



Organic litter dynamics in headwater streams draining contrasting land uses

Marian C. Pye · Ian P. Vaughan ·
Steve J. Ormerod · Isabelle Durance

Received: 7 March 2022 / Revised: 6 November 2022 / Accepted: 7 November 2022 / Published online: 29 November 2022
© The Author(s) 2022

Abstract Climate change could alter fluxes of organic matter and macronutrients through freshwater ecosystems potentially affecting stream organisms. However, riparian controls on litter dynamics offer an opportunity to adapt headwaters to climate change by protecting or restoring riparian vegetation. We assessed how riparian land cover and climatic variability affected the supply, retention and downstream transport of particulate organic matter (POM) in headwaters—the most extensive small water bodies in temperate landscapes. Leaf litter inputs, benthic stocks and suspended organic matter were measured nominally monthly in second–third-order streams draining broadleaf woodland, conifer, acid moorland and circumneutral moorland over four years with varying discharge. Streams draining broadleaf woodland received more leaf litter from the riparian zone than conifer and moorland and transported higher concentrations of CPOM and FPOM at base flows. Broadleaf sites had higher CPOM stocks, even after hydrological events that reduced CPOM in conifer and moorland sites. In contrast, FPOM dynamics

reflected hydrological conditions irrespective of land cover. These results show how some organic matter fractions in streams are sensitive to hydrological conditions, illustrating how wetter climates will influence FPOM exports. Nevertheless, riparian broadleaves have the potential to offset climatic effects on organic matter processing in headwaters through the replenishment and retention of CPOM.

Keywords Adaptation · Climate change · Land use · Leaf litter · Nature-based solutions · Small water bodies

Introduction

Climate change poses major threats to global biodiversity and ecological functioning, with rivers among the most sensitive of all ecosystems (Ormerod, 2009). Many freshwater organisms are affected by thermal and hydrological regimes either directly, indirectly through resource availability, or through interactions between climatic effects and other stressors (Woodward et al., 2010). Among river types, headwater streams (first to third order) are at particular risk to changing temperature and precipitation because of their low thermal mass and rapid response to hydrological events (Gomi et al., 2002; Caissie, 2006). Headwaters are also the most extensive small water bodies in temperate landscapes because of their disproportionately large contribution to total river length

Guest editors: Mary Kelly-Quinn, Jeremy Biggs,
J. Iwan Jones & William D. Riley / Small Water Bodies
in the Landscape

M. C. Pye · I. P. Vaughan · S. J. Ormerod (✉) · I. Durance
Water Research Institute, Cardiff School of Biosciences,
Cardiff University, Sir Martin Evans Building Museum
Avenue, Cardiff CF10 3AX, UK
e-mail: ormerod@cardiff.ac.uk

(Biggs et al., 2017; Riley et al., 2018). Already, headwaters at higher latitudes and altitudes show evidence of increasing discharge in winter, increased frequency of hydrological events (Birsan et al., 2005; Dixon et al., 2006; Hannaford & Marsh, 2006; Marsh & Dixon, 2012), earlier spring snowmelt (Kormann et al., 2015) and rapid warming (Hassan et al., 2005). Evidence of concomitant biological change is also emerging (Durance & Ormerod, 2007), although the exact causes are unclear (Cahill et al., 2012) and likely to reflect complex mechanisms that include direct physiological effects on individual taxa as well as indirect effects on organisms, processes and functions (e.g., Durance and Ormerod, 2010).

Given their importance as biodiversity hotspots (Meyer et al., 2007; Finn et al., 2011), their value as ‘sentinel systems’ (Perkins et al., 2010), and their role as sources of water, organic matter and macronutrients for downstream ecosystems (Wipfli et al., 2007; Battin et al., 2008), there is a need to understand how headwaters respond to climate change and variation (Riley et al., 2018). One potential mechanism is through changes in the amount, composition, timing, flux or retention of key basal resources that normally support biological production (Verdonschot & van den Hoorn, 2010; Kominoski & Rosemond, 2012). Like many ecosystems (Polis et al., 1997), headwaters are fuelled by resources from outside their boundaries, as well as by in situ primary production. In upland streams, these ‘resource subsidies’ are largely composed of terrestrial detritus, mostly leaf litter from riparian vegetation, whose availability could be sensitive to changes in stream flow and thermal regimes. For example, temperatures affects the seasonality and timing of leaf fall (Duputié et al., 2015; Sanpera-Calbet et al., 2016), while warming accelerates the biological decomposition of leaves in ways that vary among species (Graça et al., 2015; Follstad Shah et al., 2017). Additionally, leaf litter retention decreases with increasing discharge (Webster et al., 1987; Pretty & Dobson, 2004; Koljonen et al., 2012), while the majority of annual litter export occurs during storm events (Webster et al., 1987; Johnson et al., 2006; Richardson et al., 2009a; Eggert et al., 2012). These effects raise the possibility that leaf litter in headwaters may be depleted more rapidly as temperatures rise and as the hydrological cycle intensifies (Acuña & Tockner, 2010; Heartsill-Scalley et al., 2012).

As well as understanding potential climatic influences on litter fluxes in headwaters, there is an opportunity to consider whether factors affecting litter inputs and dynamics could offer a means of managing climate change impacts. Interest in such ‘nature-based solutions’ to address environmental stressors is growing rapidly (Murphy et al., 2021; Seddon et al., 2020). For example, the restoration or planting of riparian trees is advocated as an adaptive management strategy to mitigate the effects of land use and climate change on stream ecosystems (e.g., Abell et al., 2007; Ormerod, 2009; Palmer et al., 2009; Seavy et al., 2009). Specifically, riparian trees moderate hydrological (Bradshaw et al., 2007) and thermal extremes in streams (Broadmeadow et al., 2011; Garner et al., 2015), reduce sediment and nutrient inputs (Broadmeadow & Nisbet, 2004; Sweeney et al., 2004), increase aquatic and terrestrial biodiversity (Naiman et al., 1993; Suurkuukka et al., 2014) and increase in-stream habitat diversity through inputs of woody debris (Naiman & Décamps, 1997; Gurnell et al., 2002). However, benefits might also arise through riparian controls on litter stocks and secondary production (Thomas et al., 2016) with associated value to food web structure (Polis et al., 1997), habitat structure (Moore et al., 2004) and ecosystem stability (Rooney et al., 2006). Indeed, a wealth of evidence demonstrates the importance of detritus in subsidising recipient food webs in forested headwater streams (e.g., Fisher and Likens, 1973; Benke et al., 1984; Wallace et al., 1999, 2015) and increasingly also even in open-canopy streams where detrital inputs here are comparatively low (e.g., Menninger and Palmer, 2007; Leberfinger et al., 2011; Dekar et al., 2012). The significance of detritus in headwaters is reflected in the trait diversity among aquatic invertebrates such that some taxa ‘shred’ coarser particles of organic matter (CPOM) while others ‘collect’ or ‘filter’ the smaller, more labile particles of fine particulate organic matter (FPOM) (Cummins et al., 1989). In combination with bacterial and fungal breakdown, these processes transfer energy and nutrients from detritus to higher trophic levels and to other downstream consumers. Interactions between climatic and land use controls on organic matter inputs and fluxes through headwaters are therefore likely to have wide ranging consequences both locally and beyond headwater

boundaries (Wipfli et al., 2007; Richardson et al., 2010; Scharnweber et al., 2014; Jonsson et al., 2015).

Despite the potential importance of interactions between climate and riparian land use in mediating the dynamics of organic matter dynamics in headwaters, understanding is currently rudimentary despite decades of research focus (Tank et al., 2010). Recent attempts to model organic matter dynamics under future climate or riparian management scenarios have been limited by gaps in empirical evidence and process-based understanding (e.g., Richardson et al., 2009a; Acuña and Tockner, 2010; Stenroth et al., 2014). To date, most field-based studies on organic matter dynamics have involved short timescales (~1 year, e.g., Abelho & Graça, 1996; González and Pozo, 1996; Cariss and Dobson, 1997; Pozo et al., 1997), or small spatial scales (~1 study site e.g., Molinero and Pozo, 2004; Mollá et al., 2006; Wallace et al., 2015). Long-term, field-based studies conducted over multiple catchments with contrasting land use are therefore a priority.

In this paper, we assess whether riparian broadleaved woodlands can offset the effects of climate-driven changes in flow regimes on organic matter dynamics in headwaters by comparing the inputs, availability and exports of particulate organic matter with adjacent conifer and moorland streams. Specifically, variations in organic matter inputs, benthic standing stocks, and suspended concentrations were measured over four years in headwater streams with contrasting riparian land cover types in central Wales, UK, to test the following predictions:

1. In all land cover types, organic matter storage and downstream transport are driven by hydrological conditions, with wetter conditions resulting in reduced standing stocks and enhanced export.
2. Despite hydrological effects, streams draining broadleaved woodlands receive, store and transport greater quantities of particulate organic matter by comparison with conifer and moorland streams.

The second of these predictions, if upheld, has particular importance for the role of riparian broadleaved woodlands in climate change management.

Materials and methods

Study sites and overall experimental design

The study was conducted in eight second- to third-order streams (catchment area 17–264 ha), located in the headwaters of the Afon Tywi, within the Llyn Brianne Stream Observatory (LBSO; <https://www.cardiff.ac.uk/llyn-brianne-observatory>) in central Wales, UK (52°8'N 3°45'W; Fig. 1; see Durance & Ormerod (2007) and Weatherley & Ormerod (1987) for full site details). The sites have a long history in global change research on a range of themes (Durance & Ormerod, 2007; Larsen et al., 2018). Regional climate is maritime and temperate, with mean daily stream temperatures between 0.5 and 16°C and annual mean rainfall ca. 1900 mm (Weatherley & Ormerod, 1990). The sites were chosen at the project's outset in 1981 to represent typical classes of land cover that occur across upland Britain, and were categorised on the dominant vegetation within 10 m of the stream bank as broadleaved woodland (Blf; site codes 'G1' and 'G2', mostly oaks *Quercus robur* L. and birch *Betula pendula* Roth), conifer plantation (Con; site codes 'L1' and 'L2' mostly Sitka spruce *Picea sitchensis* (Bong) Carr. and lodgepole pine *Pinus contorta* Douglas), acid moorland (AM; site codes 'C1' and 'C4') and circumneutral moorland (CM; site codes 'L6' and 'L7'). Although acid and circumneutral moorland streams are similar in catchment land classification, they differ in acid–base status because of local calcite veins, while there is also increased cover of bracken *Pteridium aquilinum* (L.) Kuhn with occasional mountain ash *Sorbus aucuparia* L., willow *Salix* spp and hawthorn *Crataegus monogyna* Jacq. over the brown earth soils at the CM sites. The AM sites, in contrast, have more purple moor-grass *Molinia caerulea* (L.) Moench over peaty gley soils. All study sites were located within 10 km of each other ensuring that climatic conditions were similar.

For logistical reasons reflecting the intensity of work required in assessing litter dynamics, we concentrated effort on one 'core' site from each land use category (C4, G1, L1 and L6) while ensuring some replication for less intensive measurements (C1, G2, L2, L7). Over four years between November 2010 and September 2014, inputs of leaf litter, benthic standing stocks of CPOM and FPOM, and suspended concentrations of CPOM and FPOM (hereafter "leaf

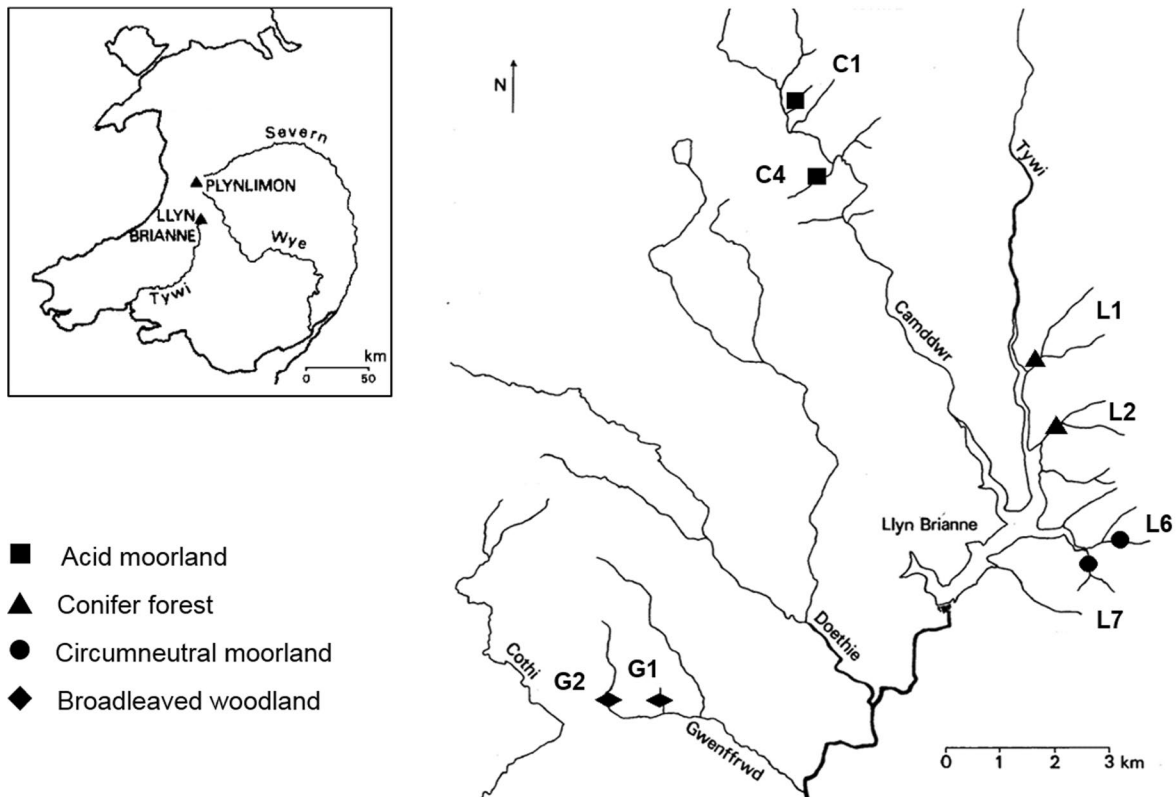


Fig. 1 Locations of the eight study streams within the Llyn Brianne Stream Observatory in central Wales, UK. Major river systems are labelled. Images adapted from Edwards et al. (1990) and Broadmeadow and Nisbet (2002)

litter inputs”, “CPOM/FPOM standing stocks” and “CPOM/FPOM concentrations”, respectively) were measured at monthly-bimonthly intervals in the four “core” catchments. Leaf litter inputs were measured during three periods of broadleaf litterfall and movement (November, late December, January/February). CPOM/FPOM standing stocks and concentrations were measured monthly/bimonthly depending on weather and flow conditions. CPOM/FPOM was sampled at 35 dates; on average, 8–9 dates were sampled every year. Standing stocks were measured in all eight catchment (i.e., two per land use type) from October 2011 onwards.

Stream discharge measurements

Stream discharge ($\text{m}^3 \text{s}^{-1}$) was recorded at 15-min intervals at one of the study sites, L1 (data supplied by Natural Resource Wales from 1991; Station number 060S0589W), and was assumed to reflect

relative flow conditions for all sites as well as wider hydro-climatic conditions. These assumptions were supported by (i) comparisons between stream flow measured at L1 and regional rainfall data (Fig. 2) and (ii) long-term observations of stream flow at several nearby catchments of identical order and similar altitude that show clear similarities in relative flow regimes (Marc & Robinson, 2007). Thus, discharge measured continuously by the UK Centre for Ecology and Hydrology on Plynlimon, 37 km to the north (Plynlimon flume; $52^{\circ}28'14'' \text{ N}$, $3^{\circ}41'16'' \text{ W}$), and at a gauged site on the Afon Cothi, 20 km to the south west ($51^{\circ}51'37'' \text{ N}$, $4^{\circ}11'00'' \text{ W}$), correlated highly significantly with measured values at Llyn Brianne ($r=0.90$, $n=289$ monthly mean values, $P<0.0001$).

Organic matter sampling and laboratory methods

Direct and indirect inputs of leaf litter were estimated on each occasion using separate proxy measurements

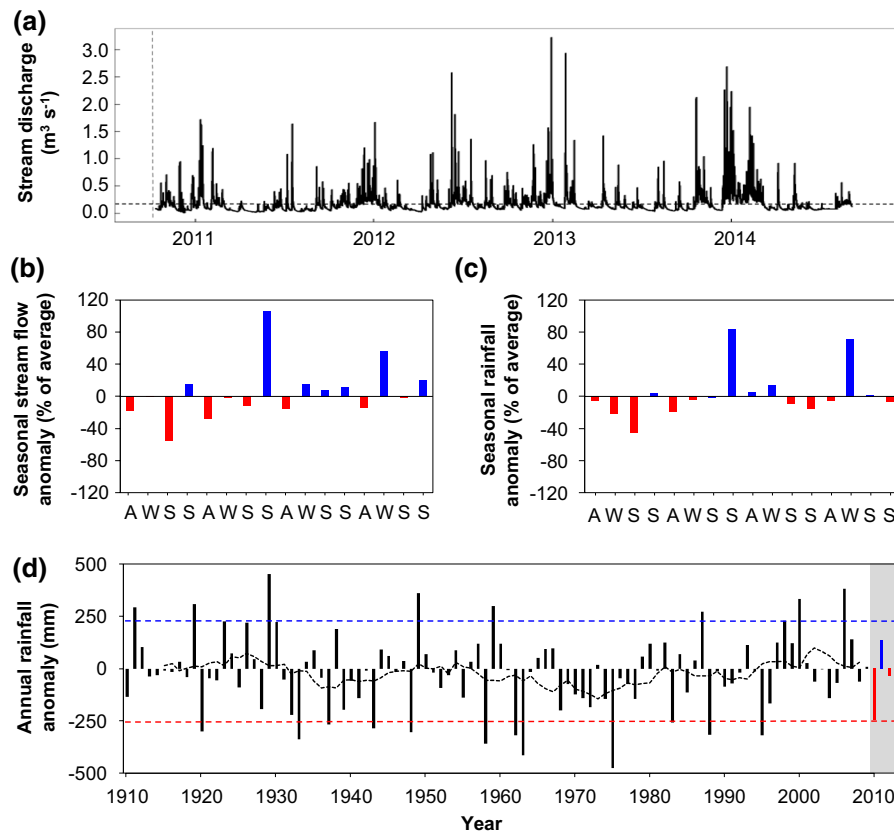


Fig. 2 Hydrological conditions over the study period, 2010–2014 and comparisons with long-term records, 1910–2014, at the local (study site L1, Llyn Brienne Stream Observatory, mid-Wales, UK) and regional (Wales, UK) scale. Figure **a** shows 15-min stream discharge ($\text{m}^3 \text{s}^{-1}$) at L1 during the study period October 2010 to September 2014. Horizontal dashed line and shaded band, respectively, depict the overall mean and range of stream flows under which organic matter sampling took place. Figure **b–c** shows seasonal anomalies in **(b)** regional rainfall and **(c)** local stream flow, respectively, during the study period October 2010 to September 2014 (corresponding to the shaded areas in **(d)**). Seasonal anomalies

represent differences in average seasonal rainfall or discharge from 1996 to 2010 averages. Seasonal averages are calculated using data over a 3-month period for Autumn (A; Sep–Oct–Nov), Winter (W; Dec–Jan–Feb), Spring (S; Mar–Apr–May) and Summer (S; Jun–Jul–Aug). Figure **d** shows annual (=Oct–Sept) anomalies in regional rainfall during 1910–2014. Blue and red dotted lines denote maximum and minimum values, respectively. Black dotted line denotes moving 10-year average. Regional rainfall data provided by © UK Meteorological Office; L1 stream discharge data provided by Natural Resources Wales (© Natural Resources Wales and database right)

of the mass and movement of leaf litter. Direct inputs (i.e., vertical inputs of leaf litter falling directly into the stream from the overhead canopy) were estimated by collecting all non-woody leaf litter from each of four 0.42 m^2 marked plots (cleared of all loose material one month prior to the first collection), which were positioned on the ground approximately 1 m from the stream bank, 10 m apart, along each stream bank ($n=8$ ‘proximal plots’ per site). This position reflected a trade-off between the quadrats being placed close enough to the stream to represent likely

inputs and the risk of samples being lost during storm events. Note, also, that the Brienne streams are mostly 0.5–2 m in width, so that lateral variations in direct litterfall into the streams are likely to be small. Litter samples were air-dried in the laboratory and weighed to the nearest 0.01 g. To correct for any losses of leaf litter from each plot, set numbers of painted leaves were placed in adjacent 0.42 m^2 plots on each sampling occasion. Painted leaves were used as markers of leaf residence and throughout, and the proportion of remaining painted leaves collected and recorded

on each subsequent sampling occasion. These marked leaves included the dominant species present in each catchment (acid moorland = purple moor-grass); broadleaf woodland = common oak; conifer forest = Sitka spruce). The mass of leaf litter samples in each distal plot was then divided by the proportion of painted leaves remaining and the number of days since the last sampling occasion to estimate the mass per unit area of direct leaf litter input per day for each sampling period.

Indirect inputs (i.e., leaf litter entering the stream indirectly via lateral movement from the stream bank; measured during Oct 2013–Sep 2014 only) were estimated by measuring the mean distance moved (in m) by set numbers of painted leaves (using the same species as in the proximal plots, see above), which were placed in four marked 0.42 m² plots positioned on the ground approximately 10 m from the stream bank, 10 m apart, along each stream bank ($n=8$ distal plots per site), on each sampling occasion. The mean distance moved (m) from each distal plot was then multiplied by the mean mass of direct inputs (g m⁻² per day, estimated from all proximal plots) and then multiplied by 2 (two sides of stream) to estimate the mass of indirect leaf litter input per m⁻² per day (assuming a 1 m-wide stream), for each sampling occasion.

Benthic coarse and fine POM (benthic CPOM = non-woody detritus > 2 mm; benthic FPOM = > 0.5 mm < 2 mm) was sampled on each occasion using a randomly positioned Hess sampler ($n=5$ replicates per site; area 0.707 m²; mesh aperture 500 µm; sampling depth 10–15 cm) and preserved on-site in 70% industrial methylated spirit (IMS; Fisher Scientific, UK). In the laboratory, all macroinvertebrates were removed; then, the remaining sample material was rinsed under tap water to remove sediment and retained on graduated 0.5- and 2-mm sieves (Endecotts Ltd., UK), air-dried and weighed to the nearest 0.01 g.

Suspended fine and coarse POM (suspended FPOM = suspended particles > 10 µm and < 1 mm; suspended CPOM = suspended particles > 1 mm) was sampled on each occasion ($n=3$ replicates per reach) by filtering known volumes (range = 10–600 l as measured by repeated use of a 5 l container; mean = 142.6 l) of stream water through a stacked pair of 10 µm (fine) and 1 mm (coarse) mesh filters, with care taken not to resuspend particles from the stream bed. Upon collection, suspended POM

samples were refrigerated at ~4 °C, returned to the laboratory and frozen within 24 h. Frozen suspended POM samples were then freeze-dried at -20 °C for 48–72 h and weighed to the nearest 0.001 g.

Ash-free dry mass (AFDM) of all samples was estimated by combusting a subset (~1/3) of samples from each site at 550 °C for 5 h in a muffle furnace and applying ash-free conversion factors to the air-dried mass. Leaf litter input data were expressed in g AFDM m⁻² day⁻¹; CPOM and FPOM standing stock data were expressed in g AFDM m⁻² and suspended CPOM and FPOM concentration data in mg AFDM l⁻¹.

Data analysis

To determine whether quantities of leaf litter inputs, POM standing stocks and POM concentrations differed among riparian land cover types, each response variable was modelled using a linear mixed-effects model with ‘Land cover’ (acid moorland, broadleaf woodland, circumneutral moorland, conifer forest) as a fixed term. ‘Sampling date’ was included as a random term in all models to account for unexplained temporal variation likely to affect all locations (e.g., seasonal variation or flow conditions). In leaf litter inputs models, the random term ‘Quadrat ID’ was crossed with ‘Sampling date’ to account for the non-independence of samples collected from the same quadrat. In POM standing stock models, the random term ‘Site’ was crossed with ‘Sampling date’ to account for the non-independence of samples collected from the same site on each sampling occasion. All models were fitted using restricted maximum likelihood (REML) and validated by visual inspection of the distribution of the standardised residuals versus the fitted values and of the distribution of the random effects (Zuur et al., 2009).

To determine whether temporal variations in CPOM and FPOM standing stocks and concentrations were determined by riparian land cover and/or stream discharge patterns, each of the four response variables was modelled using global linear mixed-effects models, which were then refined using a backwards selection procedure (after Zuur et al., 2009). First, the initial global models were fitted with ‘Riparian land cover’, ‘Discharge’ and a two-way ‘Riparian land cover x Discharge’ interaction as fixed terms. Then, non-significant terms were removed sequentially

using likelihood ratio tests with maximum likelihood estimation, selecting the models with the lowest Akaike Information Criterion (AIC) in each case until only significant terms remained (Zuur et al., 2009). The final optimal models were then re-fitted using REML and their residual distributions checked (Zuur et al., 2009). ‘Discharge’ was represented by the magnitude of antecedent high flows (‘Q5’; determined as stream discharge ($\text{m}^3 \text{s}^{-1}$) equalled or exceeded in 5% of the 30-day flow record prior to each sampling occasion) for the CPOM and FPOM standing stocks models, and mean discharge on the day of sampling (‘Q-day’; determined as mean stream discharge ($\text{m}^3 \text{s}^{-1}$) was recorded over 24 h on the calendar date of sampling) for the CPOM and FPOM concentration models. Both discharge variables were derived from the 15-min discharge data recorded at L1.

In all final models, the *P*-values of the fixed effects were estimated using conditional *F*-tests based on Kenward–Roger approximation for degrees of freedom (Kenward & Roger, 1997), using the R package *Pbkrtest* (Halekoh & Højsgaard, 2014). In addition, the predictive power of the model parameters (i.e., marginal R^2 ; the proportion of variance explained by the fixed factors alone, and conditional R^2 ; the proportion of variance explained by both the fixed and random factors) was estimated using the *r.squared*. *GLMM* function in the R package *MuMin* (Nakagawa & Schielzeth, 2013; Bartón, 2015). Where necessary, response and explanatory variables were transformed to homogenise variances. All mixed models were fitted using the *lmer* function within the *lme4* package (Bates et al., 2015) in R (R Development Core Team, 2016).

Results

Hydrological conditions

Over the four-year study period, stream discharge at the gauged index site, L1, ranged between 0.001 and $4.080 \text{ m}^3 \text{ s}^{-1}$ with an overall median of $0.120 \text{ m}^3 \text{ s}^{-1}$ (Fig. 2a). Seasonal anomalies in stream flow (Fig. 2b) were similar to regional rainfall patterns (Fig. 2c), which in turn reflected long-term historical inter-annual variability (Fig. 2d). Relative to historical averages, the first and third years of study were relatively dry, while the second and fourth years were relatively wet (Fig. 2d). The two wet years notably included the wettest summer and the wettest winter in Wales in the preceding 100 years (data not shown).

Riparian land cover and organic matter dynamics

Across all years of the study, the broadleaf woodland site supplied significantly greater amounts of leaf litter directly and indirectly to the associated stream than the acid moorland, circumneutral moorland and conifer forest sites, among which litter inputs were not distinguishable (Table 1; Fig. 3a). Standing stocks of CPOM and FPOM were more similar across land cover types (Table 1; Fig. 3b), with broadleaf sites storing significantly more CPOM than circumneutral sites but not acid moorland and conifer sites. FPOM followed similar patterns, though there were no significant differences among riparian land cover types.

Concentrations of suspended CPOM and FPOM were significantly greater in the broadleaf stream than in all the other riparian land cover types (Table 1; Fig. 3b). Otherwise, CPOM and FPOM

Table 1 Summary GLMM output for all individual responses to riparian land cover

Response	<i>Df</i>	<i>F</i> -value	<i>P</i> -value	Post-hoc	r^2_m	r^2_c
<i>Input rates</i>						
Direct	3	31.82	< 0.001	Br > AM, CM, Co	0.43	0.65
Indirect	3	25.02	< 0.001	Br > AM, CM, Co	0.32	0.45
<i>Standing stocks</i>						
CPOM	3	7.39	0.042	Br > CM	0.36	0.55
FPOM	3	3.96	0.109	–	0.25	0.60
<i>Concentrations</i>						
CPOM	3	52.96	< 0.001	Br > AM, CM, Co	0.18	0.55
FPOM	3	106.89	< 0.001	Br > AM, CM, Co; AM > Co; Co > CM	0.21	0.74

The results of the post hoc tests indicate significant differences in rank order among the sites

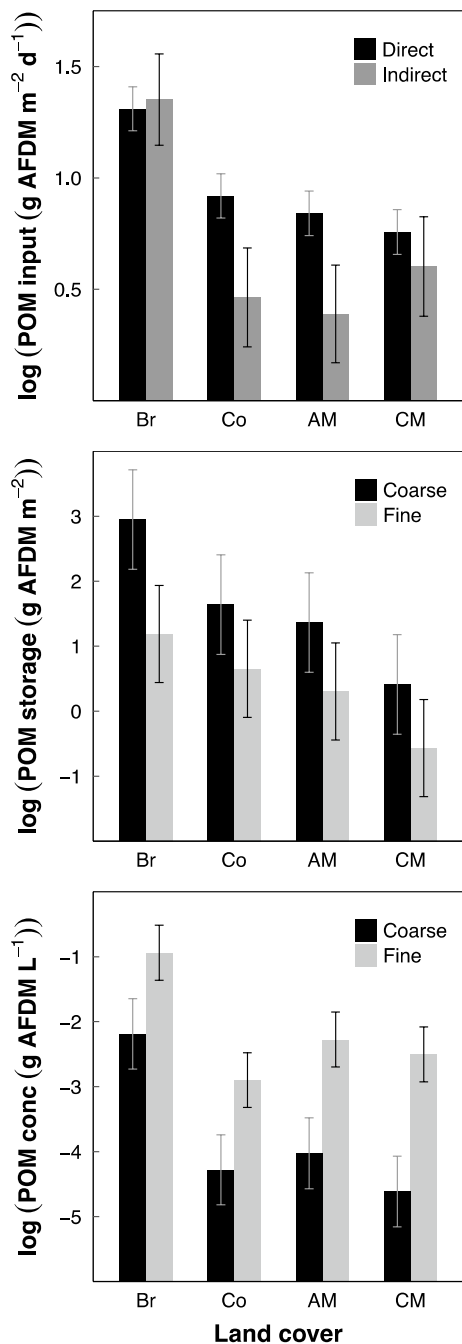


Fig. 3 Estimated **a** inputs, **b** standing stocks and **c** concentrations of particulate organic matter versus riparian land cover (Br=Broadleaf woodland; Co=Conifer forest; AM=Acid moorland; CM=Circumneutral moorland) for each of the four core streams at Llyn Brianne (all data are means with 95% confidence intervals)

concentrations were similar among the conifer and moorland sites, though CPOM concentrations were lower in the circumneutral moorland site than the acid moorland site, while the conifer site had lower FPOM concentrations than the acid moorland site. Across all sites, standing stocks of POM occurred largely in the form of coarse particles, whereas POM in suspension was dominated by fine particles (Fig. 3b, c).

Hydrological conditions and organic matter dynamics

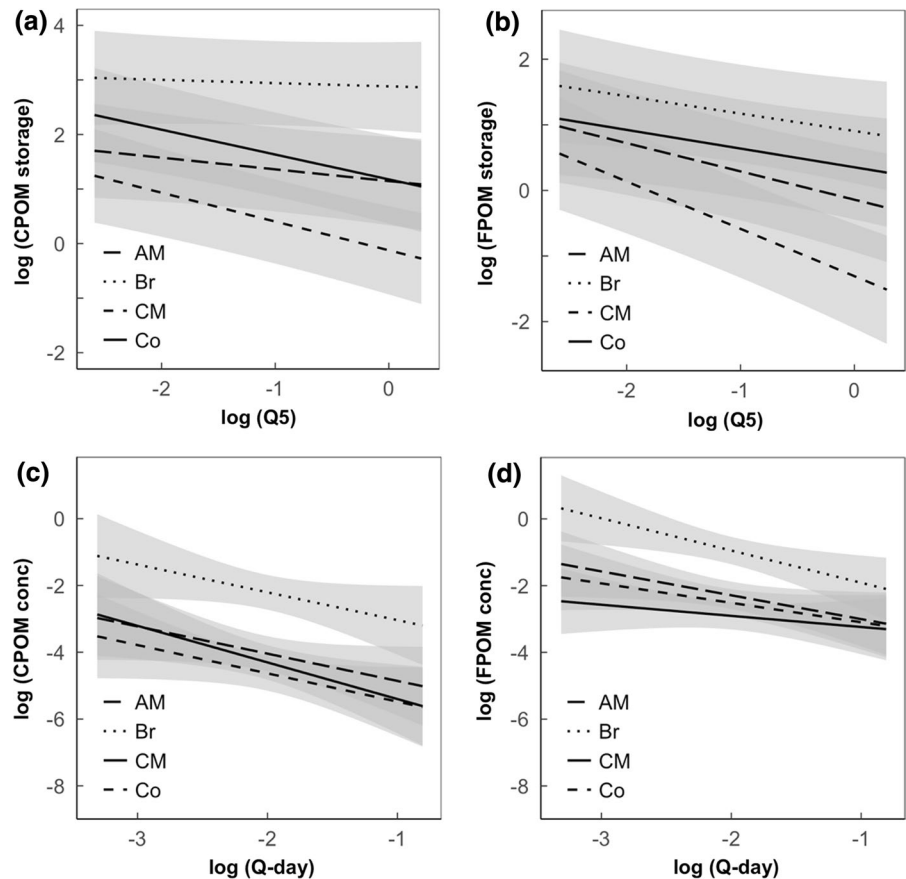
Following larger floods, benthic FPOM standing stocks were reduced in all land cover types, with this effect most pronounced in circumneutral moorland sites ($F_{3,1196.5}=8.97$, $P<0.001$; $r^2_m=0.31$, $r^2_c=0.61$; Fig. 4b). In contrast, benthic CPOM standing stocks were reduced in streams draining all land cover types except broadleaf woodland ($F_{3,1200.3}=5.77$, $P<0.001$; $r^2_m=0.38$, $r^2_c=0.56$; Fig. 4a).

Concentrations of suspended CPOM were consistently reduced at higher stream discharge levels ($F_{1,32.8}=5.36$, $P=0.027$; $r^2_m=0.23$, $r^2_c=0.56$; Fig. 4c), implying dilution effects, but remained highest in broadleaves. For FPOM, the effect of stream discharge depended on land cover type, with broadleaf sites transporting the highest concentrations of FPOM at base flows, whereas concentrations were similar among sites at higher flows ($F_{3,366.1}=3.68$, $P=0.012$; $r^2_m=0.26$, $r^2_c=0.75$; Fig. 4d).

Discussion

Leaf litter dynamics provide an important research focus in freshwater ecology, particularly set against the need to address climate change effects on river ecosystems. As a fundamental resource for temperate stream organisms, the input, storage and export of autochthonous litter in headwaters are expected to be controlled hydrologically, while temperature also affects its breakdown (Webster et al., 1999; Northington & Webster, 2017; Follstad Shah et al., 2017). Additionally, management proposals to reduce the risks of climate change to streams include the restoration of riparian woodlands both to moderate temperatures and to enhance resource supply to freshwater organisms (Thomas et al., 2016). So far, however, there have been few empirical comparisons of these effects across different riparian land

Fig. 4 Estimated slopes and 95% confidence intervals for modelled **a** CPOM standing stocks and **b** FPOM standing stocks (g AFDM m^{-2}) versus the magnitude of high flows (Q5: stream discharge exceeded 5% of the time), and modelled **c** CPOM concentrations and **d** FPOM concentrations (mg AFDM l^{-1}) versus mean discharge on the day of sampling, for each land cover type (AM= Acid moorland; Br= Broadleaf woodland; CM= Circumneutral moorland; Co= Conifer forest). Stream discharge variables derived from 15-min data recorded at study site L1, provided by Natural Resources Wales (© Natural Resources Wales and database right)



uses. We therefore aimed in this investigation to test two related hypotheses that (i) organic matter storage in upland streams is reduced through downstream export under wetter conditions and (ii) streams draining broadleaved woodlands receive and store more particulate organic matter than other streams, thus offsetting any flow-related losses. Both hypotheses were supported with minor qualification: wetter periods reduced FPOM standing stocks across all land cover types, while CPOM stocks were reduced at conifer and moorland sites. In contrast, at broadleaf sites CPOM stocks were maintained following hydrological events, losses of FPOM here were lower, and suspended concentrations were effectively maintained during high flow. Moreover, broadleaf sites received greater quantities of leaf litter from the riparian zone than conifer and moorland sites, reflected also in greater CPOM and FPOM in suspension at low flows. There was some departure from expectation in that variations in benthic FPOM and CPOM stocks were masked by inter-site variability, and only for CPOM

were stocks greater in broadleaf than in circumneutral moorland. Overall, support for the first hypothesis implies that any increased discharge resulting from climate change has the potential to reduce litter stocks for consumers, while general support for the second hypothesis illustrates further the value of riparian broadleaves along temperate headwaters in climate change adaptation (Thomas et al., 2016).

As with all field investigations, several caveats apply to our results. For example, we made no assessments of the phenology or quality of litter inputs to streams, which could differ in important ways between native, deciduous woodlands and non-native conifer catchments. The life cycles of temperate stream organisms that rely on litter inputs are more likely to be attuned to the seasonality of resource inputs to streams in native deciduous woodland (Huryn & Wallace, 2000). Additionally, the quality of organic litter from deciduous and conifer canopies can differ markedly with consequences for stream ecosystem processes and the abundances of stream

organisms (Thomas et al., 2016). More fundamentally, rather than controlled, randomised experiments with replicated treatment effects, our assessments depended on cross-sectional analyses across a small number of years and a limited number of catchments with low replication. These limitations are inevitable given the ecosystem-scale processes we investigated, and few other studies achieve replication at catchment scales over prolonged timescales. At Llyn Brianne, also, there is some risk of spatial auto-correlation because catchments with the same land uses occur mostly in adjacent locations, although we have no evidence that this pattern results in significant error.

At a more detailed level, there were uncertainties over the exact relationship between discharge and the downstream fluxes of organic matter. In the absence of a broadleaf canopy, CPOM stocks declined at conifer and moorland sites following wetter periods, while FPOM declined at all sites. These results illustrate that downstream export at high flow was sufficient to reduce amounts of benthic litter at the whole stream scale even though concentrations of suspended organic matter declined as flow increased. Sample collection was not practicable during storm events, however, nor during all stages of the storm hydrograph. This meant that definitive input–output budgets for organic matter could be calculated. These limitations should be noted given that the majority of downstream organic matter transport probably occurs during storms (Golladay et al., 1987; Wallace et al., 1995; Johnson et al., 2006). As well as discharge pattern, litter dynamics in upland streams are influenced by retention effects resulting from bed roughness and in-stream structure created, for example, by debris dams and snags. This effect has been demonstrated experimentally at Llyn Brianne (Dobson et al., 1995), where streams draining moorland and broadleaves have more vegetated and woody features than the streams draining conifer (Rutt et al., 1989). The management of litter storage would ideally take such effects into account as a possible additional measure to increase climate resilience.

Notwithstanding these limitations, our four-year study captured substantial variations in rainfall and discharge, representative of long-term pattern (Fig. 2). Moreover, the use of the Llyn Brianne Stream Observatory provides a research context for the study that stretches from 1981 to the present day, and work to understand the implications

of our findings is continuing (Durance & Ormerod, 2007). Some of the clearest effects we observed were related to land use, and to the apparent effects of broadleaf trees in the catchments studied: broadleaves (i) supplied more litter to the streams than any other land use; (ii) stored the greatest masses of coarse litter in the benthos which were maintained after events, and (iii) produced the highest suspended concentrations of FPOM and CPOM which were most effectively maintained during floods. All of these effects are likely to be important to organisms dependent of benthic or suspended organic matter in headwaters, such as leaf shredders, detritivores and filter feeders. The role of organic litter from riparian broadleaf trees in temperate headwaters is one of the most widely recognised principles in stream ecology (e.g., Fisher and Likens, 1973; Wallace et al., 2015; Campbell et al., 1992; Delong and Brusven, 1994; Benfield, 1997; Hart et al., 2013). Not only does this organic subsidy drive major ecological processes through energetic transfer and secondary production, but it has also shaped trait development in a wide range of stream organisms whose feeding methods, life cycles and morphology are tied to the annual input and subsequent processing of allochthonous litter.

In contrast, there is less recognition in climate change adaptation of the importance of protecting or restoring riparian broadleaves because of their role in organic subsidies (Thomas et al., 2016). Typically, the value of riparian trees to climate change management is seen more from the perspective of carbon sequestration (i.e., climate mitigation: Dewar & Cannell, 1992), stream thermal damping (Broadmeadow et al., 2011), reduced pollutant flux (Sweeney & Newbold, 2014), enhanced connectivity or landscape permeability to dispersing organisms (Manning et al., 2009) and, increasingly, natural flood management (Kay et al., 2019). As well as confirming the potential adaptive value of riparian broadleaves in increasing litter inputs to streams that could maintain production, our data illustrated the processes involved: in these upland streams broadleaves contributed litter to streams in roughly equal amounts between direct and indirect pathways, and in quantities significantly greater than any other site type by 2.5–4X through direct input and by 6–9X through indirect pathways (Fig. 3). These effects reflect likely overall litter production and less ground vegetation acting as barriers

to lateral movement (Scarsbrook et al., 2001; Hart et al., 2013).

Although the difference in inputs was not reflected clearly in organic matter standing stocks overall, input masses offer the most plausible reason to explain why broadleaf sites maintained higher standing stocks of benthic CPOM than all other land cover types following wetter periods. Our data illustrate how catchment or riparian broadleaves could replenish losses during events through the influx of leaf litter from terrestrial sources, which are transported to the stream via surface runoff during rainfall events (Maridet et al., 1995; Naiman & Décamps, 1997; Hart et al., 2013). As well as the quantities added, laterally transported litter may also be qualitatively important to consumers because of its higher nitrogen concentration than that of litter falling directly into the stream (Benson & Pearson, 1993). We suggest that these lateral inputs provide an important, high-quality replenishment of resources that are apparently depleted in other catchment types (Hart et al., 2013; Riedl et al., 2013). As well as lateral inputs, the re-surfacing of buried organic matter from the stream channel during turbulent flows could also replenish benthic standing stocks (Cornut et al., 2012). In addition to having greater resource availability, streams bordered by mature broadleaved tree species are also likely to have a greater capacity to retain organic matter than their coniferous or moorland counterparts. This is due to the characteristics of the leaf litter itself (Pretty & Dobson, 2004; Quinn et al., 2007; Cordova et al., 2008; Hoover et al., 2010) and the presence of large woody retention structures in the form of fallen branches and mature trees, which together promote retention and longer-term storage, particularly of CPOM (e.g., Muotka and Laasonen, 2002; Lepori et al., 2005; Flores et al., 2011; Eggert et al., 2012). In turn, this constant, heterogeneous supply of food resources is expected to sustain a diverse array of stream organisms (Petersen & Cummins, 1974; Webster & Benfield, 1986; Moore et al., 2004; Rooney et al., 2006). In contrast, conifer and moorland streams are likely to be limited by litter supply, and at Llyn Brianne also they are less retentive and more likely to export litter downstream at rates faster than can be maintained by supply (Rutt et al., 1989). Woody debris and litter retention could, nevertheless, be enhanced in conifer sites if riparian zones were appropriately managed for broadleaf tree species and woody debris left in place (Ormerod et al., 1993).

Conclusions

Overall, our study demonstrates an interaction between riparian land cover, hydrological conditions and organic matter dynamics in headwater catchments. If organic matter supplies are limited and retention capacity is low, organic matter stocks in headwaters are likely to be depleted under wetter climatic conditions. A reduction in the amount of basal resources retained within headwater streams, particularly structurally complex resources such as particulate organic matter, could have ecological implications. Fewer resources at the base of the stream food web will ultimately reduce the amount of energy and matter available to be biologically processed and transferred to higher trophic levels (Wallace et al., 1997), and therefore limit overall food web productivity in the upper reaches of river networks. These effects might not only be local to headwater reaches, but could extend beyond their aquatic boundaries and downstream: streams, like many ecosystems, are open and permeable, and reciprocate subsidies to the adjacent terrestrial ecosystem in the form of emerging adult aquatic insects, which, in turn, provide important prey items for organisms such as riparian and river birds (Polis et al., 2004; Marczak et al., 2007). While further studies are needed to investigate the energetic contribution of headstreams to downstream rivers and estuaries, there is some expectation that upstream contributions of organic matter can affect the functioning of downstream ecosystems, including fish production (Wipfli et al., 2007).

As an option to effectively adapt river ecosystem functions and services to climate change, our data are consistent with the notion of protecting and restoring tree cover in temperate headwater catchments. While there is a need for fuller quantification of input–output budgets of organic material at catchment scales, on the basis of current evidence we advocate greater attention to headwater streams in water policies (Lassaletta et al., 2010; Biggs et al., 2017). Second, we suggest that adaptive management actions should consider organic matter processes in ecosystem function and resilience, and their sensitivity to future climate. Management actions warranting attention could include: (1) increasing organic matter supplies to river networks by enhancing broadleaved tree cover in headwater catchments via catchment-wide tree planting; (2) increasing the retentiveness of headwaters

by introducing organic matter retention structures, such as log jams and boulders, to stream reaches; (3) allowing the development of mature woodlands along river margins to establish complex and sustainable stream-riparian linkages; and (4) protecting existing natural woodlands in headwater catchments from deforestation to maintain complex ecological properties.

Acknowledgements We thank two referees for comments on the manuscript. The authors declare that they have no competing interests and that data can be made available on request.

Funding This work was funded by the Natural Environment Research Council under the DURESS programme and by the Esmee Fairbairn Foundation. Natural Resources Wales provided extensive support in kind and through site access, also providing stream flow data. Clare Wilkinson provided significant help with fieldwork.

Data availability Enquiries about data availability should be directed to the authors.

Declarations

Conflict of interest The authors have not disclosed any competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Abelho, M. & M. A. S. Graça, 1996. Effects of eucalyptus afforestation on leaf litter dynamics and macroinvertebrate community structure of streams in Central Portugal. *Hydrobiologia* 324: 195–204.
- Abell, R., J. D. Allan & B. Lehner, 2007. Unlocking the potential of protected areas for freshwaters. *Biological Conservation* 134: 48–63.
- Acuña, V. & K. Tockner, 2010. The effects of alterations in temperature and flow regime on organic carbon dynamics

- in Mediterranean river networks. *Global Change Biology* 16: 2638–2650.
- Bartón, K., 2015. MuMin: multi-model inference R package version No 1.
- Bates, D., M. Mächler, B. Bolker & S. Walker, 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48.
- Battin, T. J., L. A. Kaplan, S. Findlay, C. S. Hopkinson, E. Marti, A. I. Packman, J. D. Newbold & F. Sabater, 2008. Biophysical controls on organic carbon fluxes in fluvial networks. *Nature Geoscience* 1: 95–100.
- Benfield, E. F., 1997. Comparison of litterfall input to streams. *Journal of the North American Benthological Society* 16: 104–108.
- Benke, A. C., T. C. Van Arsdall, G. M. Gillespie & F. K. Parrish, 1984. Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. *Ecological Monographs* 54: 25–63.
- Benson, L. J. & R. G. Pearson, 1993. Litter inputs to a tropical Australian rainforest stream. *Austral Ecology* 18: 377–383.
- Biggs, J., S. von Fumetti & M. Kelly-Quinn, 2017. The importance of small waterbodies for biodiversity and ecosystem services: implications for policy makers. *Hydrobiologia* 793: 3–39.
- Birsan, M. V., P. Molnar, P. Burlando & M. Pfaundler, 2005. Streamflow trends in Switzerland. *Journal of Hydrology* 314: 312–329.
- Bradshaw, C. J. A., N. S. Sodhi, K.S.-H. Peh & B. W. Brook, 2007. Global evidence that deforestation amplifies flood risk and severity in the developing world. *Global Change Biology* 13: 2379–2395.
- Broadmeadow, S. B. & T. R. Nisbet, 2002. The Effect of riparian forest management on the freshwater environment: SNIFFER Scotland and Northern Ireland forum for environmental research. Report SR02.06F, Foundation for Water Research, Marlow Bucks., 162.
- Broadmeadow, S. B. & T. R. Nisbet, 2004. The effects of riparian forest management on the freshwater environment: a literature review of best management practice. *Hydrology and Earth System Sciences* 8: 286–305.
- Broadmeadow, S. B., J. G. Jones, T. E. L. Langford, P. J. Shaw & T. R. Nisbet, 2011. The influence of riparian shade on lowland stream water temperatures in southern England and their viability for brown trout. *River Research and Applications* 27: 226–237.
- Cahill, A. E., M. E. Aiello-Lammens, M. C. Fisher-Reid, X. Hua, C. J. Karanewsky, H. Y. Ryu, G. C. Sbeglia, F. Spagnolo, J. B. Waldron, O. Warsi & J. J. Wiens, 2012. How does climate change cause extinction? *Proceedings of the Royal Society of London B: Biological Sciences* 280: 20121890.
- Caissie, D., 2006. The thermal regime of rivers: a review. *Freshwater Biology* 51: 1389–1406.
- Campbell, I. C., K. R. James, B. T. Hart & A. Devereaux, 1992. Allochthonous coarse particulate organic material in forest and pasture reaches of two south-eastern Australian streams. *Freshwater Biology* 27: 353–365.
- Cariss, H. & M. Dobson, 1997. Transport and retention of detritus in upland streams: A comparison of an open

- stream and an adjacent wooded site. *Limnetica* 13: 85–91.
- Cordova, J. M., E. J. Rosi-Marshall, J. L. Tank & G. A. Lamberti, 2008. Coarse particulate organic matter transport in low-gradient streams of the Upper Peninsula of Michigan. *Journal of the North American Benthological Society* 27: 760–771.
- Cornut, J., A. Elger, A. Greugny, M. Bonnet & E. Chauvet, 2012. Coarse particulate organic matter in the interstitial zone of three French headwater streams. *Annales De Limnologie - International Journal of Limnology* 48: 303–313.
- Cummins, K. W., M. A. Wilzbach, D. M. Gates, J. B. Perry & W. B. Taliaferro, 1989. Shredders and riparian vegetation. *BioScience* 39: 24–30.
- Dekar, M. P., R. S. King, J. A. Back, D. F. Whigham & C. M. Walker, 2012. Allochthonous inputs from grass-dominated wetlands support juvenile salmonids in headwater streams: evidence from stable isotopes of carbon, hydrogen, and nitrogen. *Freshwater Science* 31: 121–132.
- Delong, M. D. & M. A. Brusven, 1994. Allochthonous input of organic matter from different riparian habitats of an agriculturally impacted stream. *Environmental Management* 18: 59–71.
- Dewar, R. C. & M. G. R. Cannell, 1992. Carbon sequestration in the trees, products and soils of forest plantations: an analysis using UK examples. *Tree Physiology* 11: 49–71.
- Dixon, H., D. M. Lawler & A. Y. Shamseldin, 2006. Stream-flow trends in western Britain. *Geophysical Research Letters* 33: L19406.
- Dobson, M., S. A. A. G. Hildrew, S. Orton & S. J. Ormerod, 1995. Increasing litter retention in moorland streams: ecological and management aspects of a field experiment. *Freshwater Biology* 33: 325–337.
- Duputié, A., A. Rutschmann, O. Ronce & I. Chuine, 2015. Phenological plasticity will not help all species adapt to climate change. *Global Change Biology* 21: 3062–3073.
- Durance, I. & S. J. Ormerod, 2007. Climate change effects on upland stream macroinvertebrates over a 25-year period. *Global Change Biology* 13: 942–957.
- Durance, I. & S. J. Ormerod, 2010. Evidence for the role of climate in the local extinction of a cool-water trichod. *Journal of the North American Benthological Society* 29: 1367–1378.
- Edwards, R. W., A. S. Gee & J. H. Stoner, 1990. Acid waters in Wales, Springer, Netherlands, Dordrecht., 356.
- Eggert, S. L., J. B. Wallace, J. L. Meyer & J. R., Webster, 2012. Storage and export of organic matter in a headwater stream: responses to long-term detrital manipulations. *Ecosphere* 3: 1–25.
- Finn, D. S., N. Bonada, C. Múrria & J. M. Hughes, 2011. Small but mighty: headwaters are vital to stream network biodiversity at two levels of organization. *Journal of the North American Benthological Society* 30: 963–980.
- Fisher, S. G. & G. E. Likens, 1973. Energy flow in bear brook, New Hampshire: an integrative approach to stream ecosystem metabolism. *Ecological Monographs* 43: 421–439.
- Flores, L., A. Larrañaga, J. Díez & A. Elosegi, 2011. Experimental wood addition in streams: effects on organic matter storage and breakdown. *Freshwater Biology* 56: 2156–2167.
- Follstad Shah, J. J., J. S. Kominoski, M. Ardón, W. K. Dodds, M. O. Gessner, N. A. Griffiths, C. P. Hawkins, S. L. Johnson, A. Lecerf, C. J. LeRoy, D. W. Manning, A. D. Rosemond, R. L. Sinsabaugh, C. M. Swan, J. R. Webster & L. H. Zeglin, 2017. Global synthesis of the temperature sensitivity of leaf litter breakdown in streams and rivers. *Global Change Biology* 23: 3064–3075.
- Garner, G., I. A. Malcolm, J. P. Sadler, C. P. Millar & D. M. Hannah, 2015. Inter-annual variability in the effects of riparian woodland on micro-climate, energy exchanges and water temperature of an upland Scottish stream. *Hydrological Processes* 29: 1080–1095.
- Golladay, S. W., J. R. Webster & E. F. Benfield, 1987. Changes in stream morphology and storm transport of seston following watershed disturbance. *Journal of the North American Benthological Society* 6: 1–11.
- Gomi, T., R. C. Sidle & J. S. Richardson, 2002. Understanding processes and downstream linkages of headwater systems. *BioScience* 52: 905–916.
- González, J. M. & J. Pozo, 1996. Longitudinal and temporal patterns of benthic coarse particulate organic matter in the Agüera stream northern Spain. *Aquatic Sciences* 58: 355–366.
- Graça, M. A. S., V. Ferreira, C. Canhoto, A. C. Encalada, F. Guerrero-Bolaño, K. M. Wantzen & L. Boyero, 2015. A conceptual model of litter breakdown in low order streams. *International Review of Hydrobiology* 100: 1–12.
- Gurnell, A. M., H. Piegay, F. J. Swanson & S. V. Gregory, 2002. Large wood and fluvial processes. *Freshwater Biology* 47: 601–619.
- Halekoh, U. & S. Højsgaard, 2014. A Kenward-Roger approximation and parametric bootstrap methods for tests in linear mixed models—the R package pbkr test. *Journal of Statistical Software* 59: 1–32.
- Hannaford, J. & T. Marsh, 2006. An assessment of trends in UK runoff and low flows using a network of undisturbed catchments. *International Journal of Climatology* 26: 1237–1253.
- Hart, S. K., D. E. Hibbs & S. S. Perakis, 2013. Riparian litter inputs to streams in the central Oregon Coast Range. *Freshwater Science* 32: 343–358.
- Hassan, R., R. Scholes & N. Ash, 2005. Ecosystems and human well-being: current state and trends, Vol. 1. Island Press, Washington:
- Heartsill-Scalley, T., F. N. Scatena, S. Moya & A. E. Lugo, 2012. Long-term dynamics of organic matter and elements exported as coarse particulates from two Caribbean montane watersheds. *Journal of Tropical Ecology* 28: 127–139.
- Hoover, T. M., L. B. Marczak, J. S. Richardson & N. Yone-mitsu, 2010. Transport and settlement of organic matter in small streams. *Freshwater Biology* 55: 436–449.
- Hury, A. D. & J. B. Wallace, 2000. Life history and production of stream insects. *Annual Review of Entomology* 45: 83–110.

- Johnson, M. S., J. Lehmann, E. C. Selva, M. Abdo, S. Riha & E. G. Couto, 2006. Organic carbon fluxes within and streamwater exports from headwater catchments in the southern Amazon. *Hydrological Processes* 20: 2599–2614.
- Jonsson, M., P. Hedström, K. Stenroth, E. R. Hotchkiss, F. R. Vasconcelos, J. Karlsson & P. Byström, 2015. Climate change modifies the size structure of assemblages of emerging aquatic insects. *Freshwater Biology* 60: 78–88.
- Kay, A. L., G. H. Old, V. A. Bell, H. N. Davies & E. J. Trill, 2019. An assessment of the potential for natural flood management to offset climate change impacts. *Environmental Research Letters* 14: 044017.
- Kenward, M. G. & J. H. Roger, 1997. Small sample inference for fixed effects from restricted maximum likelihood. *Biometrics* 53: 983–997.
- Koljonen, S., P. Louhi, A. Mäki-Petäys, A. Huusko & T. Muotka, 2012. Quantifying the effects of in-stream habitat structure and discharge on leaf retention: implications for stream restoration. *Freshwater Science* 31: 1121–1130.
- Kominoski, J. S. & A. D. Rosemond, 2012. Conservation from the bottom up: forecasting effects of global change on dynamics of organic matter and management needs for river networks. *Freshwater Science* 31: 51–68.
- Kormann, C., T. Francke, M. Renner & A. Bronstert, 2015. Attribution of high resolution streamflow trends in Western Austria—an approach based on climate and discharge station data. *Hydrology and Earth System Sciences* 19: 1225–1245.
- Larsen, S., J. M. Chase, I. Durance & S. J. Ormerod, 2018. Lifting the veil: richness measurements fail to detect systematic biodiversity change over three decades. *Ecology* 99: 1316–1326.
- Lassaletta, L., H. García-Gómez, B. S. Gimeno & J. V. Rovira, 2010. Headwater streams: neglected ecosystems in the EU water framework directive. Implications for nitrogen pollution control. *Environmental Science & Policy* 13: 423–433.
- Leberfinger, K., I. Bohman & J. Herrmann, 2011. The importance of terrestrial resource subsidies for shredders in open-canopy streams revealed by stable isotope analysis. *Freshwater Biology* 56: 470–480.
- Lepori, F., D. Palm & B. Malmqvist, 2005. Effects of stream restoration on ecosystem functioning: detritus retentiveness and decomposition. *Journal of Applied Ecology* 42: 228–238.
- Manning, A. D., P. Gibbons & D. B. Lindenmayer, 2009. Scattered trees: a complementary strategy for facilitating adaptive responses to climate change in modified landscapes? *Journal of Applied Ecology* 46: 915–919.
- Marc, V. & M. Robinson, 2007. The long-term water balance 1972–2004 of upland forestry and grassland at Plynlimon, mid-Wales. *Hydrology and Earth System Sciences* 11: 44–60.
- Marczak, L. B., R. M. Thompson & J. S. Richardson, 2007. Meta-analysis: trophic level, habitat, and productivity shape the food web of resource subsidies. *Ecology* 88: 140–148.
- Maridet, L., J. G. Wasson, M. Philippe & C. Amoros, 1995. Benthic organic matter dynamics in three streams: riparian vegetation or bed morphology control? *Archiv Für Hydrobiologie* 132: 415–425.
- Marsh, T. J. & H. Dixon, 2012. The UK water balance: how much has it changed in a warming world? In *Proceedings of the Eleventh National BHS Symposium: “Hydrology for a changing world.”* British Hydrological Society, Dundee.
- Menninger, H. L. & M. A. Palmer, 2007. Herbs and grasses as an allochthonous resource in open-canopy headwater streams. *Freshwater Biology* 52: 1689–1699.
- Meyer, J. L., D. L. Strayer, J. B. Wallace, S. L. Eggert, G. S. Helfman & N. E. Leonard, 2007. The contribution of headwater streams to biodiversity in river networks. *Journal of the American Water Resources Association* 43: 86–103.
- Molinero, J. & J. Pozo, 2004. Impact of a *Eucalyptus globulus* labill plantation on the nutrient content and dynamics of coarse particulate organic matter CPOM in a small stream. *Hydrobiologia* 528: 143–165.
- Mollá, S., S. Robles & C. Casado, 2006. Seasonal variability of particulate organic matter in a mountain stream in central Spain. *International Review of Hydrobiology* 91: 406–422.
- Moore, J. C., E. L. Berlow, D. C. Coleman, P. C. de Ruiter, Q. Dong, A. Hastings, N. Collins Johnson, K. S. McCann, K. Melville, P. J. Morin, K. Nadelhoffer, A. D. Rosemond, D. M. Post, J. L. Sabo, K. M. Scow, M. J. Vanni & D. H. Wall, 2004. Detritus, trophic dynamics and biodiversity. *Ecology Letters* 7: 584–600.
- Muotka, T. & P. Laasonen, 2002. Ecosystem recovery in restored headwater streams: the role of enhanced leaf retention. *Journal of Applied Ecology* 39: 145–156.
- Murphy, T. R., M. E. Hanley, J. S. Ellis & P. H. Lunt, 2021. Native woodland establishment improves soil hydrological functioning in UK upland pastoral catchments. *Land Degradation and Development* 32: 1034–1045.
- Naiman, R. J. & H. Décamps, 1997. The Ecology of Interfaces: riparian zones. *Annual Review of Ecology and Systematics* 28: 621–658.
- Naiman, R. J., H. Decamps & M. Pollock, 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* 3: 209–212.
- Nakagawa, S. & H. Schielzeth, 2013. A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4: 133–142.
- Northington, R. M. & J. R. Webster, 2017. Experimental reductions in stream flow alter litter processing and consumer subsidies in headwater streams. *Freshwater Biology* 62: 737–750.
- Ormerod, S. J., 2009. Climate change, river conservation and the adaptation challenge. *Aquatic Conservation: Marine and Freshwater Ecosystems* 19: 609–613.
- Ormerod, S. J., S. D. Rundle, E. C. Lloyd & A. A. Douglas, 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.
- Palmer, M. A., D. P. Lettenmaier, N. L. Poff, S. L. Postel, B. Richter & R. Warner, 2009. Climate change and river

- ecosystems: protection and adaptation options. *Environmental Management* 44: 1053–1068.
- Perkins, D. M. J., J. Reiss, G. Yvon-Durocher & G. Woodward, 2010. Global change and food webs in running waters. *Hydrobiologia* 657: 181–198.
- Petersen, R. C. & K. W. Cummins, 1974. Leaf processing in a woodland stream. *Freshwater Biology* 4: 343–368.
- Polis, G. A., W. B. Anderson & R. D. Holt, 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28: 289–316.
- Polis, G. A., M. E. Power & G. R. Huxel (eds), 2004. *Food webs at the landscape level*. University of Chicago Press, Chicago, 548.
- Pozo, J., E. González, J. Díez & A. Elosegi, 1997. Leaf-litter budgets in two contrasting forested streams. *Limnetica* 13: 77–84.
- Pretty, J. L. & M. Dobson, 2004. Leaf transport and retention in a high gradient stream. *Hydrology and Earth System Sciences* 8: 560–566.
- Quinn, J. M., N. R. Phillips & S. M. Parkyn, 2007. Factors influencing retention of coarse particulate organic matter in streams. *Earth Surface Processes and Landforms* 32: 1186–1203.
- R Development Core Team, 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.r-project.org>.
- Richardson, D. C., L. A. Kaplan, J. D. Newbold & A. K. Aufdenkampe, 2009a. Temporal dynamics of seston: a recurring nighttime peak and seasonal shifts in composition in a stream ecosystem. *Limnology and Oceanography* 54: 344–354.
- Richardson, J. S., T. M. Hoover & A. Lecerf, 2009b. Coarse particulate organic matter dynamics in small streams: towards linking function to physical structure. *Freshwater Biology* 54: 2116–2126.
- Richardson, J. S., Y. Zhang & L. B. Marczak, 2010. Resource subsidies across the land-freshwater interface and responses in recipient communities. *River Research and Applications* 26: 55–66.
- Riedl, H. L., L. B. Marczak, N. A. McLenaghan & T. M. Hoover, 2013. The role of stranding and inundation on leaf litter decomposition in headwater streams. *Riparian Ecology and Conservation* 1: 3–10.
- Riley, W. D., E. C. E. Potter, J. Biggs, A. L. Collins, H. P. Jarvie, J. I. Jones, M. Kelly-Quinn, S. J. Ormerod, D. A. Sear, R. L. Wilby, S. Broadmeadow, C. D. Brown, P. Chanin, G. H. Copp, I. G. Cowx, A. Grogan, D. D. Hornby, D. Huggett, M. G. Kelly, M. Naura, J. R. Newman & G. M. Siriwardena, 2018. Small water bodies in Great Britain and Ireland: ecosystem function, human-generated degradation, and options for restorative action. *Science of the Total Environment* 645: 1598–1616.
- Rooney, N., K. McCann, G. Gellner & J. C. Moore, 2006. Structural asymmetry and the stability of diverse food webs. *Nature* 442: 265–269.
- Rutt, G. P., N. S. Weatherly & S. J. Ormerod, 1989. Microhabitat availability in Welsh moorland and forest streams as a determinant of macroinvertebrate distribution. *Freshwater Biology* 22: 247–261.
- Sanpera-Calbet, I., V. Acuña, A. Butturini, R. Marcé & I. Muñoz, 2016. El Niño southern oscillation and seasonal drought drive riparian input dynamics in a Mediterranean stream. *Limnology and Oceanography* 61: 214–226.
- Scarsbrook, M. R., J. M. Quinn, J. Halliday & R. Morse, 2001. Factors controlling litter input dynamics in streams draining pasture, pine, and native forest catchments. *New Zealand Journal of Marine and Freshwater Research* 35: 751–762.
- Scharnweber, K., M. J. Vanni, S. Hilt, J. Syväranta & T. Mehner, 2014. Boomerang ecosystem fluxes: organic carbon inputs from land to lakes are returned to terrestrial food webs via aquatic insects. *Oikos* 123: 1439–1448.
- Seavy, N. E., T. Gardali, G. H. Golet, F. T. Griggs, C. A. Howell, R. Kelsey, S. L. Small, J. H. Viers & J. F. Weigand, 2009. Why climate change makes riparian restoration more important than ever: recommendations for practice and research. *Ecological Restoration* 27: 330–338.
- Seddon, N., A. Chausson, P. Berry, C. A. J. Girardin, A. Smith & B. Turner, 2020. Understanding the value and limits of nature-based solutions to climate change and other global challenges. *Philosophical Transactions of the Royal Society B, Biological Sciences* 375: 20190120.
- Stenroth, K., T. M. Hoover, J. Herrmann, I. Bohman & J. S. Richardson, 2014. A model-based comparison of organic matter dynamics between riparian-forested and open-canopy streams. *Riparian Ecology and Conservation* 2: 1–13.
- Suurkuukka, H., R. Virtanen, V. Suorsa, J. Soininen, L. Paasivirta & T. Muotka, 2014. Woodland key habitats and stream biodiversity: does small-scale terrestrial conservation enhance the protection of stream biota? *Biological Conservation* 170: 10–19.
- Svenning, J.-C., 2002. A review of natural vegetation openness in north-western Europe. *Biological Conservation* 104: 133–148.
- Sweeney, B. W. & J. D. Newbold, 2014. Streamside forest buffer width needed to protect stream water quality, habitat, and organisms: a literature review. *Journal of the American Water Resources Association* 50: 560–584.
- Sweeney, B. W., T. L. Bott, B. W. Sweeney, T. L. Bott, J. K. Jackson, L. A. Kaplan, J. D. Newbold, L. J. Standley, W. C. Hession & R. J. Horwitz, 2004. Riparian deforestation, stream narrowing, and loss of stream ecosystem services. *Proceedings of the National Academy of Sciences of the USA* 101: 14132–14137.
- Tank, J. L., E. J. Rosi-Marshall, N. A. Griffiths, S. A. Entekin & M. L. Stephen, 2010. A review of allochthonous organic matter dynamics and metabolism in streams. *Journal of the North American Benthological Society* 29: 118–146.
- Thomas, S. M., S. W. Griffiths & S. J. Ormerod, 2016. Beyond cool: adapting upland streams for climate change using riparian woodlands. *Global Change Biology* 22: 310–324.
- Verdonschot, P. F. M. & M. van den Hoorn, 2010. Using discharge dynamics characteristics to predict the effects of climate change on macroinvertebrates in lowland streams. *Journal of the North American Benthological Society* 29: 1491–1509.
- Wallace, J. B., M. R. Whiles, S. L. Eggert, T. F. Cuffney, G. J. Lughart & K. Chung, 1995. Long-term dynamics

- of coarse particulate organic matter in three Appalachian mountain streams. *Journal of the North American Benthological Society* 14: 217–232.
- Wallace, J. B., S. L. Eggert, J. L. Meyer & J. R. Webster, 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* 277: 102–104.
- Wallace, J. B., S. L. Eggert, J. L. Meyer & J. R. Webster, 1999. Effects of resource limitation on a detrital-based ecosystem. *Ecological Monographs* 69: 409–442.
- Wallace, J. B., S. L. Eggert, J. L. Meyer, J. R. Webster & W. V. Sobczak, 2015. Stream invertebrate productivity linked to forest subsidies: 37 stream-years of reference and experimental data. *Ecology* 96: 1213–1228.
- Weatherley, N. S. & S. J. Ormerod, 1987. The impact of acidification on macroinvertebrate assemblages in Welsh Streams: towards an empirical model. *Environmental Pollution* 46: 223–240.
- Weatherley, N. S. & S. J. Ormerod, 1990. Forests and the temperature of upland streams in Wales: a modelling exploration of the biological effects. *Freshwater Biology* 24: 109–122.
- Webster, J. R. & E. F. Benfield, 1986. Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics* 17: 567–594.
- Webster, J. R., E. F. Benfield, S. W. Golladay, B. H. Hill, L. E. Hornick, R. F. J. Kazmierczak & W. B. Perry, 1987. Experimental studies of physical factors affecting seston transport in streams. *Limnology and Oceanography* 32: 848–863.
- Webster, J. R., E. F. Benfield, T. P. Ehrman, M. A. Schaeffer, J. L. Tank, J. J. Hutchens & D. J. D'Angelo, 1999. What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta. *Freshwater Biology* 41: 687–705.
- Wipfli, M. S., J. S. Richardson & R. J. Naiman, 2007. Ecological linkages between headwaters and downstream ecosystems: transport of organic matter, invertebrates, and wood down headwater channels. *Journal of the American Water Resources Association* 43: 72–85.
- Woodward, G., D. M. Perkins & L. E. Brown, 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 365: 2093–2106.
- Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev & G. M. Smith, 2009. *Mixed effects models and extensions in ecology with R*, Springer, New York:
- Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.