscapes. *Earth-Science Reviews*, *82*, 75–100.

Hornig, C. E., & Brusven, M. A. (1986). Effects of suspended sediments of leaf processing by *Hesperophylax occidentalis* (Trichoptera, Limnephilidae) and *Pteronarcys californica* (Plecoptera, Pteronarcyidae). *Great Basin Naturalist*, *46*, 33–38.

Izagirre, O., Bermejo, M., Pozo, J., & Elosegi, A. (2007). RIVERMET: An excel-based tool to calculate river metabolism from diel oxygen-concentration curves. *Environmental Modelling & Software*, *22*, 24–35.

Izagirre, O., Serra, A., Guasch, H., & Elosegi, A. (2009). Effects of sediment deposition on periphytic biomass, photosynthetic activity and algal community structure. *Science of the Total Environment*, *407*, 5694–5700.

James, A. B. W., Dewson, Z. S., & Death, R. G. (2008). The effect of experimental flow reductions on macroinvertebrate drift in natural and streamside channels. *River Research and Applications*, *24*, 22–35.

Johnson and Dunham (1963). *The geology of Moor House, a national nature reserve in North East Westmorland. Monographs of the Nature Conservancy 2*. London: HMSO.

Jones, A., Duck, R., Reed, R., & Weyers, J. (1999). Environmental analysis. In A. Jones, R. Duck, R. Reed, & J. Weyers (Eds.), *Practical skills in environmental science*)Prentice Hall.

Jones, J. I., Murphy, J. F., Collins, A. L., Sear, D. A., Naden, P. S., & Armitage, P. D. (2012a). The impact of fine sediment on macroinvertebrates. *River Research and Applications*, *28*, 1055–1071. https://doi.org/10.1002/rra.1516

Jones, J. I., Collins, A. L., Naden, P. S., & Sear, D. A. (2012b). The relationship between fine sediment and macrophytes in rivers. *River Research and Applications*, *28*, 1006–1018.

Jones, J. I., Duerdoth, C. P., Collins, A. L., Naden, P. S., & Sear, D. A. (2014). Interactions between diatoms and fine sediment. *Hydrological Processes*, *28*, 1226–1237.

Kemp, P. S., Sear, D. A., Collins, A. L., Naden, P., & Jones, J. I. (2011). The impacts of fine sediment on riverine fish. *Hydrological Processes*, *25*, 1800–1821.

Kokelj, S. V., Lacelle, D., Lantz, T. C., Tunnicliffe, J., Malone, L., Clark, I. D., & Chin, K. S. (2013). Thawing of massive ground ice in mega slumps drives increases in stream sediment and solute flux across a range of watershed scales. *Journal of Geophysical Research - Earth Surface*, *118*, 681–692.

Larsen, S., & Ormerod, S. J. (2010). Low-level effects of inert sediments on temperate stream invertebrates. *Freshwater Biology*, *55*, 476–486.

Larsen, S., Pace, G., & Ormerod, J. (2010). Experimental effects of sediment deposition on the structure and function of macroinvertebrate assemblages in temperate streams. *River Research and Applications*, *26*, 1–11.

Mainstone, C.P., Hall, R. and Diack, I. (2016) A narrative for conserving freshwater and wetland habitats in England. Natural England research report NERR064. Natural England, Sheffield.

Marzolf, E. R., Molholland, P., & Steinman, A. D. (1994). Improvements to the diurnal upstream-downstream dissolved oxygen change technique for determining whole stream metabolism in small streams. *Canadian Journal of Fisheries and Aquatic Sciences*, *51*, 1591–1599.

Matthaei, C. D., Weller, F., Kelly, D. W., & Townsend, C. R. (2006). Impacts of fine sediment addition to tussock, pasture, dairy and deer farming streams in New Zealand. *Freshwater Biology*, *51*, 2154–2172.

Mayer, L. M., Schick, L. L., Skorko, K., & Boss, E. (2006). Photodissolution of particulate organic matter from sediments. *Limnology and Oceanography*, *51*, 1064–1071.

Nogaro, G., Datry, T., & Mermillod-Blondi, F. (2010). Influence of streambed sediment clogging on microbial processes in the hyporheic zone. *Freshwater Biology*, *55*, 1288–1302.

O'Driscoll, C., de Eyto, E., O'Connor, M., Asam, Z. U. Z., Rodgers, M., & Xiao, L. (2013). Biotic response to forest harvesting in acidic blanket peat fed streams: A case study from Ireland. *Forest Ecology and Management*, *310*, 729–739.

O'Driscoll, C., O'Connor, M., Asam, Z. U. Z., de Eyto, E., Brown, L. E., & Xiao, L. (2016). Forest clearfelling effects on dissolved oxygen and metabolism in peatland streams. *Journal of Environmental Management*, *166*, 250–259.

O'Hara, R. B., & Kotze, D. J. (2010). Do not log-transform count data. *Methods in Ecology and Evolution*, *1*, 118–122.

Palmer, S. M., Evans, C. D., Chapman, P. J., Burden, A., Jones, T. G., Allott, T. E. H., … Holden, J. (2015). Sporadic hotspots for physico-chemical retention of aquatic organic carbon: From peatland headwater source to sea. *Aquatic Sciences*, 1–14. https://doi.org/10.1007/s00027-015-0448-x

Pawley, S., Dobson, M. & Fletcher, M. (2011) Guide to British freshwater macroinvertebrates for biotic assessment, Freshwater Biological Association, Scientific Publication No. 67., Ambleside, Cumbria. pp. 80

Piggott, J. J., Lange, K., Townsend, C. R., & Matthaei, C. D. (2012). Multiple stressors in agricultural streams: A mesocosm study of interactions among raised water temperature, sediment addition and nutrient enrichment. *PloS One*, *7*, e49873.

Piggott, J. J., Townsend, C. R., & Matthaei, C. D. (2015). Climate warming and agricultural stressors interact to determine stream macroinvertebrate community dynamics. *Global Change Biology*, *21*, 1887–1906.

Ramchunder, S. J., Brown, L. E., & Holden, J. (2009). Environmental effects of drainage, drain-blocking and prescribed vegetation burning in UK upland peatlands. *Progress in Physical Geography*, *33*, 49–79.

Ramchunder, S. J., Brown, L. E., Holden, J., & Langton, R. (2011). Spatial and seasonal variability of peatland stream ecosystems. *Ecohydrology*, *4*, 577–578.

Ramchunder, S. J., Brown, L. E., & Holden, J. (2012). Catchment-scale peatland restoration benefits stream ecosystem biodiversity. *Journal of Applied Ecology*, *49*, 182–191.

Ramchunder, S. J., Brown, L. E., & Holden, J. (2013). Rotational vegetation burning effects on peatland stream ecosystems. *Journal of Applied Ecology*, *50*, 636–648.

Roberts, B. J., Mulholland, P. J., & Hill, H. R. (2007). Multiple scales of temporal variability in ecosystem metabolism rates: Results from 2 years of continuous monitoring in a forested headwater stream. *Ecosystems*, *10*, 588–606.

Roulet, N., & Moore, T. R. (2006). Browning the waters. *Nature*, *444*, 283–284.

Suren, A. M., & Jowett, I. G. (2001). Effects of deposited sediment on invertebrate drift: An experimental study. *New Zealand Journal of Marine and Freshwater Research*, *35*, 725–737.

Turley, M. D., Bilotta, G. S., Chadd, R. P., Extence, C. A., Brazier, R. E., Burnside, N. G., & Pickwell, A. G. G. (2016). A sediment-specific family-level biomonitoring tool to identify the impacts of fine sediment in temperate rivers and streams. *Ecological Indicators*, *70*, 151–165.

Von Schiller, D., Marti, E., Riera, J. L., Ribot, M., Marks, J. C., & Sabater, F. (2008). Influence of land use on steam ecosystem function in a Mediterranean catchment. *Freshwater Biology*, *53*, 2600–2612.

Wood, P. J., & Armitage, P. D. (1997). Biological effects of fine sediment in the lotic environment. *Environmental Management*, *21*, 203–217.

Wood, P. J., Toone, J., Greenwood, M. T., & Armitage, P. D. (2005). The response of four lotic macroinvertebrate taxa to burial by sediments. *Archiv für Hydrobiologie*, *163*, 145–162.