Received: 31 May 2023 | Revised: 8 April 2024 | Accepted: 9 April 2024
DOI: 10.1002/eco.2654

RESEARCH ARTICLE

WILEY

Effects of natural flood management woody dams on benthic macroinvertebrates and benthic metabolism in upland streams: Importance of wood-induced geomorphic changes

Ho Wen Lo[1,2] | Megan Klaar[1] | Mark Smith[1] | Clare Woulds[1]

[1]School of Geography, University of Leeds, United Kingdom

[2]Earth and Environmental Sciences Programme, Chinese University of Hong Kong, Ma Liu Shui, Hong Kong

Correspondence
Ho Wen Lo, Earth and Environmental Sciences Programme, Chinese University of Hong Kong, Ma Liu Shui, Hong Kong.
Email: owenhwlo@cuhk.edu.hk

Abstract

Natural Flood Management (NFM) aims to reduce flood hazard by working with nature and is gaining prominence worldwide. One particular NFM technique involves the use of channel-spanning woody dams that maintain a clearance height above baseflow. These dams function by increasing channel roughness during high flows and by forcing excessive water onto the floodplain. Whether these dams provide additional benefits to nature remains unclear. While there are many existing studies on natural in-stream wood structures, very few have documented the impact of NFM woody dams in particular. This study adopted a multidisciplinary approach and a Before–After Control–Impact (BACI) research design to assess whether NFM woody dams installed in a small upland catchment had driven changes in benthic macroinvertebrate assemblages and benthic metabolic activities through the geomorphic changes that they had created. Statistical results indicate that macroinvertebrate density, richness, and diversity did not show any difference between stream reaches with and without NFM woody dams. The metrics were generally not related to grain-size parameters and volumes of sediments eroded or deposited. However, individual genera such as *Baetis* and *Rhithrogena* became more dominant in the control reach towards the end of the study period, likely due to the higher flow velocities and coarser sediments there resulting from the lack of flow resistance in the absence of NFM woody dams. Rates of benthic respiration (but not rates of photosynthesis) were consistently significantly higher in woody dam reaches than in control reaches, likely due to the presence of patches of finer sediments in the former.

KEYWORDS
BACI study, benthic macroinvertebrates, benthic metabolism, in-stream wood, Natural Flood Management

1 | INTRODUCTION

Natural Flood Management (NFM) refers to the use and promotion of natural processes to slow and store flood water and is becoming increasingly popular worldwide (Lane, 2017). One particular NFM intervention involves deploying woody dams that span the channel while maintaining a clearance height above baseflow (Figure 1a; the term 'NFM woody dams' is used hereafter to refer specifically to this

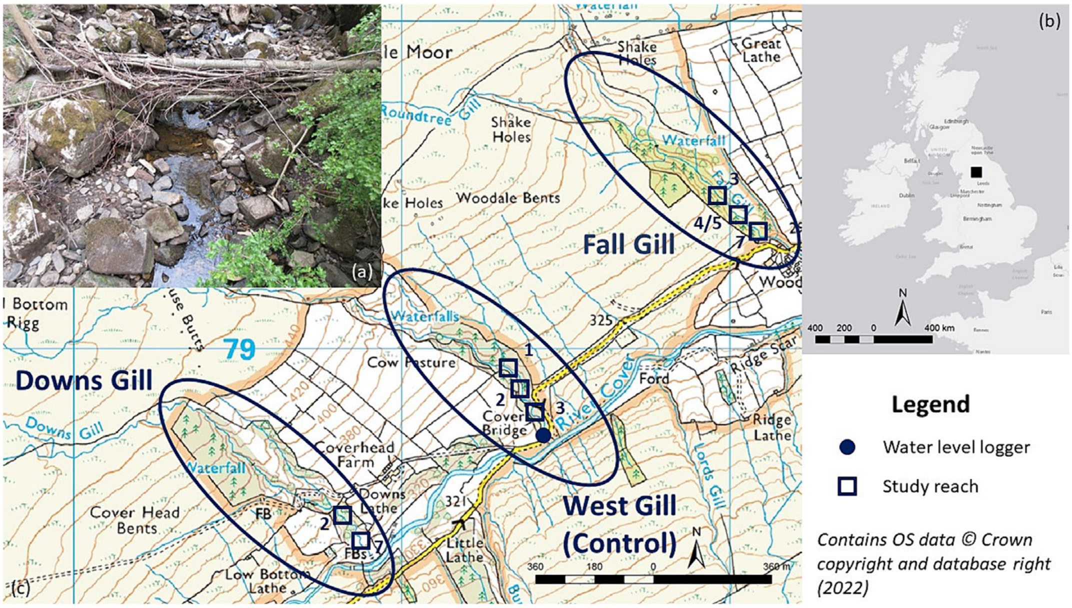


FIGURE 1 Details of the upper River Cover catchment – (a) example of a Natural Flood Management woody dam, showing its suspension above baseflow; (b) location of the catchment within the United Kingdom; (c) locations of intensively-monitored reaches shown in squares (woody dams on Downs Gill and Fall Gill numbered sequentially from upstream to downstream).

type of NFM wood structure). These dams increase flow resistance during high flows and divert excessive water onto the floodplain. Before further promoting the use of NFM woody dams, a full assessment of their potential benefits is required to evaluate whether they are beneficial for nature, including freshwater biodiversity and various ecosystem processes (Ellis et al., 2021; Lo et al., 2021). Freshwater biodiversity has been found to provide a range of ecosystem services (Durance et al., 2016). For example, benthic macroinvertebrates, through their position in the aquatic food chain, have implications for fisheries (Brittain & Sartori, 2009; Finlay et al., 2002; Stewart, 2009). Ecosystem processes such as metabolic activities have an impact on energy transfer and the global carbon cycle (Battin et al., 2009; Cole et al., 2007).

Natural in-stream wood has been found to positively influence aquatic macroinvertebrates (Benke & Wallace, 2003). First, the wood surface acts as a unique habitat for various functional feeding groups, including scrapers, collector-gatherers, and filter-feeders (Anderson et al., 1984; Collier et al., 2004; Collier & Halliday, 2000; Cudney & Wallace, 1980; Smock et al., 1989). Second, in-stream wood has been found to benefit macroinvertebrate communities (i.e., increased density and diversity) in the surrounding stream bed, because of wood-induced flow and substrate variability (Frainer et al., 2017; Magliozzi et al., 2019, 2020; Pilotto et al., 2014). Particulate organic matter such as leaf litter retained upstream of in-stream wood favours the colonisation of detritivores (Gerhard & Reich, 2000; Winkler, 1991).

It is unclear whether NFM woody dams are associated with the same benefits. Since NFM woody dams only come into contact with streamflow during flood events, their surfaces are not expected to be persistently colonised by aquatic macroinvertebrates (Lo et al., 2021). Moreover, NFM woody dams are not in contact with the stream bed, so they are unlikely to lead to the formation of distinct accumulations of particulate organic matter immediately upstream. However, they may still influence benthic macroinvertebrate communities through modifications of channel morphology. For example, they may buffer the stream bed against textural coarsening during flood events by offering extra flow resistance (Manga & Kirchner, 2000). The finer substrates typically found in stream reaches with woody dams may then support a macroinvertebrate assemblage distinct from that in reaches without woody dams (Reice, 1980). Textural fining may provide a greater surface area for the attachment of biofilms and organic matter (Sutherland, 1999), increasing the density of benthic macroinvertebrates by supplying them with alternative food sources (Kiffney et al., 2014). NFM woody dams may also enhance heterogeneity in the stream bed by creating pools (when water is forced underneath them) and deposition zones (for clasts larger than their clearance heights) in different parts of the channel (Lo et al., 2022). These channel units may be inhabited by different assemblages (Hilderbrand et al., 1997), resulting in a higher reach-scale diversity. Previous research by Deane et al. (2021) recorded responses of benthic macroinvertebrates to wood structures deployed for NFM, but the structures studied were more similar to natural accumulations that maintained contact with the stream bed. Moreover, only one stream was studied, with no data collected prior to wood input for comparison.

It has also been found that in-stream wood contributes to increases in reach-scale metabolic rates (Blaen et al., 2018). First, wood surfaces provide additional sites for the colonisation of heterotrophic microorganisms that degrade wood tissues as well as organic matter intercepted from the water column into carbon dioxide (Collier & Smith, 2003; Gulis et al., 2008; Tank et al., 1993). Second, in-stream wood favours the establishment of benthic macroinvertebrate communities, resulting in enhanced biological transformation of organic matter into carbon dioxide (Flores et al., 2013; Frainer et al., 2017). Third, in-stream wood also leads to increases in microbial metabolic rates in benthic sediments (Groffman et al., 2005; Hedin, 1990). Complete knowledge about the third mechanism appears to be still lacking, but it is likely the result of increased hyporheic exchange (Krause et al., 2014) and temperature variability under the presence of in-stream wood (Klaar et al., 2020).

Increased benthic metabolic rates in the presence of in-stream wood may also be the result of a cascade effect involving wood-induced changes in sedimentary characteristics. Changes in the *average* grain size drive changes in the available surface area for the attachment of organic matter, with patches consisting of finer grains normally having higher organic matter concentrations (Hargrave, 1972; Sutherland, 1999), hence sustaining higher rates of microbial respiration per unit stream bed area. Changes in the *variation* of grain size also lead to changes in benthic metabolism, with more heterogeneous stream bed areas associated with higher rates of benthic respiration and photosynthesis due to the creation of near-bed turbulence that would supply benthic biofilms with more nutrients and dissolved oxygen (Cardinale et al., 2002). The *stability* of grains also influences benthic metabolism, with streams dominated by mobile sand grains less colonised by benthic microorganisms and therefore having lower metabolic rates (Atkinson et al., 2008). Overall, the connection between sedimentary characteristics and benthic metabolism has been relatively well documented, but to date very few studies have examined how in-stream wood influences benthic metabolism through modifications of sedimentary characteristics. Since NFM woody dams are expected to buffer against stream bed coarsening during high flows (Lo et al., 2021), they are expected to influence biofilms and metabolic activities on benthic sediment surfaces.

These possible effects of the installation of NFM woody dams on benthic macroinvertebrates and benthic metabolism are currently not well documented in the extant literature. The aim of this paper is therefore to quantify these effects, with particular attention given to wood-induced geomorphic and sedimentary characteristics as possible mechanisms driving any biological change observed.

2 | METHODS

2.1 | Study site

The study site (upper River Cover catchment, Yorkshire Dales National Park, United Kingdom; Figure 1) has been previously described in detail in Lo et al. (2022). The lithology of the catchment is dominated by horizontally-bedded Carboniferous limestone (British Geological Survey, 2022). Towards the end of the Last Glacial Period, glacial meltwater carved the bedrock and gave rise to deeply-incised V-shaped valleys currently drained by headwater streams exhibiting step-pool morphologies (Yorkshire Dales National Park Authority, 2002). The current study focused on three such streams, namely Downs Gill, West Gill, and Fall Gill (Figure 1). Eight NFM woody dams were installed on Downs Gill and seven on Fall Gill between August and September 2018. No woody dam was built on West Gill, which served as the control stream.

2.2 | Benthic macroinvertebrates

A full Before–After Control–Impact (BACI; Underwood, 1992) research design was employed to isolate the effects of NFM woody dams on benthic macroinvertebrate communities from natural population fluctuations. A control stream was necessary for the quantification of natural changes that were unrelated to NFM woody dams (Figure S1).

Baseline sampling took place in spring (May and June) 2018 to reveal the structure of the benthic macroinvertebrate communities prior to the installation of woody dams. Three patches were sampled for each of the three control reaches on West Gill (Figures 1, 2). Five reaches that would later receive woody dams were selected for baseline sampling — two on Downs Gill and three on Fall Gill (Figure 1). These reaches were chosen such that the influence of confounding factors was minimised. For example, the hydraulic influence of boulders (Tritico & Hotchkiss, 2005) and channel banks at bends (Asahi et al., 2013) could be significant, rendering it difficult to isolate the effects of woody dams. Therefore, only locations within relatively straight and low-gradient sections were chosen. Bedrock-controlled sections were avoided because they were not expected to undergo substantial geomorphic changes (Wohl, 2015). Moreover, without bed sediments, it would be impossible to identify cascade effects on ecological and biogeochemical processes induced by changes in sedimentary characteristics. Six patches were sampled for each of these five reaches, except for the upper reach identified on Downs Gill, where 10 patches were sampled (Figure 2). Each reach was sampled once before dam installation. Because of the large number of study reaches, it was not possible to sample all of them within the same day, and baseline fieldwork was spread across two weeks between late May and early June 2018. We ensured that (antecedent) flow conditions were similar on the different dates of sampling.

A total of six NFM woody dams were eventually constructed on the five monitored reaches on Downs Gill and Fall Gill. They were, counting from upstream to downstream, the second and seventh dams on Downs Gill, and the third, fourth, fifth, and seventh dams on Fall Gill. The fourth and fifth dams on Fall Gill were constructed within the same reach (labelled ‘4/5’ in Figure 1). Three monitoring fieldwork campaigns were conducted in autumn (November) 2018, spring (May and June) 2019, and autumn (September) 2020. To minimise any possible seasonal effect, the original plan was to conduct the final fieldwork campaign in spring 2020, exactly one year after the previous monitoring survey and two years after the baseline survey. However, it was delayed to September 2020 because of COVID-19 restrictions. During each of these three fieldwork campaigns, benthic macroinvertebrates were collected from the three

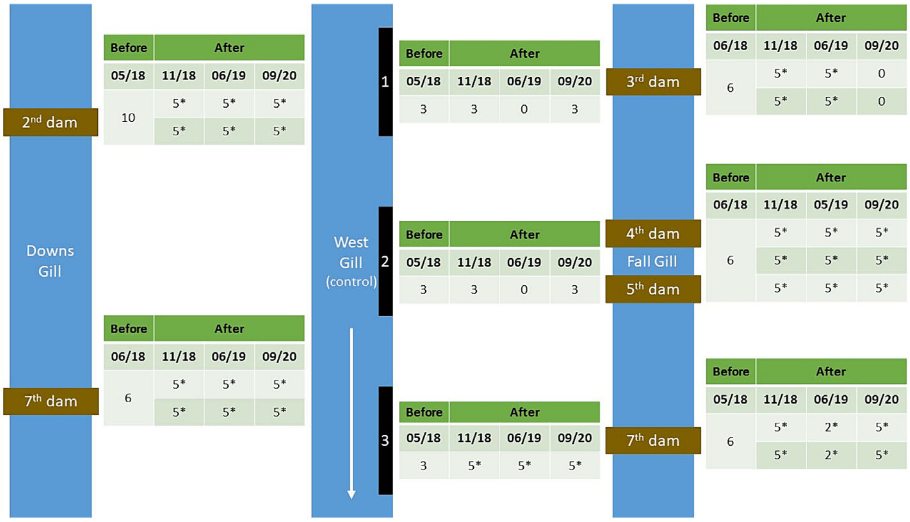


FIGURE 2 Schematic diagram showing the number of patches sampled for each study reach within each sampling season; asterisk (*) indicates that patch-scale variables were also recorded.

10 m control reaches on West Gill and the 10 m reaches upstream and downstream of the six closely-monitored woody dams. Attention was given to the 10 m within the NFM woody dams as most physical habitat changes were identified within this range (Lo et al., 2022). The reach upstream of the fifth dam on Fall Gill completely overlapped the reach downstream of the fourth dam, so there were 14 study reaches in total (five upstream of dams, five downstream of dams, one in between two dams, and three control reaches) following dam construction.

The target was to sample five patches for each 10 m reach. Exceptions included the top two control reaches, where fewer patches were sampled because of time and weather constraints. For the seventh dam on Fall Gill, samples for some patches in June 2019 were lost, so only two patches remained for both the upstream and downstream reaches. In addition, the third dam on Fall Gill had been displaced by high flows, and by September 2020, the dam had clearly integrated with the left bank and was no longer interacting with the active channel. Therefore, no macroinvertebrate sample was collected at this site in September 2020. Each study reach was sampled once within each season. Because of the large number of study reaches, it was not possible to sample all of them within the same day, and fieldwork was normally spread across two weeks within the same season. This explains why the spring 2019 survey covered May and June. We ensured that (antecedent) flow conditions were similar on the different dates of sampling within the same season.

At each patch, a Surber sampler (frame size: 0.1 m^2; mesh size: 250 μm) with the net extending in the downstream direction was deployed on the stream bed. Coarse sediments within the frame were picked up and rubbed by hand in the net of the Surber sampler, so that all benthic macroinvertebrates attached to their surfaces would be washed into a plastic container attached to the terminal end of the net. Finer sediments and dead plant litter were also flushed into the plastic container. All substrates and macroinvertebrates collected by the plastic container were then transferred to a storage bag, preserved in 70% methylated spirit, and transported to the laboratory.

In the laboratory, macroinvertebrates were visually sorted from the substrates. Using the taxonomic guide published by Dobson et al. (2012), specimens of macroinvertebrates were identified to at least the genus level using a light microscope (Leica M60) with 25x magnification. The genus level is commonly used in studies evaluating the response of benthic macroinvertebrates to in-stream wood (e.g., Baillie et al., 2019; Stewart et al., 2012; Testa et al., 2011; Warren & Kraft, 2006; Wellnitz et al., 2014), so identification to this level is not expected to obscure any wood-induced effect. Genus-level identification has previously been shown to be adequate for multivariate analyses or environmental monitoring (Bailey et al., 2001).

Three basic biotic measures (i.e., density D in m^{-2}, taxa richness S, and Shannon diversity index H') were calculated for each patch. Density was defined as the number of individuals present in a patch divided by 0.1 m^2 (i.e., the area enclosed by the frame of the Surber sampler). Taxa richness referred to the number of taxa recorded in the patch. Shannon diversity index was calculated using the following formula (DeJong, 1975):

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

where p_i is the proportion of individuals belonging to the ith taxon. Taxonomic compositions (i.e., relative abundances of individual taxa) were also recorded for all the patches.

2.3 | Benthic metabolism

Three fieldwork campaigns were conducted: November 2018, June 2019, and September 2020 (two months, nine months, and two years after the installation of NFM woody dams respectively). With limited apparatus, it was not possible to measure benthic metabolic rates at all study reaches described above. To facilitate the transport of water and sediment samples, only the third control reach, the seventh dam on Downs Gill, and seventh dam on Fall Gill (Figure 1) were selected for metabolic measurements, owing to their accessibility. Attention was given to the 10 m upstream and downstream of each them, yielding five study reaches in total (two upstream, two downstream, and one control). In each study reach, three submerged patches 0.1 m^2 in area were selected randomly for the collection of stream bed sediments. Only the surface layer was removed. During transport, all grains were completely submerged in 5 L of stream water collected from the same location.

In the laboratory, metabolic rates of each patch were determined by incubating stream bed sediments in a gas-tight plexiglass chamber (14 cm in diameter and 16.6 cm in height; Figure 3). Changes in dissolved oxygen (DO) concentrations within the chamber over time were recorded (Bott et al., 1978). After placing the sediments, the chamber was fully filled with stream water, and a lid was fitted on top such that no air bubbles would be trapped inside. A PyroScience OXR230 fibre-optic oxygen probe (connected to a PyroScience FireStingO2 oxygen meter transmitting data to the Pyro Oxygen Logger software) was inserted into the chamber through an air-tight aperture drilled in the lid. The chamber was then placed into an incubator, with the temperature inside the incubator set as that measured in the field to reproduce field conditions (Table 1), so that the impact of NFM woody dams on benthic metabolism in the natural environment could be approximated as closely as possible. To ensure that dissolved contents were evenly distributed, water inside the chamber was continuously mixed by a magnetic stir bar driven by an external motor. The sediments were first incubated in darkness for 10 h, allowing only respiration to take place. After that, LED lamps (Arcadia LED Stretch CS18XM; 7 W provided by a total of 10 bulbs) inside the incubator were turned on for another 10 h, allowing both respiration and photosynthesis to take place. At the end of each incubation experiment, the mass of sediments (to the nearest g) and volume of water (to the nearest mL) incubated were measured.

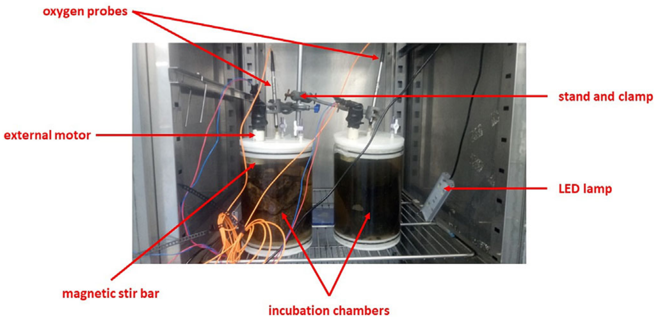


FIGURE 3 Experimental set-up of the incubation chambers in the laboratory.

The oxygen sensor made discrete measurements at 1 s intervals, and a scatter plot of DO concentration versus time was yielded for each incubation. A best-fit regression line was then added to each plot. In general, the equation of the regression line is as follows:

$$\mathrm{DO}(t) = \mathrm{DO}(t_0) + (r_\mathrm{P} - r_\mathrm{R})(t)$$

where r_P is the rate of increase in DO concentration (in μmol O_2 L^{-1} s^{-1}) due to photosynthesis; r_R is the rate of decrease in DO concentration (in μmol O_2 L^{-1} s^{-1}) due to respiration; t_0 is the time when the incubation experiment began; and t is the time (in s) elapsed since t_0. This equation represents the change in DO from the initial concentration via the addition of DO produced by photosynthesis and the subtraction of DO consumed by respiration. The slope of the regression line for the dark treatment would be $-r_\mathrm{R}$ since $r_\mathrm{P} = 0$ (i.e., no photosynthesis). The slope of the regression line for the light treatment would be $r_\mathrm{P} - r_\mathrm{R}$, which enables the calculation of r_P by substituting r_R from the dark treatment. The rates of respiration and photosynthesis per unit stream bed area (in g O_2 m^{-2} d^{-1}) were then calculated using the following equations:

$$R = \frac{r_\mathrm{R} \times 10^{-6} \times 32 \times V \times 86400}{0.1}$$

$$P = \frac{r_\mathrm{P} \times 10^{-6} \times 32 \times V \times 86400}{0.1}$$

where $10^{-6} \times 32$ is the mass (in g) of 1 μmol of O_2; V is the volume of water (in L) added to the incubation chamber; 86,400 is the number of seconds in one day; and 0.1 is the area of stream bed (in m^2) sampled.

2.4 | Patch-scale geomorphic variables

Geomorphic parameters were measured at two spatial scales, patch and reach, at the same time as macroinvertebrate surveys and metabolic measurements. At the patch scale, grain size distributions by mass (Gordon et al., 2004) were measured within the 0.1 m^2 where macroinvertebrates were sampled and at locations where sediments

TABLE 1 Temperature (°C) used for each incubation experiment.

Sampling time	West Gill 3 Control	Downs Gill (7th dam) Upstream	Downstream	Fall Gill (7th dam) Upstream	Downstream
11/2018	7.3	4.8	4.9	4.9	4.9
06/2019	10.0	14.3	14.4	9.0	9.0
09/2020	10.9	15.8	15.9	14.0	14.0

were collected for benthic metabolic measurements. Using sieves, sediments in each patch were divided into multiple size classes with intervals of one φ (Table 2). The φ scale and metric scale (d; in mm) can be interconverted using the following equations:

$$d = 2^{-\varphi}$$

$$-\varphi = \log_2 d$$

The mass of each size class was measured to the nearest g, and it was divided by the total mass of that sample to give the proportion of mass represented by that size class. The cumulative proportion of total mass finer than each φ value was recorded. Three percentile values ($-\varphi_{16}$, $-\varphi_{50}$, and $-\varphi_{84}$; $-\varphi_i$ is the grain size larger than $i\%$ of the total mass) and the sorting index (s_p) were then calculated for each sample using the following formulae (Chaddock, 1921; Gordon et al., 2004):

$$-\varphi_i = L + \frac{i - f_c}{f_m} \times (U - L)$$

$$s_p = \frac{(-\varphi_{84}) - (-\varphi_{16})}{2}$$

where i is the percentile value (16, 50, or 84); f_c is the cumulative percentage of mass represented by all the size classes preceding the one containing φ_i; f_m is the percentage of mass represented by the size class containing φ_i; L is the lower boundary (in $-\varphi$) of the size class containing φ_i; and U is the upper boundary (in $-\varphi$) of the size class containing φ_i.

Hydraulic parameters were also measured at each patch during macroinvertebrate sampling as they might be influenced by channel morphology. Water depth (z) was determined to the nearest mm using a tape measure, and average flow velocity (v) was measured at 60% depth over a period of 5 s (Schwendel et al., 2010) using a Global Water FP111 impeller-type flow probe.

TABLE 2 Conversion between the metric scale and the φ scale.

Grain size in mm	Grain size in φ	Grain size in $-\varphi$
0.125	3	−3
0.25	2	−2
0.5	1	−1
1	0	0
2	−1	1
4	−2	2
8	−3	3
16	−4	4
32	−5	5
64	−6	6
128	−7	7

2.5 | Reach-scale geomorphic variables

At the reach scale, data previously presented by Lo et al. (2022) were utilised. Three-dimensional (3D) surveys employing Structure-from-Motion (SfM) photogrammetry were conducted within the same month as macroinvertebrate surveys and metabolic measurements. Survey extent encompassed the 10 m upstream and downstream of the NFM woody dams marked in Figure 1, plus the three 10 m control reaches. By quantitatively comparing 3D models (cell size: 0.1 m) of the same reach generated from two successive surveys, volumes of sediments eroded, volumes of sediments deposited, and net volume changes were calculated. Lo et al. (2022) found no significant difference in these volumes between the treatment types, but it remains unclear whether reach-scale erosion or deposition could have driven changes in macroinvertebrate communities and metabolic rates. This consideration could reveal whether NFM woody dams could potentially lead to biotic changes through inducing greater geomorphic changes.

SfM surveys also generated orthophotographs (pixel size: 1 mm) of the study reaches, allowing the spatial extents of channel units (in particular the percentage of reach area covered by scour pools) to be quantified. During each geomorphological fieldwork campaign, pebble counts (Wolman, 1954) were also conducted. The count for each 10 m study reach involved measuring 100 clasts while wading from the downstream end of the reach to its upstream end in a zigzag pattern. The intermediate axis of each clast was measured using a 5 m tape measure (to the nearest cm for coarser grains) or a calliper (to the nearest mm for finer grains). The following metrics were then computed for each count: median grain size (d_{50}; mm), grain size at the 16^{th} percentile (d_{16}; mm), grain size at the 84^{th} percentile (d_{84}; mm). The sorting index (s_r; dimensionless) was also calculated, using the following formula (Gordon et al., 2004):

$$s_r = \frac{1}{2}\left(\frac{d_{84}}{d_{50}} + \frac{d_{50}}{d_{16}}\right)$$

A higher value of s_r indicates a more poorly-sorted stream bed, which is assumed to represent higher stream bed heterogeneity.

2.6 | Statistical analyses

All patch-scale biotic metrics were two-way classified into groups based on 'sampling time' (pre-intervention spring 2018, post-intervention autumn 2018, spring 2019, autumn 2020) and 'treatment type' (control, upstream of dam, downstream of dam). The 34 patches sampled on Downs Gill and Fall Gill in spring 2018 served as the common baseline for both 'upstream' and 'downstream' reaches. Moreover, it should be noted that the reach between the fourth and fifth dams on Fall Gill was classified as a 'downstream' reach as clearly no backwater effect (i.e., zone of slow flows and sediment accumulations) was observed immediately upstream of the fifth dam. Shapiro–Wilk tests were run to check whether data within each group were normally distributed. Where necessary, the data were $\ln(x+1)$ transformed to attain normality. Levene's tests were conducted to ensure that all groups had equal variances. The mean of each group was computed by aggregating all patches belonging to the same treatment type within the same sampling season. Two-way ANOVA tests were then performed on the means of the various biotic measures, with 'sampling time' and 'treatment type' as factors. NFM woody dams were considered to have an impact if the interaction between 'sampling time' and 'treatment type' had a significant ($p < 0.05$) effect. In case of significance, Tukey's HSD tests were performed to reveal which factor caused the significance. All statistical tests were performed using R v4.1.3 (R Core Team, 2022).

Non-metric multidimensional scaling (NMDS) was employed using the 'metaMDS' function in the 'vegan' package (Oksanen et al., 2008) to graphically display taxonomic compositions of all the patches sampled throughout the study period. The number of dimensions sought was three (i.e., assigning each patch at each sampling time a set of three-dimensional co-ordinates), a compromise between maintaining true ecological distances between patches and enabling the resulting NMDS plots to be interpreted (Dexter et al., 2018). The three-dimensional configuration was projected along the third axis (which captured the least variation) to generate a two-dimensional NMDS plot. In other words, each patch had a horizontal (NMDS1) co-ordinate and a vertical (NMDS2) co-ordinate. The plot was simplified to produce a second NMDS plot, displaying only the centroid of each 10 m study reach at each sampling time. The position of the centroid was determined by taking the mean of the co-ordinates of the relevant patches. The second plot was further simplified to include only the centroid of each treatment type (i.e., upstream of dam, downstream of dam, or control) at each sampling time, showing how taxonomic compositions associated with the three treatment types had changed over time. NMDS was supplemented by a PERMANOVA test performed on taxonomic compositions with 'sampling time' and 'treatment type' as independent variables. A test result giving $p < 0.05$ would indicate that some divergence had occurred between the three treatment types, but more PERMANOVA tests were required to reveal precisely when taxonomic compositions had diverged and which treatment(s) in particular had caused the divergence.

The 'envfit' procedure in 'vegan' was used to repeat a linear regression analysis for each taxon to establish a relationship between its relative abundance in a patch and the NMDS co-ordinates of the patch in the first NMDS plot. Significant relationships (i.e., $p < 0.05$) were displayed as vectors (i.e., resultants of the relationships with both the vertical and the horizontal co-ordinates; lengths dependent on R^2) in the first NMDS plot, providing insights into taxa driving differences in taxonomic compositions between the patches. The 'envfit' procedure was also employed to identify relationships between the sedimentary characteristics of a patch and the NMDS co-ordinates of the patch in the first NMDS plot as well as relationships between reach-scale geomorphic parameters and reach-averaged NMDS co-ordinates in the second NMDS plot. Significant relationships ($p < 0.05$) were included into the respective NMDS plot as vectors, revealing patch-scale and reach-scale physical variables driving differences in taxonomic compositions.

To assess whether biotic differences observed between the three treatment types were due to differences in geomorphic characteristics induced by NFM woody dams, linear regression was performed to identify relationships between patch-scale biotic variables (i.e., macroinvertebrate metrics: D, S, and H'; metabolic rates: R and P) and the geomorphic ($-\varphi_{16}$, $-\varphi_{50}$, $-\varphi_{84}$, and s_p) and hydraulic (z and v) characteristics of the corresponding patches. Linear regression was also performed to identify relationships between changes in reach-averaged biotic variables (i.e., D, S, H', R, and P) and reach-scale volume changes (i.e., volume of sediments eroded, volume of sediments deposited, and net volume change) as well as relationships between reach-averaged biotic variables (i.e., D, S, H', R, and P) and reach-scale geomorphic parameters (i.e., percentage of reach area covered by scour pools, d_{16}, d_{50}, d_{84}, s_r). To test whether temperature was a confounding variable in the current study, linear regression was performed to identify relationships between water temperatures (Table 1) and reach-averaged metabolic rates. Shapiro–Wilk tests were performed to ensure normality of the variables, and $\ln(x+1)$ transformation was applied where necessary. Normally, $p < 0.05$ would indicate a significant relationship, but since there were multiple (n) independent variables for each dependent variable, Bonferroni correction was adopted and only relationships with $p < 0.05/n$ were considered significant.

3 | RESULTS

3.1 | Macroinvertebrates

A total of 15,044 individuals from 81 taxa were collected over the entire study period. The mean abundance of benthic macroinvertebrates per patch was 69 (range: 2–719), and the mean number of taxa was 12 (range: 2–27).

The two-way ANOVA test performed on log-transformed macroinvertebrate density $\ln(D+1)$ suggests that changes were not different across the three treatment types over time (Figure 4a; Table S1: interaction between 'sampling time' and 'treatment type' had no significant effect on log-transformed density). However, the main effect of 'treatment type' was significant (Table S1), with the Tukey's HSD test revealing that the control reaches had consistently (both before and after the construction of NFM woody dams) greater densities than reaches upstream and downstream of NFM woody dams (both $p < 0.0001$; Figure 4a). The two-way ANOVA test performed on macroinvertebrate taxa richness suggests that changes were not different across the three treatment types over time (Figure 4b; Table S1: interaction between 'sampling time' and 'treatment type' had no significant effect on richness). The two-way ANOVA test performed on Shannon index suggests that changes were different across the three treatment types over time (Figure 4c; Table S1: interaction between 'sampling time' and

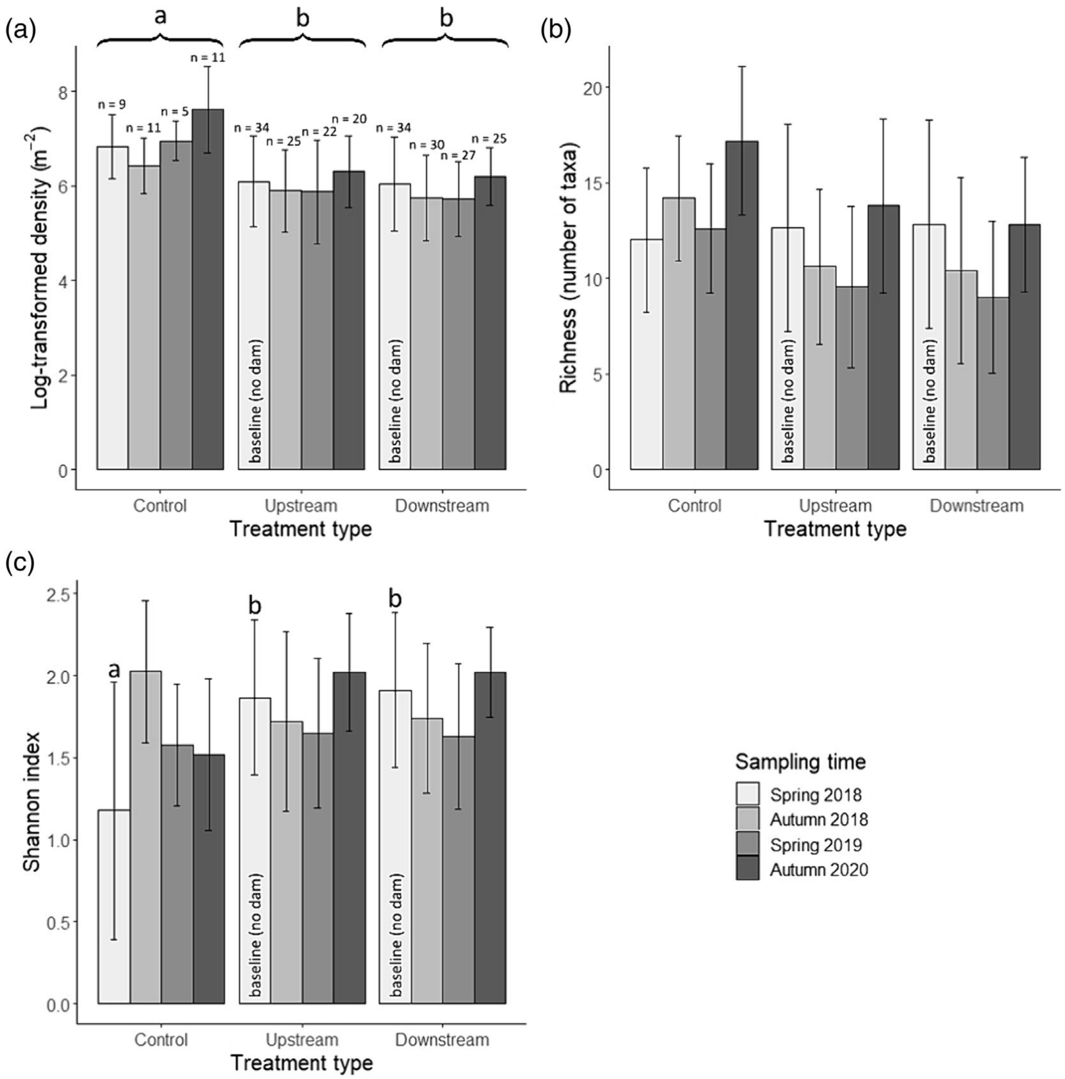


FIGURE 4 Means of macroinvertebrate community metrics recorded in the three treatment types throughout the study period; box heights represent means; error bars show ±1 standard deviation; different alphabets above bars indicate significant differences; n numbers in panel (a) refer to numbers of patches that have been taken into account during the computation of means; same numbers of patches are used for the calculation of means in panels (b) and (c).

'treatment type' had a significant effect on Shannon index). The Tukey's HSD test suggests that this significant interaction effect arose from the unique trend displayed by the control reaches, which had a Shannon index significantly lower than both reaches upstream of dams ($p = 0.005$) and reaches downstream of dams ($p = 0.001$) in spring 2018 (before the construction of NFM woody dams), but this difference was not maintained for the rest of the study period (Figure 4c).

At the patch scale, regression analyses suggest that all of the above community metrics had no obvious relationship with log-transformed water depth and any of the grain size parameters (Figure S2), but log-transformed flow velocity (Figure S2) had positive relationships with log-transformed density ($\beta = 1.682$, $R^2 = 0.070$, $p < 0.001$; Table S2) and richness ($\beta = 7.496$, $R^2 = 0.053$, $p = 0.002$; Table S2). At the reach scale, volumes of sediments eroded (Figure S4) had a positive relationship with changes in taxa richness ($\beta = 1.734$, $R^2 = 0.151$, $p = 0.011$; Table S3). Results from further regression analyses (Table S4) suggest that the percentage of channel area occupied by scour pools (Figure S5) and reach-scale grain size parameters determined by pebble counts (Figure S6) were in general not significant in explaining any of the three reach-averaged macroinvertebrate community metrics.

The first PERMANOVA test performed on taxonomic compositions indicates a significant interaction between 'sampling time' and 'treatment type' (pseudo-$F = 1.575$, $p = 0.014$), suggesting that the community compositions at the three reach types had diverged sometime during the study period. Follow-up stepwise PERMANOVA tests suggest that the divergence had taken place sometime between spring 2019 and autumn 2020 (pseudo-$F = 1.880$, $p = 0.034$; Table S5). Throughout the study period, communities upstream and downstream of woody dams remained similar (pseudo-$F = 0.506$, $p = 0.988$), suggesting that the divergence between spring 2019 and autumn 2020 was caused by the control reaches accommodating a taxonomic composition different from the woody dam reaches. During the first three fieldwork campaigns, the three treatment types had similar NMDS1 co-ordinates (Figure 5), but in autumn 2020, the control reaches clearly had smaller NMDS1 values (i.e., shifting to the left of the NMDS plot) than the woody dam reaches.

The 'envfit' procedure in 'vegan' reveals that seven important taxa (Figure 6a) had driven the difference in taxonomic composition observed between patches: Orthocladiinae (Diptera: Chironomidae; $R^2 = 0.840$, $p = 0.001$), *Baetis* (Ephemeroptera: Baetidae; $R^2 = 0.783$, $p = 0.001$), *Leuctra* (Plecoptera: Leuctridae; $R^2 = 0.514$, $p = 0.001$), *Rhithrogena* (Ephemeroptera: Heptageniidae; $R^2 = 0.297$, $p = 0.001$), Oligochaeta (Annelida; $R^2 = 0.265$, $p = 0.001$), *Isoperla* (Plecoptera: Perlodidae; $R^2 = 0.250$, $p = 0.001$), and *Nemoura* (Plecoptera: Nemouridae; $R^2 = 0.217$, $p = 0.001$).

Further analyses with the 'envfit' function suggest that three patch-scale physical variables (Figure 6b) were significantly related to the taxonomic compositions of the sampled patches: $-\varphi_{16}$ ($R^2 = 0.058$, $p = 0.008$), log-transformed velocity v ($R^2 = 0.051$, $p = 0.012$), and log-transformed s_p ($R^2 = 0.041$, $p = 0.026$). The fitting of reach-scale environmental vectors to the NMDS plot (Figure 6c) indicates that differences in reach-averaged taxonomic compositions were related to the sorting index s_r ($R^2 = 0.162$, $p = 0.018$) and the proportion of channel area occupied by scour pools ($R^2 = 0.141$, $p = 0.032$).

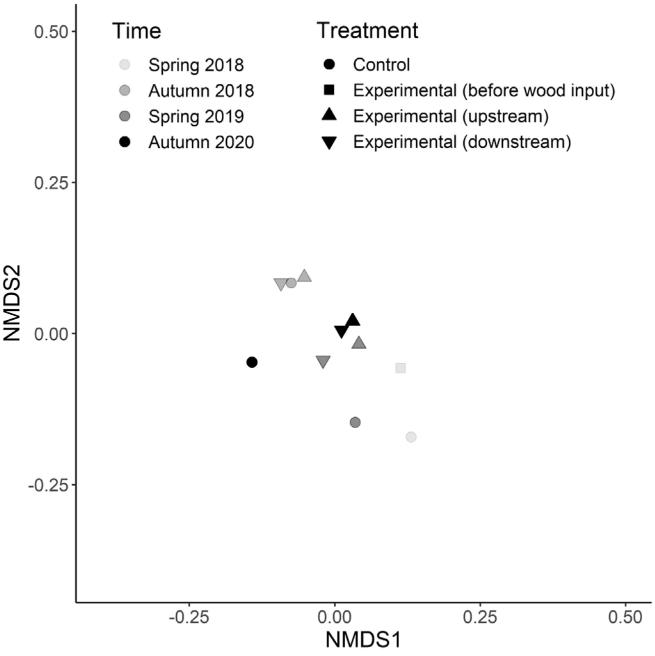


FIGURE 5 NMDS plot showing how taxonomic compositions associated with each treatment type evolved over time during the study period; simplified from Figures S7 and S8.

3.2 | Benthic metabolism

Over the entire study period, the mean rate of respiration per unit stream bed area (Figure 7a) was 0.07 g O_2 m^{-2} d^{-1} at West Gill (control), 0.12 g O_2 m^{-2} d^{-1} at Downs Gill (upstream of dam), 0.13 g O_2 m^{-2} d^{-1} at Downs Gill (downstream of dam), 0.10 g O_2 m^{-2} d^{-1} at Fall Gill (upstream of dam), and 0.12 g O_2 m^{-2} d^{-1} at Fall Gill (downstream of dam). The mean rate of photosynthesis per unit stream bed area (Figure 7b) was 0.11 g O_2 m^{-2} d^{-1} at West Gill (control), 0.11 g O_2 m^{-2} d^{-1} at Downs Gill (upstream of dam), 0.13 g O_2 m^{-2} d^{-1} at Downs Gill (downstream of dam), 0.11 g O_2 m^{-2} d^{-1} at Fall Gill (upstream of dam), and 0.13 g O_2 m^{-2} d^{-1} at Fall Gill (downstream of dam). It is noted that one of the patches sampled on the control reach in 2019 had abnormally high metabolic rates (one order of magnitude greater than most other patches). The reason for this is unclear. It could be due to the presence of particularly fine sediments at the sampling location. It is also possible that a part of the equipment was not functioning normally. To be conservative and to avoid over-interpreting an anomalous result, the patch was excluded from all analyses.

The two-way ANOVA test performed on log-transformed rates of respiration per unit stream bed area shows that 'treatment type' had a significant main effect ($F_{2,35} = 4.325$, $p = 0.021$; Table S1), with the Tukey's HSD test indicating that the control reach had consistently lower log-transformed rates of respiration per unit stream bed area than the downstream reaches ($p = 0.032$; Figure 7a). Conversely, the two-way ANOVA on log-transformed rates of photosynthesis per unit stream bed area shows that the main effect of 'treatment type' was not significant ($F_{2,35} = 2.755$, $p = 0.077$; Table S1). However, the interaction between 'sampling time' and 'treatment type' had a significant effect ($F_{4,35} = 2.692$, $p = 0.047$; Table S1). The Tukey's HSD test shows that the mean photosynthesis rate in upstream reaches decreased significantly between 2018 and 2019 ($p = 0.012$) but not in other treatment types.

After removing the 2019 outlier, the log-transformed rate of respiration per unit stream bed area was found to be negatively related to the patch-scale grain sizes (Figure S3) $-\varphi_{50}$ ($\beta = -0.056$, $R^2 = 0.176$, $p = 0.005$; Table S2) and $-\varphi_{84}$ ($\beta = -0.097$, $R^2 = 0.260$, $p < 0.001$; Table S2). At the same time, the log-transformed rate of photosynthesis per unit stream bed area was found to be negatively related to $-\varphi_{84}$ ($\beta = -0.061$, $R^2 = 0.091$, $p = 0.026$; Table S2).

At the reach scale, there was no observable linkage between the rates of benthic metabolic activities and the volume of sediments eroded or deposited (Table S3). Further evidence suggesting that reach-averaged benthic metabolic rates were not controlled by reach-scale geomorphology was provided by the insignificant regression results reported in Table S4 — reach-averaged rates of benthic respiration and photosynthesis were not related to any of the reach-scale geomorphic and sedimentary variables.

Water temperatures were found to be negatively related to rates of respiration, but the slope was very close to 0 ($\beta = -0.007$, $R^2 = 0.365$, $p = 0.010$). There was no significant relationship between water temperatures and rates of photosynthesis.

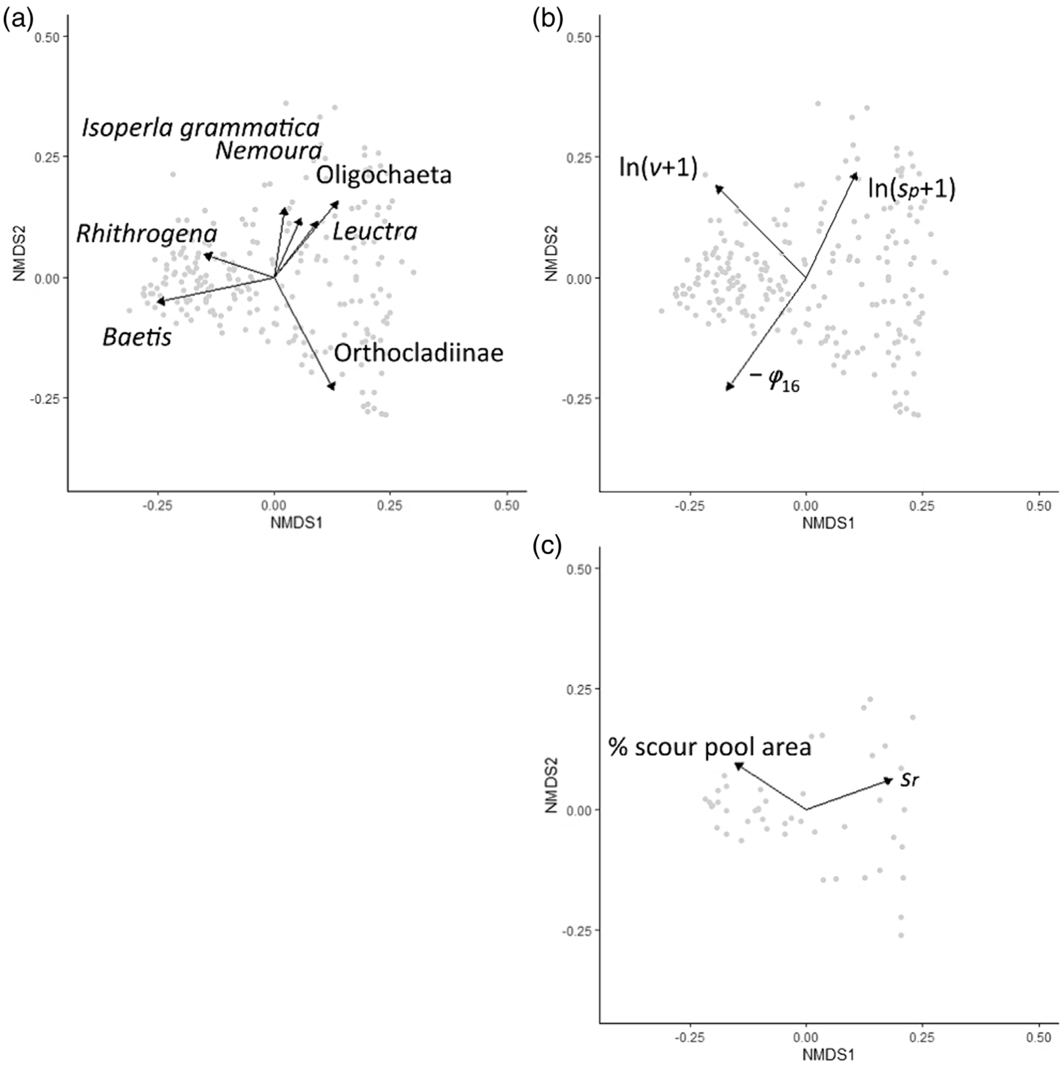


FIGURE 6 Reproduction of the NMDS plots (Figures S7 and S8), with significant (a) taxa, (b) patch-scale and (c) reach-scale geomorphic/hydraulic variables shown as vectors.

4 | DISCUSSION

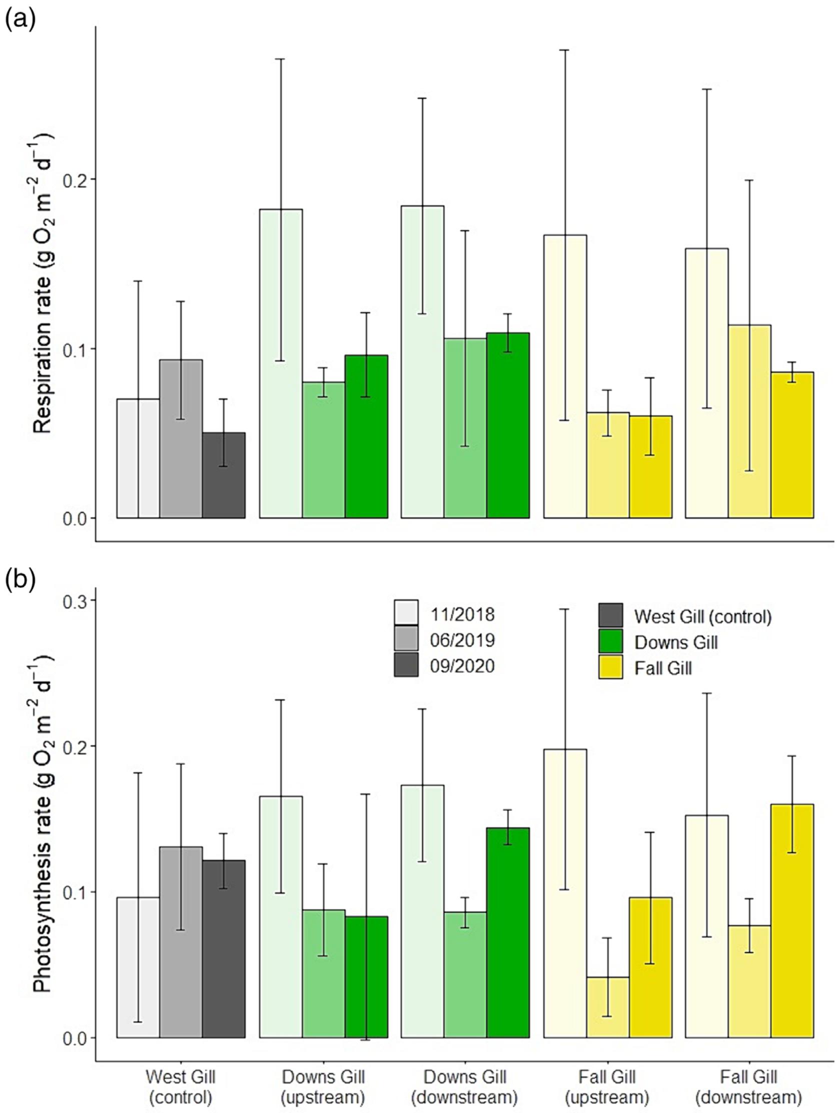
The current study found that the woody dam reaches differed from the control reaches in macroinvertebrate taxonomic compositions in autumn 2020, near the end of the study period. Rates of benthic respiration were also consistently higher in the woody dam reaches. The following discussion considers whether the biotic changes observed were due to the geomorphic changes induced by the installation of NFM woody dams and whether greater biotic changes would have been observed if there had been greater geomorphic changes.

4.1 | Benthic macroinvertebrates

In this study, no relationship was identified between any of the macroinvertebrate community metrics and the sedimentary characteristics of the sampled patches. This seems to suggest that benthic macroinvertebrate communities would not have shown any response even if the NFM woody dams had led to greater changes in stream bed sedimentary characteristics. However, it is worth noting the small range of patch-scale sorting index recorded in the current study (i.e., between 0.35 and 1.62). Gayraud and Philippe (2003) documented patch-scale sorting index values between 0.16 and 3.56, and they found that patches with higher sorting index values (i.e., more poorly-sorted patches) had greater densities of benthic macroinvertebrates as these patches contained greater volumes of interstitial space. In other words, the most poorly-sorted patch in the current study may still not contain sufficient interstitial space to support a significantly higher density. To result in more poorly sorted patches and hence higher macroinvertebrate densities, the NFM woody dams should be installed closer to the stream bed, so that they can induce greater hydraulic and substrate variability (Klaar et al., 2011; Pinto et al., 2019; Wellnitz et al., 2014).

Moreover, even if one patch contained a lot of sand and had a small overall grain size, the amount of sand was insignificant at the reach scale (as reported by Lo et al., 2022). New taxa preferring

FIGURE 7 Mean rates of benthic (a) respiration and (b) photosynthesis per unit stream bed area; box heights represent means (three patches were used for calculating each mean, except the mean of West Gill in June 2019, which was computed from only two patches); error bars show ±1 standard deviation; degree of shading shown in the legend applies to all colours.



sand-sized sediments would not be attracted, and the patch would still be dominated by macroinvertebrates preferring coarse grains migrating from neighbouring coarse patches (Beisel et al., 2000). Erman and Erman (1984) also observed no effect of substrate heterogeneity on taxa richness within sampling trays that were 29.5 cm long by 23.5 cm wide (i.e., similar to the frame size of the Surber sampler used in the current study). To increase the diversity of benthic macroinvertebrates, NFM woody dams need to induce the formation of distinct sediment facies at the reach scale that support different macroinvertebrate assemblages (Hasselquist et al., 2018; Mathers et al., 2017). This condition did not arise in the current study as the monitored dams were all suspended above baseflow and unable to retain large volumes of finer sediments. Only dams with clearance heights < 0.3 m from the stream bed were likely to result in significant sediment storage at the study location (Lo et al., 2022). Although finer grains accumulated immediately upstream of the seventh dam on Downs Gill, they only occupied less than 2 m of the 10 m study reach (Lo et al., 2022). The accumulated grains were mostly pebbles, which would support taxa similar to those inhabiting cobbles elsewhere in the study reach (Doeg et al., 1989).

Unlike the current study, Deane et al. (2021) found significantly increased macroinvertebrate biodiversity in the vicinity of in-stream wood deployed for NFM in Black Brook, Peak District National Park, United Kingdom. Their study stream had physical and chemical characteristics similar to the tributaries monitored in the current study, but the in-stream wood accumulations in their study were structurally different from those in the upper River Cover catchment. The wood structures that Deane et al. (2021) monitored resembled natural fallen wood, which maintained contact with base flow and even the stream bed. Consequently, the wood structures in their study may be more easily colonised by aquatic macroinvertebrates than those in the current study.

Nevertheless, NFM woody dams in the current study appeared to have a detectable impact on taxonomic compositions towards the end of the study period. The control reaches shifted to the left side of the NMDS plot in autumn 2020, but there was no such shift in the woody dam reaches (Figure 5). This shift represents an increase in dominance by the mayflies *Baetis* and *Rhithrogena*, as well as faster flows and coarser sediments measured in the field, agreeing with previous studies concerning the habitat preferences of *Baetis* and *Rhithrogena* (Céréghino et al., 2004; Shelly, 1979). The shift also indicates that the control reaches had lower sorting index s_r values (i.e., better sorted and more homogeneous stream beds) than the woody dam reaches in autumn 2020, confirming the preference of the two taxa for structurally simple habitats such as cobble surfaces (Mcclelland & Brusven, 1980). Overall, these observations suggest that NFM woody dams may have favoured macroinvertebrate diversity at the landscape scale by reducing stream bed coarsening and preserving taxa that preferred slower flows found on the right side of the NMDS plot (Figure 6a), such as *Leuctra* and *Nemoura* (Beauger et al., 2006; Dolédec et al., 2007; Williams et al., 1995). This was likely achieved during flood events, when the dams would have interacted with the water and offered flow resistance (Manga & Kirchner, 2000), thereby lowering the average flow velocity and resulting in less energy available for sediment entrainment. The maximum grain size that was eroded from the stream bed should therefore be lower in the woody dam reaches than in the control reaches, leading to less coarsening in the former after flood events.

The current study has provided some evidence that scouring could increase taxa richness (Table S3) and influence taxonomic compositions (Figure 6c), agreeing with various previous studies (e.g., Hilderbrand et al., 1997; Stewart et al., 2012). It may therefore be argued that the lack of new pools formed by the NFM woody dams in the current study was one of the reasons why diversity did not increase. As discussed in Lo et al. (2022), bank erosion was more prominent than pool formation as the bank was much softer than the stream bed in the study catchment. The flow during the first half of the study period was also not strong enough to form pools. Only two underflow pools were formed towards the end of the monitoring, at the fifth and seventh dams on Fall Gill respectively, and they might have contributed to the small (but not statistically significant) increase in richness and Shannon index observed in autumn 2020. More time and high flows may be needed before macroinvertebrates that prefer deeper water depths could colonise these newly-formed habitats. If the NFM woody dams eventually lead to the formation of persistent pools while preserving some finer sediments elsewhere (hence increasing the reach-scale variation in grain size), then they may drive an increase in reach-scale biodiversity.

An essential limitation associated with the use of benthic macroinvertebrates for habitat monitoring arises from the biphasic life cycles of a number of taxa (Brittain & Sartori, 2009; Morse, 2009; Stewart, 2009). Community metrics recorded during field surveys therefore might not only reflect in-stream habitat conditions, but also the state of the surrounding terrestrial environment that provides the streams with colonists (Arnaiz et al., 2011; Collier, 1995; Moraes et al., 2014). If the riparian area is impaired or not fully natural, there may not be sufficient insects in their adult, terrestrial stages to produce eggs and aquatic larvae to colonise the stream bed even when wood may have created complex and favourable in-stream habitats (Jähnig et al., 2010; McKie & Cranston, 2001). This may have been the case in the upper River Cover catchment as the study tributaries were all draining homogeneous moors and conifer plantations, which were found to accommodate a limited diversity of macroinvertebrates (Ormerod et al., 1993). Consequently, even when new channel units arose under the influence of NFM woody dams, there may have been no new taxa to colonise them.

Moreover, there was some evidence that benthic macroinvertebrate communities in the current study were different between the tributaries even before the construction of NFM woody dams. As shown in Figures S7 and S8, Downs Gill samples were separate from Fall Gill samples and that West Gill (control) samples were more similar to the latter group in taxonomic compositions. This agrees with previous research suggesting high taxa turnover across space in headwater areas (Clarke et al., 2008), where the taxonomic composition of one tributary may differ completely from that of the next tributary (while the diversity of each tributary can remain low). Instead of showing consistent responses, they may have reacted to the installation of NFM woody dams in different site-specific ways (de Brouwer et al., 2020), consequently rendering the detection of impacts difficult.

4.2 | Benthic metabolism

There was a significant negative relationship between patch-scale grain sizes ($-\varphi_{50}$ and $-\varphi_{84}$) and rates of benthic respiration, indicating that the rate increased when the size of stream bed sediments decreased. If the outlier (i.e., the 2019 West Gill patch that had abnormally high metabolic rates) was not removed, the relationships would be even stronger as it was one of the samples with the smallest median grain size (39.78 mm). Finer grains provide larger surface areas for the adsorption of organic matter, resulting in a higher mass of organic matter per unit stream bed area (Hargrave, 1972; Sutherland, 1999). The organic matter is the substrate for respiration and favours the growth of heterotrophic microorganisms, which transform the organic matter into carbon dioxide. This postulation is supported by Hedin (1990) and Groffman et al. (2005), who both found that debris dam sediments had higher organic matter concentrations and yielded higher rates of respiration than sediments collected from other stream bed areas.

Overall, the reason why the woody dam reaches had slightly higher measured rates of respiration than the control reaches (by 0.06 g O_2 m^{-2} d^{-1}) was likely because finer patches had been sampled in the former. These patches could be biogeochemical hotspots (Krause et al., 2014), but they did not occur extensively in the study site. For example, although finer gravels accumulated immediately upstream of the seventh dam on Downs Gill, they only occupied less than 2 m of the 10 m study reach (Lo et al., 2022). Consequently, there was no significant difference in reach-scale grain size between the woody dam reaches and the control reaches, and no significant relationship between grain sizes and rates of respiration was detected at the reach scale. As explained in Section 4.1, the NFM woody dams may have resulted in less coarsening in the woody dam reaches than in the control reaches immediately after flood events. However, when the water level dropped, there would be no more interaction between the dams and the stream water. As a result, flow velocities and grain sizes deposited during baseflow should be similar in the control reach and the woody dam reaches. In this study, sediments for incubation were mostly collected during baseflow, so enough time may have passed since the last flood event for the difference in grain size between the control reach and the woody dam reaches to diminish.

A statistically significant negative relationship was recorded between temperatures and rates of benthic respiration. However, the regression slope was very small, so temperature could in essence be interpreted as having no effect on benthic respiration in the current study. This is unexpected as higher temperatures should increase metabolic rates by speeding up the chemical reactions that constitute metabolic processes (Acuña et al., 2008; Perkins et al., 2012). The range of temperatures recorded in the current study (between 4.8 and 15.9°C; Table 1) was smaller than that recorded by the previous studies cited (> 20°C) and so may not have produced significant differences in rates of benthic respiration. Substrate availability (as determined by grain sizes) may have been more important in limiting benthic respiration (Roman & Sabater, 1999).

As in previous studies (e.g., Frainer et al., 2017; Kiffney et al., 2014), the current study did not detect any difference in primary productivity between reaches with wood and those without. However, there was a negative relationship between $-\varphi_{84}$ and rates of photosynthesis (Table S2). The rate of benthic photosynthesis is normally positively correlated to the biomass of benthic algae (Aristegi et al., 2010; Bott et al., 1985; Busch & Fisher, 1981; Fellows et al., 2006), so the reason why smaller cobbles support higher rates of primary production may be due to the larger overall surface area available for the attachment of more benthic algae. Since algae require sunlight to carry out photosynthesis, the undersides of cobbles are unlikely to be colonised. In other words, when the magnitude of sediment fining and the associated increase in grain surface area remain the same, the increase in the biomass of algae should be smaller than that in the biomass of heterotrophic micro-organisms. This explains why the slope of the relationship between the rate of benthic photosynthesis and $-\varphi_{84}$ was less negative than that of the relationship between the rate of benthic respiration and $-\varphi_{84}$ (-0.0011 vs. -0.0967). This also explains why the patches sampled in the woody dam reaches had higher rates of benthic respiration but not higher rates of benthic photosynthesis than the patches sampled in the control reach. It should be noted that, even if the NFM woody dams had led to the accumulation of fine sediments, rates of benthic photosynthesis might not have increased significantly. This is because very fine grains are unfavourable to algal growth (Atkinson et al., 2008; Cahoon et al., 1999; Uehlinger et al., 2002). In fact, the current study identified no significant relationship between $-\varphi_{16}$ (i.e., grain size of the finer portion of a patch) and rates of photosynthesis (Table S2).

Overall, these findings suggest that wood-induced geomorphic changes, more specifically changes in stream bed grain size, could drive changes in benthic metabolic rates. The reason why the current study did not detect an impact of NFM woody dams on benthic metabolism at the reach scale was because of the small textural changes that they caused. As described by Lo et al. (2022), only dams with clearance heights <0.3 m from the stream bed could result in significant sediment storage. If greater amounts of small gravels had accumulated upstream of the dams, there might have been higher rates of respiration at the reach scale, resulting in more rapid organic matter turnover. This assertion can be verified in the future by measuring benthic metabolism at the two non-monitored sites on Fall Gill where finer grains were found to have accumulated immediately upstream of the dams. Moreover, Lo et al. (2022) observed that the NFM woody dams monitored led to bank erosion more frequently than stream bed scouring. This was likely because bank materials (soil) at the study were softer and less resistant than stream bed materials (cobbles, boulders, or even bedrock). This could potentially explain why benthic ecosystems were not significantly altered at the reach scale. Only two underflow pools developed on Fall Gill, towards the end of the three-year study period (Lo et al., 2022). More time and a higher frequency of flood events may be required for these topographic features to become well developed such that they can have more long-lasting influence on benthic metabolism. This is difficult as the NFM woody dams had low persistence, and once they are displaced their geomorphic influence will be greatly reduced (Lo et al., 2022).

Although benthic biofilms (i.e., the drivers of benthic metabolism) are theoretically less directly impacted by disturbances in the surrounding terrestrial environment than macroinvertebrates that have biphasic life cycles, it should be noted that some wider-scale variables independent of the presence of NFM woody dams and their effects on stream bed texture, such as the concentration of nutrients (Martin et al., 2010) and dissolved organic carbon (McDowell, 1985), might influence metabolic rates. Future studies must therefore ensure that these factors will not confound the interpretation of the effects of NFM woody dams, for example by selecting streams that have similar water chemistry.

5 | CONCLUSION

The NFM woody dams were found to have increased rates of benthic respiration through minor modifications of stream bed grain sizes. However, the NFM woody dams have not modified benthic macroinvertebrate communities significantly. There was no linkage identified between channel morphology and benthic macroinvertebrates, with only some evidence suggesting that coarse sediments and low stream bed heterogeneity favoured the dominance of *Baetis* and *Rhithrogena*. It is envisaged that river managers and NFM practitioners worldwide could make use of the findings of the current study to design better woody dams that can simultaneously reduce flood risks and enhance aquatic biodiversity (e.g., by reducing the clearance heights to encourage localised sediment deposition). Future research should expand to other upland catchments in the temperate climatic region to investigate if other larger-scale site-specific factors (e.g., riparian cover and stream water quality) may be more important than geomorphic variables in governing benthic metabolic and macroinvertebrate responses to the construction of NFM woody dams. Moreover, although some of the intensively-monitored dams had been displaced by high flows, those that were suspended higher above baseflow remained stable. Longer-term monitoring incorporating the full lifespans of NFM woody dams can reveal if they will ultimately lead to more extensive geomorphic changes and alter benthic metabolism or diversify macroinvertebrate communities at the reach scale.

ACKNOWLEDGEMENTS

We would like to thank Prof. Ian Maddock and Prof. Paul Kay for providing comments to an earlier version of this paper. We would like to express our gratitude to Dr. Karen Bacon and Prof. Lee Brown for giving suggestions during the research implementation stage. Thanks also go to Dr. Zora van Leeuwen for her efforts in setting up the field site. Finally, we are indebted to the Mawle family for allowing us to conduct fieldwork on their estate.

This paper is dedicated to the memory of Dr. Mervyn Peart (1954–2023), whose passion for nature had inspired the first author.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Ho Wen Lo https://orcid.org/0000-0002-4766-6032

REFERENCES

Acuña, V., Wolf, A., Uehlinger, U., & Tockner, K. (2008). Temperature dependence of stream benthic respiration in an Alpine river network under global warming. *Freshwater Biology*, *53*, 2076–2088.

Anderson, N. H., Steedman, R. J., & Dudley, T. (1984). Patterns of exploitation by stream invertebrates of wood debris (xylophagy). *Internationale Vereinigung für Theoretische Und Angewandte Limnologie: Verhandlungen*, *22*, 1847–1852. https://doi.org/10.1080/03680770.1983.11897584

Aristegi, L., Izagirre, O., & Elosegi, A. (2010). Metabolism of Basque streams measured with incubation chambers. *Limnetica*, *29*(2), 301–310. https://doi.org/10.23818/limn.29.25

Arnaiz, O. L., Wilson, A. L., Watts, R. J., & Stevens, M. M. (2011). Influence of riparian condition on aquatic macroinvertebrate communities in an agricultural catchment in south-eastern Australia. *Ecological Research*, *26*, 123–131. https://doi.org/10.1007/s11284-010-0767-2

Asahi, K., Shimizu, Y., Nelson, J., & Parker, G. (2013). Numerical simulation of river meandering with self-evolving banks. *Journal of Geophysical Research: Earth Surface*, *118*, 2208–2229. https://doi.org/10.1002/jgrf.20150

Atkinson, B. L., Grace, M. R., Hart, B. T., & Vanderkruk, K. E. N. (2008). Sediment instability affects the rate and location of primary production and respiration in a sand-bed stream. *Journal of the North American Benthological Society*, *27*(3), 581–592. https://doi.org/10.1899/07-143.1

Bailey, R. C., Norris, R. H., & Reynoldson, T. B. (2001). Taxonomic resolution of benthic macroinvertebrate communities in bioassessments. *Journal of the North American Benthological Society*, *20*(2), 280–286. https://doi.org/10.2307/1468322

Baillie, B. R., Hicks, B. J., Hogg, I. D., van den Heuvel, M. R., & Kimberley, M. O. (2019). Debris dams as habitat for aquatic invertebrates in forested headwater streams: A large-scale field experiment. *Marine and Freshwater Research*, *70*(5), 734–744. https://doi.org/10.1071/MF18216

Battin, T. J., Luyssaert, S., Kaplan, L. A., Aufdenkampe, A. K., Richter, A., & Tranvik, L. J. (2009). The boundless carbon cycle. *Nature Geoscience*, *2*, 598–600. https://doi.org/10.1038/ngeo618

Beauger, A., Lair, N., Reyes-Marchant, P., & Peiry, J. L. (2006). The distribution of macroinvertebrate assemblages in a reach of the River Allier (France), in relation to riverbed characteristics. *Hydrobiologia*, *571*, 63–76. https://doi.org/10.1007/s10750-006-0217-x

Beisel, J., Usseglio-Polatera, P., & Moreteau, J. (2000). The spatial heterogeneity of a river bottom: A key factor determining macroinvertebrate communities. *Hydrobiologia*, *422*(423), 163–171. https://doi.org/10.1023/A:1017094606335

Benke, A. C., & Wallace, J. B. (2003). Influence of wood on invertebrate communities in streams and rivers. *American Fisheries Society Symposium*, *37*, 149–177.

Blaen, P. J., Kurz, M. J., Drummond, J. D., Knapp, J. L. A., Mendoza-Lera, C., Schmadel, N. M., Klaar, M. J., Jäger, A., Folegot, S., Lee-Cullin, J., Ward, A. S., Zarnetske, J. P., Datry, T., Milner, A. M., Lewandowski, J., Hannah, D. M., & Krause, S. (2018). Woody debris is related to reach-scale hotspots of lowland stream ecosystem respiration under baseflow conditions. *Ecohydrology*, *11*, e1952. https://doi.org/10.1002/eco.1952

Bott, T. L., Brock, J. T., Cushing, C. E., Gregory, S. V., King, D., & Petersen, R. C. (1978). A comparison of methods for measuring primary production and community respiration in streams. *Hydrobiologia*, *60*(1), 3–12. https://doi.org/10.1007/BF00018681

Bott, T. L., Brock, J. T., Dunn, C. S., Naiman, R. J., Ovink, R. W., & Petersen, R. C. (1985). Benthic community metabolism in four temperate stream systems: An inter-biome comparison and evaluation of the river contiuum concept. *Hydrobiologia*, *123*, 3–45. https://doi.org/10.1007/BF00006613

British Geological Survey. (2022). Geology of Britain Viewer. Retrieved from http://mapapps.bgs.ac.uk/geologyofbritain/home.html

Brittain, J. E., & Sartori, M. (2009). Ephemeroptera (Mayflies). In V. H. Resh & R. T. Cardé (Eds.), *Encyclopedia of insects* (pp. 328–333). Academic Press. https://doi.org/10.1016/B978-0-12-374144-8.00100-4

Busch, D. E., & Fisher, S. G. (1981). Metabolism of a desert stream. *Freshwater Biology*, *11*, 301–307. https://doi.org/10.1111/j.1365-2427.1981.tb01263.x

Cahoon, L. B., Nearhoof, J. E., & Tilton, C. L. (1999). Sediment grain size effect on benthic microalgal biomass in shallow aquatic ecosystems. *Estuaries*, *22*, 735–741. https://doi.org/10.2307/1353106

Cardinale, B. J., Palmer, M. A., Swan, C. M., Brooks, S., & Poff, N. L. (2002). The influence of substrate heterogeneity on biofilm metabolism in a stream ecosystem. *Ecology*, *83*(2), 412–422. https://doi.org/10.1890/0012-9658(2002)083[0412:TIOSHO]2.0.CO;2

Céréghino, R., Legalle, M., & Lavandier, P. (2004). Drift and benthic population structure of the mayfly *Rhithrogena semicolorata* (Heptageniidae) under natural and hydropeaking conditions. *Hydrobiologia*, *519*, 127–133. https://doi.org/10.1023/B:HYDR.0000026499.53979.69

Chaddock, R. E. (1921). The graphic representation of a frequency distribution. *Quarterly Publications of the American Statistical Association*, *17*(134), 769–777. https://doi.org/10.1080/15225445.1921.10503836

Clarke, A., MacNally, R., Bond, N., & Lake, P. S. (2008). Macroinvertebrate diversity in headwater streams: A review. *Freshwater Biology*, *53*, 1707–1721. https://doi.org/10.1111/j.1365-2427.2008.02041.x

Cole, J. J., Prairie, Y. T., Caraco, N. F., McDowell, W. H., Tranvik, L. J., Striegl, R. G., Duarte, C. M., Kortelainen, P., Downing, J. A., Middelburg, J. J., & Melack, J. (2007). Plumbing the global carbon cycle: Integrating inland waters into the terrestrial carbon budget. *Ecosystems*, *10*, 172–185. https://doi.org/10.1007/s10021-006-9013-8

Collier, K. J. (1995). Environmental factors affecting the taxonomic composition of aquatic macroinvertebrate communities in lowland waterways of Northland, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, *29*, 453–465. https://doi.org/10.1080/00288330.1995.9516679

Collier, K. J., & Halliday, J. N. (2000). Macroinvertebrate-wood associations during decay of plantation pine in New Zealand pumice-bed streams: Stable habitat or trophic subsidy? *Journal of the North American Benthological Society*, *19*(1), 94–111. https://doi.org/10.2307/1468284

Collier, K. J., & Smith, B. J. (2003). Corrigendum to “Role of wood in pumice-bed streams II: Breakdown and colonisation” [For. Ecol. Manage. 177 (2003) 261–276]. *Forest Ecology and Management*, *181*, 375–390. https://doi.org/10.1016/S0378-1127(03)00222-6

Collier, K. J., Smith, B. J., & Halliday, N. J. (2004). Colonization and use of pine wood versus native wood in New Zealand plantation forest streams: Implications for riparian management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *14*, 179–199. https://doi.org/10.1002/aqc.599

Cudney, M. D., & Wallace, J. B. (1980). Life cycles, microdistribution and production dynamics of six species of net-spinning caddisflies in a large southeastern (U.S.A.) river. *Holarctic Ecology*, *3*, 169–182. https://doi.org/10.1111/j.1600-0587.1980.tb00723.x

de Brouwer, J. H. F., Verdonschot, P. F. M., Eekhout, J. P. C., & Verdonschot, R. C. M. (2020). Macroinvertebrate taxonomic and trait-based responses to large-wood reintroduction in lowland streams. *Freshwater Science*, *39*(4), 693–703. https://doi.org/10.1086/710710

Deane, A., Norrey, J., Coulthard, E., McKendry, D. C., & Dean, A. P. (2021). Riverine large woody debris introduced for natural flood management leads to rapid improvement in aquatic macroinvertebrate diversity. *Ecological Engineering*, *163*, 106197. https://doi.org/10.1016/j.ecoleng.2021.106197

DeJong, T. M. (1975). A comparison of three diversity indices based on their components of richness and evenness. *Oikos*, *26*, 222–227. https://doi.org/10.2307/3543712

Dexter, E., Rollwagen-Bollens, G., & Bollens, S. M. (2018). The trouble with stress: A flexible method for the evaluation of nonmetric multidimensional scaling. *Limnology and Oceanography Methods*, *16*(7), 434–443.

Dobson, M., Pawley, S., Fletcher, M., & Powell, A. (2012). *Guide to freshwater invertebrates*. Freshwater Biological Association.

Doeg, T. J., Marchant, R., Douglas, M., & Lake, P. S. (1989). Experimental colonization of sand, gravel and stones by macroinvertebrates in the Acheron River, Southeastern Australia. *Freshwater Biology*, *22*, 57–64. https://doi.org/10.1111/j.1365-2427.1989.tb01083.x

Dolédec, S., Lamouroux, N., Fuchs, U., & Mérigoux, S. (2007). Modelling the hydraulic preferences of benthic macroinvertebrates in small European streams. *Freshwater Biology*, *52*, 145–164. https://doi.org/10.1111/j.1365-2427.2006.01663.x

Durance, I., Bruford, M. W., Chalmers, R., Chappell, N. A., Christie, M., Cosby, B. J., Noble, D., Ormerod, S. J., Prosser, H., Weightman, A., & Woodward, G. (2016). The challenges of linking ecosystem services to biodiversity: Lessons from a large-scale freshwater study. *Advances in Ecological Research*, *54*, 87–134. https://doi.org/10.1016/bs.aecr.2015.10.003

Ellis, N., Anderson, K., & Brazier, R. (2021). Mainstreaming natural flood management: A proposed research framework derived from a critical evaluation of current knowledge. *Progress in Physical Geography*, *45*(6), 819–841. https://doi.org/10.1177/0309133321997299

Erman, D. C., & Erman, N. A. (1984). The response of stream macroinvertebrates to substrate size and heterogeneity. *Hydrobiologia*, *108*, 75–82. https://doi.org/10.1007/BF02391635

Fellows, C. S., Clapcott, J. E., Udy, J. W., Bunn, S. E., Harch, B. D., Smith, M. J., & Davies, P. M. (2006). Benthic metabolism as an indicator of stream ecosystem health. *Hydrobiologia*, *572*, 71–87. https://doi.org/10.1007/s10750-005-9001-6

Finlay, J. C., Khandwala, S., & Power, M. E. (2002). Spatial scales of carbon flow in a river food web. *Ecology*, *83*(7), 1845–1859. https://doi.org/10.1890/0012-9658(2002)083[1845:SSOCFI]2.0.CO;2

Flores, L., Díez, J. R., Larrañaga, A., Pascoal, C., & Elosegi, A. (2013). Effects of retention site on breakdown of organic matter in a mountain stream. *Freshwater Biology*, *58*, 1267–1278. https://doi.org/10.1111/fwb.12125

Frainer, A., Polvi, L. E., Jansson, R., & McKie, B. G. (2017). Enhanced ecosystem functioning following stream restoration: The roles of habitat heterogeneity and invertebrate species traits. *Journal of Applied Ecology*, *55*, 377–385. https://doi.org/10.1111/1365-2664.12932

Gayraud, S., & Philippe, M. (2003). Influence of bed-sediment features on the interstitial habitat available for macroinvertebrates in 15 French streams. *International Review of Hydrobiology*, *88*(1), 77–93. https://doi.org/10.1002/iroh.200390007

Gerhard, M., & Reich, M. (2000). Restoration of streams with large wood: Effects of accumulated and built-in wood on channel morphology, habitat diversity and aquatic fauna. *International Review of Hydrobiology*, *85*(1), 123–137. https://doi.org/10.1002/(SICI)1522-2632(200003)85:1<123::AID-IROH123>3.0.CO;2-T

Gordon, N. D., McMahon, T. A., Finlayson, B. L., Gippel, C. J., & Nathan, R. J. (2004). *Stream hydrology: An introduction for ecologists* (Second ed.). John Wiley & Sons Ltd.

Groffman, P. M., Dorsey, A. M., & Mayer, P. M. (2005). N processing within geomorphic structures in urban streams. *Journal of the North American Benthological Society*, *24*(3), 613–625. https://doi.org/10.1899/04-026.1

Gulis, V., Suberkropp, K., & Rosemond, A. D. (2008). Comparison of fungal activities on wood and leaf litter in unaltered and nutrient-enriched headwater streams. *Applied and Environmental Microbiology*, *74*(4), 1094–1101. https://doi.org/10.1128/AEM.01903-07

Hargrave, B. T. (1972). Aerobic decomposition of sediment and detritus as a function of particle surface area and organic content. *Limnology and Oceanography*, *17*(4), 583–596. https://doi.org/10.4319/lo.1972.17.4.0583

Hasselquist, E. M., Polvi, L. E., Kahlert, M., Nilsson, C., Sandberg, L., & McKie, B. G. (2018). Contrasting responses among aquatic organism groups to changes in geomorphic complexity along a gradient of stream habitat restoration: Implications for restoration planning and assessment. *Water*, *10*, 1465. https://doi.org/10.3390/w10101465

Hedin, L. O. (1990). Factors controlling sediment community respiration in woodland stream ecosystems. *Oikos*, *57*, 94–105. https://doi.org/10.2307/3565742

Hilderbrand, R. H., Lemly, A. D., Dolloff, C. A., & Harpster, K. L. (1997). Effects of large woody debris placement on stream channels and benthic macroinvertebrates. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*, 931–939. https://doi.org/10.1139/f96-334

Jähnig, S. C., Brabec, K., Buffagni, A., Erba, S., Lorenz, A. W., Ofenböck, T., Verdonschot, P. F. M., & Hering, D. (2010). A comparative analysis of restoration measures and their effects on hydromorphology and benthic invertebrates in 26 central and southern European rivers. *Journal of Applied Ecology*, *47*, 671–680. https://doi.org/10.1111/j.1365-2664.2010.01807.x

Kiffney, P. M., Buhle, E. R., Naman, S. M., Pess, G. R., & Klett, R. S. (2014). Linking resource availability and habitat structure to stream organisms: An experimental and observational assessment. *Ecosphere*, *5*(4), 39. https://doi.org/10.1890/ES13-00269.1

Klaar, M. J., Hill, D. F., Maddock, I., & Milner, A. M. (2011). Interactions between instream wood and hydrogeomorphic development within recently deglaciated streams in Glacier Bay National Park, Alaska. *Geomorphology*, *130*, 208–220. https://doi.org/10.1016/j.geomorph.2011.03.017

Klaar, M. J., Shelley, F. S., Hannah, D. M., & Krause, S. (2020). Instream wood increases riverbed temperature variability in a lowland sandy stream. *River Research and Applications*, *36*, 1529–1542. https://doi.org/10.1002/rra.3698

Krause, S., Klaar, M. J., Hannah, D. M., Mant, J., Bridgeman, J., Trimmer, M., & Manning-Jones, S. (2014). The potential of large woody debris to alter biogeochemical processes and ecosystem services in lowland rivers. *WIREs Water*, *1*, 263–275. https://doi.org/10.1002/wat2.1019

Lane, S. N. (2017). Natural flood management. *WIREs*. *Water*, *4*, e1211. https://doi.org/10.1002/wat2.1211

Lo, H. W., Smith, M., Klaar, M., & Woulds, C. (2021). Potential secondary effects of in-stream wood structures installed for natural flood management: A conceptual model. *WIREs Water*, *8*(5), e1546. https://doi.org/10.1002/wat2.1546

Lo, H. W., van Leeuwen, Z., Klaar, M., Woulds, C., & Smith, M. (2022). Geomorphic effects of natural flood management woody dams in upland streams. *River Research and Applications*, *38*(10), 1787–1802. https://doi.org/10.1002/rra.4045

Magliozzi, C., Meyer, A., Usseglio-Polatera, P., Robertson, A., & Grabowski, R. C. (2020). Investigating invertebrate biodiversity around large wood: Taxonomic vs functional metrics. *Aquatic Sciences*, *82*, 69. https://doi.org/10.1007/s00027-020-00745-9

Magliozzi, C., Usseglio-Polatera, P., Meyer, A., & Grabowski, R. C. (2019). Functional traits of hyporheic and benthic invertebrates reveal importance of wood-driven geomorphological processes in Rivers. *Functional Ecology*, *33*(9), 1758–1770. https://doi.org/10.1111/1365-2435.13381

Manga, M., & Kirchner, J. W. (2000). Stress partitioning in streams by large woody debris. *Water Resources Research*, *36*(8), 2373–2379. https://doi.org/10.1029/2000WR900153

Martin, A. E., Wipfli, M. S., & Spangler, R. E. (2010). Aquatic community responses to salmon carcass analog and wood bundle additions in restored floodplain habitats in an Alaskan stream. *Transactions of the American Fisheries Society*, *139*, 1828–1845. https://doi.org/10.1577/T09-096.1

Mathers, K. L., Rice, S. P., & Wood, P. J. (2017). Temporal effects of enhanced fine sediment loading on macroinvertebrate community structure and functional traits. *Science of the Total Environment*, *599-600*, 513–522. https://doi.org/10.1016/j.scitotenv.2017.04.096

Mcclelland, W. T., & Brusven, M. A. (1980). Effects of sedimentation on the behavior and distribution of riffle insects in a laboratory stream. *Aquatic Insects: International Journal of Freshwater Entomology*, *2*(3), 161–169. https://doi.org/10.1080/01650428009361022

McDowell, W. H. (1985). Kinetics and mechanisms of dissolved organic carbon retention in a headwater stream. *Biogeochemistry*, *1*, 329–352. https://doi.org/10.1007/BF02187376

McKie, B., & Cranston, P. S. (2001). Colonisation of experimentally immersed wood in south eastern Australia: Responses of feeding groups to changes in riparian vegetation. *Hydrobiologia*, *452*, 1–14. https://doi.org/10.1023/A:1011974813551

Moraes, A. B., Wilhelm, A. E., Boelter, T., Stenert, C., Schulz, U. H., & Maltchik, L. (2014). Reduced riparian zone width compromises aquatic macroinvertebrate communities in streams of southern Brazil. *Environmental Monitoring and Assessment*, *186*, 7063–7074. https://doi.org/10.1007/s10661-014-3911-6

Morse, J. C. (2009). Trichoptera (Caddisflies). In V. H. Resh & R. T. Cardé (Eds.), *Encyclopedia of insects* (pp. 1015–1020). London: Academic Press.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2008). Vegan: Community Ecology Package. https://CRAN.R-project.org/package=vegan

Ormerod, S. J., Rundle, S. D., Clare Lloyd, E., & Douglas, A. A. (1993). The influence of riparian management on the habitat structure and macroinvertebrate communities of upland streams draining plantation forests. *Journal of Applied Ecology*, *30*, 13–24. https://doi.org/10.2307/2404266

Perkins, D.M., Yvon-Durocher, G., Demars, B.O.L., Reiss, J., Pichler, D.E., Friberg, N., Trimmer, M. & Woodward, G. (2012). Consistent temperature dependence of respiration across ecosystems contrasting in thermal history. *Global Change Biology*, *18*, 1300–1311. https://doi.org/10.1111/j.1365-2486.2011.02597.x

Pilotto, F., Bertoncin, A., Harvey, G. L., Wharton, G., & Pusch, M. T. (2014). Diversification of stream invertebrate communities by large wood. *Freshwater Biology*, *59*, 2571–2583. https://doi.org/10.1111/fwb.12454

Pinto, C., Ing, R., Browning, B., Delboni, V., Wilson, H., Martyn, D., & Harvey, G. L. (2019). Hydromorphological, hydraulic and ecological effects of restored wood: Findings and reflections from an academic partnership approach. *Water and Environment Journal*, *33*, 353–365. https://doi.org/10.1111/wej.12457

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Reice, S. R. (1980). The role of substratum in benthic macroinvertebrate microdistribution and litter decomposition in a woodland stream. *Ecology*, *61*(3), 580–590. https://doi.org/10.2307/1937424

Roman, A. M., & Sabater, S. (1999). Effect of primary producers on the heterotrophic metabolism of a stream biofilm. *Freshwater Biology*, *41*(4), 729–736. https://doi.org/10.1046/j.1365-2427.1999.00413.x

Schwendel, A. C., Death, R. G., & Fuller, I. C. (2010). The assessment of shear stress and bed stability in stream ecology. *Freshwater Biology*, *55*, 261–281. https://doi.org/10.1111/j.1365-2427.2009.02293.x

Shelly, T. E. (1979). The effect of rock size upon the distribution of species of Orthocladiinae (Chironomidae: Diptera) and *Baetis intercalaris* McDunnough (Baetidae: Ephemeroptera). *Ecological Entomology*, *4*, 95–100. https://doi.org/10.1111/j.1365-2311.1979.tb00564.x

Smock, L. A., Metzler, G. M., & Gladden, J. E. (1989). Role of debris dams in the structure and functioning of low-gradient headwater streams. *Ecology*, *70*(3), 764–775. https://doi.org/10.2307/1940226

Stewart, K. W. (2009). Plecoptera (Stoneflies). In V. H. Resh & R. T. Cardé (Eds.), *Encyclopedia of insects* (pp. 810–813). Academic Press. https://doi.org/10.1016/B978-0-12-374144-8.00214-9

Stewart, P. M., Bhattarai, S., Mullen, M. W., Metcalf, C. K., & Reátegui-Zirena, E. G. (2012). Characterization of large wood and its relationship to pool formation and macroinvertebrate metrics in southeastern coastal plain streams, USA. *Journal of Freshwater Ecology*, *27*(3), 351–365. https://doi.org/10.1080/02705060.2012.679322

Sutherland, R. A. (1999). Distribution of organic carbon in bed sediments of Manoa Stream, Oahu, Hawaii. *Earth Surface Processes and Landforms*, *24*, 571–583. https://doi.org/10.1002/(SICI)1096-9837(199907)24:7<571::AID-ESP975>3.0.CO;2-F

Tank, J. L., Webster, J. R., & Benfield, E. F. (1993). Microbial respiration on decaying leaves and sticks in a southern Appalachian stream. *Journal of the North American Benthological Society*, *12*(4), 394–405. https://doi.org/10.2307/1467620

Testa, S., Shields, D., & Cooper, C. M. (2011). Macroinvertebrate response to stream restoration by large wood addition. *Ecohydrology*, *4*, 631–643. https://doi.org/10.1002/eco.146

Tritico, H. M., & Hotchkiss, R. H. (2005). Unobstructed and obstructed turbulent flow in gravel bed rivers. *Journal of Hydraulic Engineering*, *131*(8), 635–645. https://doi.org/10.1061/(ASCE)0733-9429(2005)131:8(635)

Uehlinger, U., Naegeli, M., & Fisher, S. G. (2002). A heterotrophic desert stream? The role of sediment stability. *Western North American Naturalist*, *62*(4), 466–473.

Underwood, A. J. (1992). Beyond BACI: The detection of environmental impacts on populations in the real, but variable, world. *Journal of Experimental Marine Biology and Ecology*, *161*, 145–178. https://doi.org/10.1016/0022-0981(92)90094-Q

Warren, D. R., & Kraft, C. E. (2006). Invertebrate community and stream substrate responses to woody debris removal from an ice storm-impacted stream system, NY USA. *Hyrobiologia*, *568*, 477–488. https://doi.org/10.1007/s10750-006-0218-9

Wellnitz, T., Kim, S. Y., & Merten, E. (2014). Do installed stream logjams change benthic community structure? *Limnologica*, *49*, 68–72. https://doi.org/10.1016/j.limno.2014.09.002

Williams, D. D., Williams, N. E., & Hogg, I. D. (1995). Life history plasticity of *Nemoura trispinosa* (Plecoptera: Nemouridae) along a permanent-temporary water habitat gradient. *Freshwater Biology*, *34*, 155–163. https://doi.org/10.1111/j.1365-2427.1995.tb00432.x

Winkler, G. (1991). Debris dams and retention in a low order stream (a backwater of Oberer Seebach – Ritrodat-Lunz study area, Austria). *Internationale Vereinigung für Theoretische Und Angewandte Limnologie: Verhandlungen*, *24*(3), 1917–1920. https://doi.org/10.1080/03680770.1989.11899097

Wohl, E. (2015). Particle dynamics: The continuum of bedrock to alluvial river segments. *Geomorphology*, *241*, 192–208. https://doi.org/10.1016/j.geomorph.2015.04.014

Wolman, M. G. (1954). A method of sampling coarse river-bed material. *Transactions, American Geophysical Union*, *35*(6), 951–956.

Yorkshire Dales National Park Authority. (2002). *Geology: Foundations of natural beauty*. Leyburn.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Lo, H. W., Klaar, M., Smith, M., & Woulds, C. (2024). Effects of natural flood management woody dams on benthic macroinvertebrates and benthic metabolism in upland streams: Importance of wood-induced geomorphic changes. *Ecohydrology*, *17*(5), e2654. https://doi.org/10.1002/eco.2654