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Beyond cool: adapting upland streams for climate change using riparian woodlands

STEPHEN M. THOMAS[1,2]*, SIÂN W. GRIFFITHS[1] and S. J. ORMEROD[1]

1. *Catchment Research Group, Cardiff School of Biosciences, Cardiff University, Sir Martin Evans Building, Museum Avenue, Cardiff, CF10 3AX, UK.*
2. *Department of Environmental Sciences, University of Helsinki, P.O. Box 65, FI-00014, Finland*

***Correspondence:** Department of Environmental Sciences, University of Helsinki, Helsinki, P.O. Box 65, FI-00014, Finland; E-mail: stephen.thomas@helsinki.fi

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Abstract

Adaptive management could reduce the risks of climate change to the world's ecosystems, but there have been surprisingly few practical evaluations of the options available. For example, riparian woodland is advocated widely as shade to reduce warming in temperate streams, but few studies have considered collateral effects on species composition or ecosystem functions. Here, we use cross sectional analyses at two scales (region and within streams) to investigate whether four types of adaptive riparian management, including those proposed to reduce potential climate change impacts, might also affect the composition, functional character, dynamics and energetic resourcing of macroinvertebrates in upland Welsh streams (UK). Riparian land use across the region had only small effects on invertebrate taxonomic composition, while stable isotope data showed how energetic resources assimilated by macroinvertebrates in all functional guilds were split roughly 50:50 between terrestrial and aquatic origins irrespective of riparian management. Nevertheless, streams draining the most extensive deciduous woodland had the greatest stocks of coarse particulate matter (CPOM) and greater numbers of "shredding" detritivores. Stream-scale investigations showed that macroinvertebrate biomass in deciduous woodland streams was around twice that in moorland streams, and lowest of all in streams draining non-native conifers. The unexpected absence of contrasting terrestrial signals in the isotopic data implies that factors other than local land use affect the relative incorporation of allochthonous subsidies into riverine food webs. Nevertheless, our results reveal how planting deciduous riparian trees along temperate headwaters as an adaptation to climate change can modify macroinvertebrate function, increase biomass and potentially enhance resilience by increasing basal resources where cover is extensive (> 60m riparian width). We advocate

greater urgency in efforts to understand the ecosystem consequences of climate change adaptation in order to guide future actions.

Introduction

Although reducing greenhouse gas emissions is fundamental to mitigating future climate change, there is growing expectation that further increase in global temperature cannot now be avoided (IPCC, 2014). Interest is growing, therefore, in strategies for climate change adaptation that might minimize the worst effects on key resources (Perry, 2015). These include organisms, ecosystems and the many services that they provide, and as a result ecologists have been among the strongest advocates for climate change adaptation (Hulme, 2005; Dudgeon *et al*., 2006; Seavy *et al*., 2009). The broad aims involve predicting the effects on vulnerable species or habitats, increasing their resilience, maintaining sensitive species or assemblages, restoring lost connectivity, reducing the stressors with which climate change interacts, and providing security for critical ecosystems (Hulme, 2005; Ormerod, 2009; Palmer *et al*. 2009; Seavy et al., 2009). So far, however, there are few specific examples where approaches advocated in theory have been evaluated in practice (Mawdsley *et al*., 2009; Macgregor & van Dijk, 2014). This is an important knowledge gap given the extent of actions likely to be required to adapt ecosystems to climate change, and because of the potentially far-reaching effects on the risks, benefits and services that might arise.

Stream and river ecosystems have figured strongly in the adaptation debate for two major reasons. First, they have major global value to human life support, for example through water supply, flood regulation, pollutant disposal, support for major biogeochemical cycles, and critical roles in fisheries (Holmlund & Hammer, 1999; Wilson & Carpenter, 1999; Ormerod, 2009). Secondly, streams and rivers are among the most sensitive of all ecosystems to climate change because they are coupled directly to the global hydrological cycle, linked closely to atmospheric thermal regimes, and at risk from interactions between climate change and existing anthropogenic stressors (Dudgeon *et al.*, 2006; Durance & Ormerod, 2007; Ormerod *et al*., 2010). Moreover, because the majority of riverine organisms are poikilothermic, they are affected metabolically both by direct temperature change and by interactions between water temperature and oxygen solubility (Graham & Harrod, 2009; Jonsson & Jonsson, 2009). Many freshwater ecosystems are also coupled tightly to the surrounding riparian zones, floodplains and catchments through lateral or longitudinal fluxes of energy that are under strong climatic influence (Nakano & Murakami, 2001; Wipfli, 2005). This includes the delivery, processing and downstream transport of detrital carbon from terrestrial litter-fall that then acts as an important basis of production throughout whole river systems (Vannote *et al*., 1980; Malmqvist, 2002).

Broad suggestions for adapting rivers to climate change are the same as for other ecosystems and include enhancing resilience, connectivity and legal protection while reducing stressors such as water quality impairment (Durance & Ormerod, 2009; Ormerod, 2009; Palmer *et al*., 2009). However, some proposed adaptation strategies are specific to rivers such as reducing abstraction (ie the active removal of water for human usage) and using riparian forest to buffer rivers against temperature gain to protect sensitive organisms (Ormerod, 2009; Broadmeadow *et al*., 2011). Enhancing or restoring riparian tree cover is advocated particularly in temperate regions where much native forest has been removed for agriculture (Battin *et al*., 2007; Palmer *et al*., 2009; Seavy *et al*., 2009). Already, the value of such “buffer strips” in moderating stream temperature is well supported by evidence (Zoellick, 2004; Battin *et al*., 2007; Broadmeadow *et al*., 2011), some of it from our own study region (Weatherley & Ormerod, 1990; Clews *et al.*, 2010).

In addition to moderating thermal conditions in rivers, riparian woodlands might aid climate change adaptation through effects on ecological processes, for example by soil denitrification, nutrient flux and sediment delivery from agricultural land (Osbourne & Kovacic, 1993; Broadmeadow & Nisbet, 2004; Larsen *et al*., 2009). More generally, riparian trees might affect important aspects of stream and river energetics by two major pathways. First, shading along streams is likely to reduce autotrophic productivity potentially limiting resources for some consumers (Hill *et al*., 1995; Kiffney *et al*., 2003; 2004; Riley *et al*., 2009). Secondly, increased inputs of terrestrial organic matter from trees might provide important subsidies for consumers linked to allochthony either in the form of abscised leaf litter (Wallace *et al*., 1997; Abelho, 2001) or terrestrial invertebrates (Nakano & Murakami, 2001). Understanding any such collateral effects on important river organisms such as macroinvertebrates could aid decisions on where and when to use of riparian trees for shade and thermal damping. Additionally, allochthonous energetic subsidies might increase stream ecosystem resilience to global change by increasing in-stream biomass (Moore *et al*., 1993; Wallace *et al*., 1997; Muotka & Laasonen, 2002). There is a need to assess whether smaller riparian ‘buffers’ of native woodland could provide such benefits when used as climate change adaptation in the riparian zones of catchments managed for agriculture or production forestry in an attempt to mimic more extensive woodland (Broadmeadow & Nisbet, 2004; Wahl *et al*., 2013).

A major difficulty in assessing the effects of riparian woodlands in climate change adaptation is that several decades of tree growth are required between implementation of the concept and the full realization of effects on stream systems. Elsewhere, however, we have used cross-sectional comparison between sites with existing riparian broadleaves and other land uses to develop predictions about possible effects on stream fishes (Thomas *et al*., 2015). The same study also incorporated modern ecological methods – specifically stable isotopic analysis – as a means of assessing energetic linkages between terrestrial subsidies and aquatic organisms (Rybczynski *et al*., 2008; Ishikawa *et al*., 2012). Allochthonous and autochthonous production in streams is often distinct enough isotopically to estimate their relative origins in freshwater organisms and hence to appraise land use effects on their resource use (Doucett *et al*., 1996; Ishikawa *et al*., 2012). We know of no study, however, where these or other techniques have been used to assess the potential energetic effects of riparian adaptation strategies on macroinvertebrates – among the most functionally important of all stream organisms. In combination, stable isotopic data, quantitative estimates of macroinvertebrate biomass and taxonomic comparisons among streams draining different land-use types can help to assess the putative consequences of variations in riparian tree cover that could arise from climate change adaptation.

Here, we use cross-sectional comparisons at two scales (region and within-streams) among replicate temperate streams in contrasting land use to test the hypothesis that climate change adaptation using broadleaves can modify macroinvertebrate function and composition by changing energetic pathways. Specific predictions were that (i) streams draining deciduous woodland would be characterised by an increased abundance and biomass of leaf-shredding invertebrates, due to increased inputs of terrestrial organic matter; (ii) resource use in invertebrates in deciduous woodland streams would reflect terrestrial production more than in grassland streams; and (iii) riparian deciduous ‘buffers’ would approximate the effects on invertebrate composition and resource use in more extensive catchment woodland.

Materials and Methods

Study sites

Sites were located in and around the Brecon Beacons National Park, South Wales, UK (51° 51' 46’" N, 3° 22' 41" W Fig SM1) and the area has been described previously (Thomas *et al.*, 2015). Briefly, the region is temperate (1.1 °C - 19.1 °C mean min to mean max temperature; mean annual rainfall is 1433 mm), with brown earth, gleys and occasionally peaty soils that mostly overlay Devonian Old Red Sandstone drained by unpolluted, circumneutral and oligotrophic headwaters (pH: ~6.5 – 7.5; conductivity: ~20 – 400 μS; Ca^{2+}: ~5 – 40 mg l^{-1}; NO_3-: ~1 – 10 mg l^{-1}; PO_4^{3-}: ~0 mg l^{-1}). Temperate deciduous woodlands would form the climax vegetation, but most land is now used for rough sheep grazing and commercial forestry with non-native conifers. As such, the area is generally representative of upland land use patterns throughout the UK and western Europe more generally. Moreover, such habitats represent ideal candidates for management adaptations, as they are predicted to experience summer temperature increases of around 4-5 °C by 2080s (compared to historical averages) as a direct result of climate change (UKCP09 medium emissions scenario; Murphy *et al.*, 2009). Warming effects are already apparent in the region, with increases in mean temperatures of 1.4-1.7 °C over the 25 years between 1980 and 2005 (Durance & Ormerod, 2007), leading to local species extinction (Durance & Ormerod, 2010).

Twenty-four second-to-third-order streams at elevations of ~150 to 450 m were selected (Table S1; Fig. S1) to represent four land uses across the region: open moorland (hereafter Moorland; MO; n = 6); grassland with deciduous buffer (Buffer; GB; n = 6), where moorland catchments had buffers (~15 – 60 m) of mature deciduous alder *Alnus glutinosa*, birch *Betula pendula*, ash *Fraxinus excelsior* and oak *Quercus* spp.; deciduous woodland (Deciduous; DE; n = 6), where catchments still had relatively extensive areas of deciduous woodland in the riparian zone (width ~ 75–220 m) with grassland/moorland beyond; coniferous buffer (Coniferous; CB; n = 6), where catchments were dominated by exotic conifer plantations of mostly sitka spruce *Picea sitchensis*, with deciduous trees in the riparian zone (~ 15 – 65 m). Eight of these 24 sites (two in each land use; Table S1) were involved in an in-depth quantitative study of variations within streams.

Land use at all the sites was determined at each site using ArcGIS (ESRI 2009. ArcGIS Desktop: Release 9.2. Redlands, CA, USA; Environmental Systems Research Institute) and the *Arc Hydro Tools* package (version 9; Center for Research in Water Resources, University of Texas, TX, USA) combined with a habitat land-cover map (Countryside Council for Wales, 2004). Elevations, distance from source and riparian buffer dimensions were estimated at 100m intervals along each stream using Google Earth (Version 5.2; Google, Inc., Mountain View, CA, USA).

Water chemistry and habitat physiography

In May-June 2010, stream widths and depths were measured at four 10 m intervals along each sampling reach and water samples collected during base-flow to assess a) cations after filtration at 0.45 µm and acid fixation (inductively coupled plasma mass spectrometry; Thermo Elemental X-Series ICP-MS: Thermo Fisher Scientific, Waltham, MA, USA) and b) anions by ion chromatography (Dionex DX-80 Ion Analyser; Thermo Fisher Scientific, Inc.). Conductivity, pH and total dissolved solids (ppm) were assessed immediately following a storm event in October 2011, as these values are typically at their most extreme during high flow (Kowalik et al., 2007). Three replicate readings were taken at each 10m interval within each study reach using a Hanna HI 98129 low-range pH/Conductivity/TDS Tester (Hanna Instruments, Woonsocket, RI, USA).

Regional macroinvertebrate communities

During May-June 2010, benthic macroinvertebrates were collected from a 30 m reach at all 24 sites by separate kick-sample (D-frame kick net: net mesh 1 mm) respectively, in riffles (2-min sampling duration) and marginal habitats (i.e. slow-flowing depositional areas within 1 m of the stream bank; 1-min sampling duration), and preserved in 70% ethanol. This standardized procedure collects around 70% of species present at any one site and sufficient to detect differences among similar hillstreams (Bradley & Ormerod, 2002). Separating riffle and marginal samples provide a more representative species pool while also recording communities in contrastingly eroding/depositing environments where coarse particulate organic matter (CPOM) might accumulate (Bradley & Ormerod, 2002).

Kick-sample contents were sieved at 500 µm, sorted and identified as far as was practically feasible, mostly species or genus except for Diptera (Athericidae, Ceratopogonidae, Chironomidae, Pedicidae, Simuliidae, Tabanidae, Tipulidae) and some Coleoptera (Dytiscidae, Gyrindiae, Scirtidae), which were identified to family. Annelida were identified to subclass. Ephemeropterans collected from marginal areas at site MO2 deteriorated during storage and this site was excluded from some analyses. Using available data bases, taxa were assigned to one of five functional feeding groups, according to the classification of Cummins and Klug (1979): “Shredders” are adapted to process coarse particulate organic matter

(CPOM: principally decaying leaf litter and riparian grasses); “Grazers” are primarily dependent on in-stream primary production, predominantly epilithic algae; “Collector-Gatherers”, referred to as detritivores under some classifications (Moog, 1995), utilise benthic fine particulate organic matter (FPOM); “Filterers” obtain suspended materials from the water column; “Predators” capture and consume other animal taxa (Moog 1995; Meritt and Cummins 1996; Hauer & Lamberti 2006).

Macroinvertebrate and CPOM within streams

In February, June and October of 2011 and 2012 (i.e. six occasions), macroinvertebrates and CPOM standing stock were collected from fast-flowing riffles at the smaller sub-set of eight of the 24 sites in 5 x 0.07 m^2 quantitative Hess samplers (Hess, 1941; upstream net: 1mm mesh; downstream net: 500µm mesh; EFE-UK and GB Nets Lostwithiel, UK). Samples were immediately preserved in 70 % Industrial Methylated Spirits (IMS: Fisher Scientific, Loughborough, UK). Following treatment as above for kick samples, all macroinvertebrate individuals from each taxon and sample were transferred to glass vials for drying at 60 ˚C for 48 h and weighing to the nearest 0.1 mg. Biomass data were expressed per m^2 of streambed. CPOM, defined as all nonwoody vascular plant material > 1 mm^2 (Cummins, 1974), was rinsed from each sample into a 1 mm sieve, and also dried, weighed and converted to m^2 estimates of standing stock.

Stable isotopes

Samples for stable isotope analysis were collected from all 24 study sites twice over the annual cycle in May - June 2010 and again during January 2011. Benthic macroinvertebrates came from kick-samples from which dominant macroinvertebrate taxa representing each major Functional Feeding Group were removed on the bank-side, transferred to screw-top plastic vials and frozen at -18 ºC within 8 hours. Later-instar individuals were collected preferentially to minimise effects of ontogenetic dietary shifts (Dobson & Hildrew, 1992). Grazers were represented by heptageniid and baetid mayflies; Shredders by leuctrid and nemourid stoneflies along with the amphipod *Gammarus pulex*; Filterers by the Hydropsychidae (Trichoptera) and Simullidae (Diptera); and Predators by the Perlidae, Chloroperlidae (Plecoptera) and Rhyacophilidae (Trichoptera). Aggregate CPOM samples, mostly decaying broadleaf litter or riparian grasses from terrestrial production, were collected simultaneously from the streambed, while epilithic biofilm (hereafter, epilithon) representing in-stream primary production was scraped from the upper surfaces of streambed rocks. Samples were frozen as above. Based on invertebrate body size (10 – 100 mg), average stream water temperatures during the collection period (May/June: ~10 °C; January; ~5°C) and turnover equations presented elsewhere (see Thomas & Crowther, 2015), the isotopic composition of the selected consumers likely represented a relatively short-term integrator of their seasonal resource use (estimated ^{13}C half-life: ~ 13 – 25 days). The chosen sampling schedule should therefore have been sufficient to allow for detection of seasonal dietary shifts in these taxa, if present.

All samples for stable isotope analysis were rinsed with DH_2O and any non-target materials removed using forceps before freeze-drying at -60 ºC for 48 h in glass vials. Dried samples were homogenized and quantities for analysis (1 ± 0.2 mg for invertebrate tissue, 3 ± 0.2 mg for autotrophic material) were packaged within tin capsules for transport to the University of California, Davis Stable Isotope Facility. Dual δ^{13}C and δ^{15}N analysis was performed using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, U.K.). Values are reported in delta (δ) notation, as parts per thousand (‰) deviation from international standards (Vienna Pee Dee Belemnite for carbon and atmospheric air for nitrogen). Epilithic $\delta^{15}N$ from DE4 was anomalously enriched (> 13 ‰ versus a mean of 1.42 ‰ at all other sites), probably reflecting local drainage, and was excluded from analyses.

Statistical analysis

Statistical analyses were conducted in R Version 2.15.2 (R Development Core Team, 2012). Initial analysis involved a combination of principal components and Analysis of Variance to confirm expected land use variations among sites, and to appraise potential confounding influences from other physico-chemical factors. These were mostly minor, although moorland sites were at higher altitudes than others by ca. 150 m while sites in Deciduous woodlands tended to have higher conductivity reflecting generally increased ionic richness (Supplementary material). These possible confounding effects are addressed below.

Regional macroinvertebrate communities

Variations in community composition among land uses were initially plotted using Non-Metric Multidimensional Scaling (NMDS; Kruskal, 1964) using the metaMDS function within R's vegan package (version 2.0-5), based on 500 iterations (Oksanen *et al*., 2012). NMDS is a robust and well-known method that ordinates samples on overall dissimilarity (Kruskal, 1964; Clarke & Warwick, 2001; Zuur *et al*., 2007), and was here used in conjunction with the Bray-Curtis index, due to the ability of this metric to accommodate zero-skewed composition data (Clarke & Warwick, 2001). All values were fourth root transformed prior to calculation to down-weight the influence of the most abundant taxa (Clarke & Warwick, 2001). Permutational Multivariate Analysis of Variance *(PERMANOVA;* Anderson, 2001*)* was subsequently used to assess whether variations in community composition between land use types were significant. This non-parametric alternative to MANOVA compares groups in multivariate space based on dissimilarities and generates p values via a permutation procedure. PERMANOVA makes few major assumptions about the data set, and does not require multivariate normality (Anderson, 2001). To rule out potentially confounding effects of differential dispersion, PERMANOVAs were followed by betadisper tests (Anderson, 2006), a multivariate analogue of Levene's test for homogeneity of variances. Following an overall PERMANOVA to assess whether land use affected community composition, we appraised group-by-group pair-wise differences using the adonis function within vegan based on 4999 permutations (Oksanen *et al.*, 2012) following 4th root transformation. Where PERMANOVAs indicated significant differences among land uses, Similarity Percentage analysis (SIMPER; Clarke, 1993) assessed which taxa were principally responsible.

At the full suite of sites, we used General Linear Models (GLMs) to assess variations in total macroinvertebrate abundance, diversity (Shannon) and FFG representation among land use categories. Where PCAs indicated significant variations among land use categories differed in water chemistry or physical variables (see Supplementary Material), effects were controlled by first modelling dependent variables against abiotic covariates (mean pH, mean conductivity, PC1 scores from anion and cation data, elevation, mean depth, mean width, catchment area, distance from source), with stepwise deletion then used to remove all non-significant variables. Any remaining significant terms for each dependent variable were included as covariates in each GLM carried out to test for differences between land use categories.

Macroinvertebrate and CPOM within streams

At the eight sites sampled repeatedly, General linear mixed effects models (GLMMs; *lme* function within the *nlme* package, Pinheiro *et al*., 2013) were used to assess differences in macroinvertebrate biomass between land use types site-pairs and sampling periods, with site fitted as a random term, in order to account for non-independence of samples taken from the same location. Separate models were fitted to assess effects on total macroinvertebrate biomass, total macroinvertebrate density, FFG-by-FFG biomass and proportional representation, and CPOM standing stocks, with models including Land Use Type, Month and Year as explanatory variables, along with all relevant two-way (including Month:Year, to investigate sampling-period-specific differences), and three-way interactions. Where overall terms were significant, factor levels were compared using Tukey’s Honestly Significant Difference (HSD) *post-hoc* comparisons.

The relationships between total macroinvertebrate biomass, total macroinvertebrate density, FFG-by-FFG biomass, FFG-by-FFG proportional representation and the quantity of CPOM within samples and were assessed using GLMMs. CPOM biomass was fitted as a covariate, along with land use type, month and year as categorical explanatory variables, with all relevant interactions, up to four-way, included. Site was again fitted as a random term to account for non-independence. Where necessary, variables for all models were log, log + 1, square root or Box-Cox transformed prior to analysis, to meet linear model assumptions of normally distributed, homoscedastic residuals and lack of autocorrelation. Because they were proportions, FFG representation data were arcsine square root transformed (Sokal & Rohlf, 1995).

Stable isotopes

Our stable isotopic analysis depends on the assumption that the isotopic composition of consumer tissues, particularly ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$, can indicate community-wide dependence distinct food resources from different origins (Post, 2002; Layman *et al*., 2012). When applied to different taxa within a food web, isotopic signatures are then used to infer energy flow (Layman *et al*., 2012). In streams and rivers, this includes tracing back the energy sources supporting macroinvertebrate consumers to their terrestrial (allochthonous) or in-stream (autochthonous) origins, which are often isotopically distinct (Ishikawa *et al*., 2012).

Dual stable isotopic assessments of $\delta\ ^{13}C$ and $\delta\ ^{15}N$ was used here in conjunction with *R*'s SIAR *(Stable Isotope Analysis in R; version 4.1.3;* R Core Team, 2012) mixing model (Parnell *et al*., 2010) with the *SIARsolomcmcv4* function to estimate proportional contribution from terrestrial and in-stream production to consumer diets individually by site, functional feeding group and season. Mixing models were fitted for 14 sites where basal resources were isotopically distinct (GB, n = 3; CB, n = 4; DE, n = 3; MO, n = 4), but 10 sites were excluded where basal resource signatures overlapped or where consumer measurements fell outside the mixing polygons implied by basal signatures. All SIAR models were based on 500,000 iterations, with the first 50,000 discarded (Parnell *et al*., 2010). Trophic enrichment factors (TEFs) of 0.5 ± 0.5 ‰ for ^{13}C and 3.23 ± 1 ‰ for ^{15}N were assumed for primary consumers (Filterers, Grazers, Shredders) based on calculated mean difference between primary consumers and basal resources. An additional trophic level of enrichment was added for Predators (i.e. TEFs of 1 ± 1 ‰ and 6.46 ± 2 ‰ were used for ^{13}C and ^{15}N, respectively).

Variations in mean proportional contributions of terrestrial organic matter to consumer production estimated by SIAR (hereafter, ‘terrestrial resource use’) were analysed using a General Linear Mixed Model (GLMM). Riparian land use, month of sampling and Functional Feeding Group, along with all possible interactions between these factors, were included as fixed effects. Site was included as a random term to account for potential non-independence due to repeated measures at each site through time. As analysis of all proportion data resulted in normally distributed, homoscedastic residuals, no transformations were applied (Warton & Hui, 2011).

Results

Regional macroinvertebrate communities

Macroinvertebrate communities at the 24 regional sites varied among land uses in riffle ($F_{3,22}$ = 1.7442, p = 0.004), marginal ($F_{3,21}$ = 2.1634, p > 0.001) and combined samples ($F_{3,21}$ = 2.116, p > 0.001), with contrasts greatest between Moorland vs. Deciduous, Coniferous vs. Moorland and Coniferous vs. Deciduous sites (Table 1; Fig. 1). Buffer sites were generally intermediate, although communities in their marginal habitats differed from Deciduous sites (Table 1 and 2). SIMPER showed that differences in community composition were mostly due to overall changes in abundance: no single taxon contributed > 7 % of the difference between any two land use categories and those responsible represented a relatively small proportion of the total species pool (Table 2). For example, differences between Deciduous sites and other land uses were principally caused by increased abundance of the amphipod *Gammarus pulex*, decreases in the grazing mayfly *Electrogena lateralis* and variations among *Leuctra* stoneflies. Conifererous sites differed from others mostly because of increased abundances of leuctrid and nemourid stoneflies, notably *Amphinemura sulcicollis*. *Betadisper* tests confirmed that differences between land uses were not due to unequal dispersion between groups (Riffle: $F_{3, 19} = 0.140$, p = 0.935; Margin: $F_{3, 18} = 0.326$, p = 0.807; Combined: $F_{3, 18} = 0.049$, p = 0.985).

Functional group representation varied more strongly among land uses (Tables 3 and S2), and shredders contributed more to communities at Deciduous sites than any other land use in riffle, margin and combined samples (Tukey's HSD for Riffle: Deciduous v Buffer P = 0.008, Coniferous P = 0.006, Moorland P = 0.005; Margin: Deciduous v Buffer P = 0.030, Coniferous P = 0.005, Moorland P = 0.013; Combined: Deciduous v Buffer P = 0.011, Coniferous, P = 0.004, Moorland P = 0.008). Other effects were weaker: Coniferous sites contained a higher proportion of Grazers (P = 0.025) and Predators (P = 0.022) than at Deciduous sites, and a lower proportion of Collector-Gatherers (P = 0.024) than at Moorland sites.

Macroinvertebrate and CPOM within streams

At the eight sites sampled repeatedly, benthic CPOM in Hess samples varied significantly among riparian land uses ($F_{3, 213} = 43.41$, $P < 0.001$) with amounts greater at Deciduous sites than in any other site type (Tukey's HSD: $P < 0.001$ in all cases), and lowest in Moorland (Fig. 2). Standing stocks at Coniferous and Buffer sites were intermediate, and did not differ significantly from each other (P = 0.557). These differences were maintained throughout the study, and did not depend on sampling year ($F_{3, 213} = 1.04$, $P > 0.377$) or month ($F_{6, 213} = 1.15$, $P > 0.337$) despite some seasonal variations (Fig. 2).

Consistent with the variations in CPOM, total macroinvertebrate biomass ($F_{3, 213} = 14.57$, $P < 0.001$) and density ($F_{3,213} = 15.84$, $P < 0.001$) were both greater at Deciduous sites and lower at Coniferous sites (Tukey's HSD: $P < 0.01$ in all cases) than in any other land use ($P < 0.05$ in all cases) when averaged across all sampling periods (Table 4; Fig. 3). Moorland and Buffer sites had intermediate biomass, and did not differ significantly from each other ($P = 0.971$). Again, these effects occurred irrespective of variations in biomass and density among seasons and years (see Supplementary Material Appendix S2).

Biomass values in each FFG also varied among land uses when averaged across sampling periods (Table 4). Shredder biomass was higher in Deciduous streams than in all other land uses ($P < 0.05$ in all cases), which did not differ significantly from one another ($P > 0.05$ in all cases). Collector-Gatherers and Filterers had their lowest biomass in Coniferous streams (Tukey's HSD: $P < 0.05$ in all cases), while Grazer biomass was also significantly lower in Coniferous than Deciduous streams ($P = 0.03$). Predator biomass was higher in Moorland than Coniferous sites ($P = 0.002$), but otherwise did not differ among land uses ($P > 0.05$ in all cases). Land use effects on FFG biomass were consistent among months, years and individual sampling periods for Collector-Gatherers (Month: $F_{6, 213} = 0.90$, $P = 0.498$; Year: $F_{3, 213} = 1.04$, $P = 0.377$; Sampling Period: $F_{6, 213} = 1.26$, $P = 0.277$), Predators (Month: $F_{6, 213} = 0.50$, $P = 0.810$; Year: $F_{3, 213} = 2.54$, $P = 0.058$; Sampling Period: $F_{6, 213} = 2.24$, $P = 0.051$) and Shredders (Month: $F_{6, 213} = 1.10$, $P = 0.365$; Year: $F_{3, 213} = 1.42$, $P = 0.238$; Sampling Period: $F_{6, 213} = 1.26$, $P = 0.276$). Variations among land uses for Filterer ($F_{6, 213} = 2.18$, $P = 0.047$) and Grazer biomass ($F_{6, 213} = 4.31$, $P < 0.001$) were more transient, and both differed among sampling months. The biomass of several functional feeding groups also varied seasonally when averaged across land use types (see Supplementary material Appendix S2). In general, similar patterns were confirmed by proportionate variations among FFGs, and in particular Deciduous sites had a greater proportion of Shredder taxa than all other land use types ($P < 0.001$ in all cases) while Coniferous sites supported a lower proportion of Collector-Gatherer taxa and greater proportion of Grazers (Tukey's HSD: $P < 0.05$ in all cases) (See Appendix S3).

Supporting a likely effect of CPOM on macroinvertebrates across land uses, total macroinvertebrate biomass ($F_{1,\ 189} = 94.96$, $P < 0.001$) and density ($F_{1,\ 189} = 138.63$, $P < 0.001$) both increased significantly in samples with greater standing stocks of CPOM (Fig. 4; Table 5). These relationships were independent of land use type (Biomass: $F_{3,\ 189} = 2.49$, $P = 0.062$; Density: $F_{3,\ 189} = 0.53$, $P = 0.661$), month (Biomass: $F_{2,\ 189} = 0.41$, $P = 0.665$; Density: $F_{2,\ 189} = 2.12$, $P = 0.122$) or year (Biomass: $F_{1,\ 189} = 0.74$, $P = 0.393$; Density: $F_{1,\ 189} = 0.02$, $P = 0.888$). Within individual guilds, Shredder biomass also increased with CPOM biomass across samples ($F_{1,\ 189} = 7.63$, $P = 0.006$), though the relationship varied seasonally ($F_{2,\ 189} = 5.85$, $P = 0.003$). Similarly, the proportion of total macroinvertebrate biomass composed of Shredders was significantly positively related to CPOM biomass ($F_{1,\ 189} = 17.22$, $P < 0.001$), but the relationship varied between months ($F_{1,\ 189} = 4.52$, $P = 0.012$) and years of sampling ($F_{1,\ 189} = 9.93$, $P = 0.002$). The biomass or proportional representation of all other functional feeding groups was not significantly related to CPOM biomass.

Stable isotopes

Contrary to prediction (ii) and unexpectedly given the apparent relationship between land use, CPOM and macroinvertebrate biomass, terrestrial resource use by macroinvertebrates, as revealed by isotopic data, did not vary significantly among riparian land use types ($F_{3,\,95}$ = 0.416, P = 0.742; Fig. 5) even when variations between months ($F_{3,\,93}$ = 0.923, P = 0.433) or FFGs ($F_{8,\,87}$ = 0.620, P = 0.759) were considered. Across all land use categories in both months, roughly 50% (range: 33.1-75.8 %) of resources assimilated by all macroinvertebrate functional groups were of terrestrial origin (Fig. 5). When all land use categories were pooled, terrestrial resource use varied between functional feeding groups in ways that differed between months ($F_{3,\,95}$ = 3.890, P = 0.012), but this effect occurred only as significantly increased terrestrial contributions to Grazer tissues in June (P = 0.002; Fig. S 3).

Discussion

Despite increasing concern about climate change, practical evidence about the effectiveness of management adaptations that could reduce adverse effects on ecosystems is still remarkably scarce. To our knowledge this study, combined with an associated article (Thomas *et al*., 2015), is the first to appraise collateral ecological effects of using riparian trees to create shade - one of the most widely advocated adaptation measures for rivers (Ormerod 2009; Palmer *et al*., 2009; Clews *et al*., 2010). Of the three predictions we examined, only one was supported unequivocally: streams draining deciduous woodland differed clearly from others in having substantially enhanced standing stocks of CPOM as well as a greater density and biomass of macroinvertebrates, particularly Shredders. In contrast, there were no variations across land uses in functional group reliance on terrestrial resources (prediction ii), and nor were the effects of riparian buffers of 15-60m width sufficient to mimic the effects of more extensive riparian woodlands (prediction iii). These outcomes provide some support for the hypothesis that climate change adaptation using broadleaves might alter macroinvertebrate communities functionally and compositionally, also enhancing stocks of CPOM as an important basal resource. However, on our evidence this effect is likely only where broadleaf restoration or planting is extensive, and large step-changes from autochthony to allochthony may not be a major feature. Interestingly, the data support previous suggestions that narrow riparian buffer zones may be insufficient to offset some of the influences of wider catchment land use on stream communities and ecosystem functioning (Allan *et al*., 1997; Kauffman *et al*., 1997; Harding *et al*., 2006; Wahl *et al*., 2013).

Before discussing more general ramifications of this study, two important caveats must be noted. First, as with other cross-sectional investigations using space-for-time substitution, our site categories were created neither by experimental manipulation nor random allocation to treatments. Our interpretation must, therefore, rely on correlative techniques that are at risk from possible confounding effects. The land use categories differed marginally on physicochemistry, with, for example, treeless moorland streams at higher elevations than other land use types (Supplementary material). However, the range over which these variables differed appeared to be insufficient to influence community composition: moorland (MO) and buffer strip (GB) sites differed on physical criteria but supported similar communities. Similarly, buffer strip (GB) sites and those draining larger areas of deciduous woodland (DE) differed with respect to water chemistry, but not in overall macroinvertebrate community composition and the principal results were consistent across the two scales of the investigation. In other fields, such as freshwater acidification, early evidence based on space-for-time substitution (Ormerod *et al*., 1988) has since been validated using long-term data (Ormerod & Durance 2009) and coupled with studies of processes (Kowalik *et al*., 2007) to provide important insights into global chance effects. A second caveat is that the study was intended to appraise the effects of riparian management as an adaptation to climate change, yet could only be carried out under current climatic conditions. While there is already evidence of warming effects on streams in the study region (Durance & Ormerod 2007, 2010; Clews *et al*., 2010), any extrapolation requires the assumption that patterns detected here will persist under the higher temperatures, more variable rainfall and potentially extreme discharge expected in NW Europe. Interestingly, future climates could also affect streamside woodlands as well as in-stream conditions – for example through altered disease effects on tree species such as European Ash (*Fraxinus excelsior*) (Pautasso *et al*., 2013). Notwithstanding these concerns, we suggest that comparative studies like ours provide a useful basis for predicting how temperate upland streams might respond to the restoration of catchment tree cover, thereby increasing understanding of the resultant ecological changes (Naiman *et al*., 2012). Decades would be required for the experimental development of riparian tree cover, yet evidence to inform decision about climate change adaptation are required now.

The clearest overall trends we detected of increased CPOM stocks, enhanced shredder density and increased macroinvertebrate biomass in extensive deciduous woodlands are generally well known (Wallace *et al.*, 1997). Interestingly, these effects occurred in both riffles and margins, but were stronger in the latter, where leaf litter and other terrestrial organic material often accumulate in ‘softer’ habitats of woody debris, roots and vegetated features (Ormerod *et al*., 1993; Flores *et al.*, 2013). Such marginal features that increase riparian shore-length and increase litter retention could be as important in increasing CPOM stocks as the adjacent canopy is in providing inputs (Muotka & Laasonen, 2002). Deciduous woodlands would form the principal climax vegetation communities over large parts of the temperate zone and, where riparian zones are intact, the resulting litter input to headwaters is a key component of energy flux through food webs (Vannote *et al*., 1980). Where subsidies of CPOM are large enough to offset climatically mediated export, riparian woodlands might also increase the resilience of macroinvertebrate populations by increasing basal resources (Moore *et al.*, 1993; Wallace *et al.*, 1995; Eggert *et al.*, 2012). Understanding future interactions between litter subsidies, uptake into food webs, secondary production and climate change is likely to be a key area of interest: land use in the riparian zone is important in that it mediates both climatic effects and riparian subsidies (Wallace *et al.*, 1995; Broadmeadow *et al.*, 2011).

Despite apparently changing CPOM and invertebrate abundance across the study streams, however, land use did not affect the relative use of terrestrial and aquatic resource use by macroinvertebrates in any functional feeding group. Thus, while shredders apparently intercepted the terrestrial subsidy at deciduous sites and converted it into increased invertebrate biomass, they still depended in part on autotrophic production. This contrasts with the resource-use patterns typically assigned to this group (Cummins & Klug, 1979). Such effects would arise where shredding taxa ingested and assimilating algal production attached to leaf litter (Hax & Golladay, 1993). In the same way, grazing taxa can supplement their diets with fine terrestrial organic matter captured within epilithic biofilms (Hamilton *et al.*, 2005). Thus, even at open moorland sites where greater autotrophic production would be expected, roughly 50% of animal production in all FFGs originated from terrestrial sources. These results are contrary to the expectation that relative allocthony versus autochthony should differ among deciduous woodland, grassland and conifer sites (Abehlo, 2001; Kiffney *et al.*, 2003, 2004).

Such unexpected effects might be explained either by intrinsic biological processes or by extrinsic, contextual factors alone or combination. For example, autotrophic food webs persist even in streams in woodland environments prior to seasonal canopy closure or where primary production is maintained in habitats such as mosses (Wallace *et al*., 1997). Equally, allochthonous resources still occur in moorland catchments, and Menninger & Palmer (2007) illustrated how herbs and grasses provided significant inputs of litter to open-canopy piedmont streams. Leberfinger *et al*. (2011) used stable isotope analysis to show that such terrestrial organic resources were important to shredding macroinvertebrates in grassland streams despite the availability of autotrophic production. Resource-use patterns might also be mediated directly and locally by invertebrate consumers: despite varying amounts of terrestrial organic matter in different land uses, use and uptake can be constrained by the capacity for feeding plasticity in consumer taxa (e.g. morphological adaptations for rock scraping vs. leaf shredding vs. filter feeding) (Cummins & Klug, 1979; Dangles, 2002). Variations in resource quality between terrestrial and in-stream production might also constrain feeding choices, with CPOM typically less rich in macronutrients than benthic epilithon: macroinvertebrates often require elemental stochiometry with their food sources, and CPOM alone may be insufficient to support growth and metabolism (Hladyz *et al*., 2009). More extrinsically, wider catchment effects or downstream export might mask local riparian effects from land use: there is evidence to indicate that even small reductions in catchment tree cover (~10 % deforestation in otherwise totally afforested catchments) weakens terrestrial-aquatic linkages (England & Rosemond, 2004). Resource use patterns may therefore reflect whole catchment land use rather than those just in the riparian zone, even where wider riparian land uses are extensive: in woodland catchments, large areas of lateral tree cover may be needed to offset downstream subsidy export, particularly transport during high flow events (Wallace *et al*. 1995; Eggert *et al*., 2012). Finally, measurement or modelling artefacts with stable isotopes cannot be excluded. For instance, in some riverine systems it may be difficult to fully discern in-stream production using isotopic signals alone, as there can be substantial overlap in ^{13}C concentrations between autochthnous and allochthonous material (France, 1996). However, care was taken to exclude data from sites where assumptions of isotopic mixing models were violated, and repeated sampling at each site improved robustness by minimizing the effects of temporal variability. Additionally, potential error in the estimation resource isotopic composition was of explicitly incorporated into the Bayesian models used here (Parnell *et al*., 2010).

Implications for climate change adaptation

A central theme of our study is an appraisal of how the protection, management and restoration of riparian broadleaves for climate-change adaptation might have effects on temperate headwaters beyond cooling alone. Already, there is extensive investment in Britain and elsewhere to instigate riparian tree planting based on evidence that the resulting shade damps thermal variation in adjacent streams (Broadmeadow & Nisbet, 2004; Broadmeadow *et al*., 2011; Environment Agency, 2011). Here, we set out to assess whether there might also be collateral effects on important basal resources or aspects of stream function mediated by macroinvertebrates. Our previous article using data from some of the same locations showed that deciduous riparian zones were neutral for salmonids, but conifers reduced density and biomass (Thomas *et al*., 2015). The latter result is consistent with data collected here in that overall macroinvertebrate biomass and density were also lowest in coniferous catchments.

Small-scale, riparian interventions in catchments used otherwise for agriculture or urbanization are postulated often as a potentially valuable and cost-effective means of reducing warming directly, reducing stressors that could be exacerbated by warming (e.g. nutrients, sediments) and enhancing resilience by providing habitat and energetic subsidies

(Moore *et al*., 1993; Wallace *et al*., 1997; Sweeney *et al*., 2004). Our data extend understanding this technique by illustrating how riparian broadleaves used in climate change adaptation would be likely to enhance CPOM stocks, Shredder densities and overall macroinvertebrate biomass, but only where woodland is extensive. In this respect the management implications are clear. First, where narrow woodland buffers are used solely to moderate thermal regimes, large energetic benefits or effects on CPOM dynamics would, on our evidence, be unlikely. In contrast, more extensive woodland restoration would have additional further benefits beyond cooling through enhanced litter subsidies and retention in marginal habitats. Both of these effects could be enhanced by encouraging planting or natural regeneration of native riparian vegetation, for example through agri-environment schemes or as part of wider global reforestation efforts (Crowther *et al*., 2015), and by protecting retentive features such as marginal vegetation or woody debris during river management (Muotka & Laasonen, 2002; Sweeney *et al*., 2004; Flores *et al.* 2013). Such techniques could either be implemented alone, or in combination with other adaptation strategies which could act to enhance local shad and cooling (e.g. Everall *et al*., 2012). The ecological benefits locally within headwaters might include improved conservation of woodland stream organisms, restored linkage between headwaters and riparian zones, restoration of natural stream function and potentially increased resilience through enhanced basal resources (Moore *et al*., 1993; Goodwin *et al*., 1997; Muotka & Laasonen, 2002). More extensive benefits from litter processing and export to ecosystems downstream are possible, but require fuller appraisal in more extensively wooded landscapes (Wipfli, 2005; Tanentzap *et al*., 2014).

More generally, our study illustrates a possible approach to appraising the potential effectiveness of climate change adaptation – through studies of ecological processes combined with a survey of locations assumed to mimic future land cover options. With current practical knowledge of climate change adaptation in most ecosystems still rudimentary, we suggest that this subject needs greater research attention given the urgency for action and the time required to develop, implement and fully realize change at the landscape scales necessary.

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Table 1: Pairwise comparisons using PERMANOVA of macroinvertebrate community composition between streams with different land use in South Wales. P values < 0.05 are highlighted in bold. See Table 2 for main taxa contributing to these differences.

	Sample Type								
	Riffle			Margin			Combined		
Comparison	df	F	P	df	F	p	df	F	P
Buffer - Coniferous	1, 11	0.89	0.55	1,11	1.44	0.19	1,11	1.29	0.20
Buffer - Deciduous	1, 10	1.56	0.11	1,10	2.10	**0.04**	1,10	1.7337	0.07
Coniferous - Deciduous	1, 10	2.42	**0.03**	1,10	3.06	**0.01**	1,10	2.3553	**0.02**
Moorland - Buffer	1, 11	1.32	0.17	1,10	1.15	0.33	1,10	1.5292	0.06
Moorland - Coniferous	1, 11	1.77	**0.04**	1,10	2.71	**0.01**	1.10	2.2317	**0.01**
Moorland - Deciduous	1, 10	2.55	**0.02**	1,9	2.87	**0.01**	1,9	3.1994	**0.01**

Table 2: Results of SIMPER analysis comparing invertebrate communities in South Wales streams among different catchment land uses. The values in each cell are percentage of total dissimilarity (after fourth root transformation) and mean raw abundances (individuals per sample) for the five taxa contributing most to differences between riparian land use types indicated by PERMANOVA (see Table 1).

Comparison	Riffle			Margin			Combined		
	Taxon	%	Mean Abundance	Taxon	%	Mean Abundance	Taxon	%	Mean Abundance
Buffer – Deciduous	N/A			*Gammarus pulex*	5.8	10.0 vs. 84.2	N/A		
				Leuctra inermis	4.8	12.8 vs. 1.8			
				Leuctra moselyi	4.2	18.8 vs. 37.2			
				Electrogena lateralis	4.2	26.0 vs. 14.4			
				Leuctra nigra	3.4	1.3 vs. 11.2			
Coniferous - Deciduous	*Gammarus pulex*	6.5	4.0 vs. 109.0	*Gammarus pulex*	6.8	3.0 vs. 84.2	*Gammarus pulex*	5.58	7.0 vs. 193.0
	Leuctra inermis	4.6	31.0 vs. 1.8	*Leuctra nigra*	5.1	0.7 vs. 11.2	*Leuctra inermis*	4.04	36.0 vs. 3.6
	Electrogena lateralis	3.6	13.5 vs. 0.6	*Chloroperla torrentium*	4.2	9.0 vs. 1.6	*Chloroperla torrentium*	3.72	16.3 vs. 2.8
	Chloroperla torrentium	3.4	7.3 vs. 1.2	*Electrogena lateralis*	3.9	22.0 vs. 14.4	*Electrogena lateralis*	3.29	35.5 vs. 15.0
	Amphinemura sulcicollis	3.2	11.7 vs. 2.4	*Leuctra inermis*	3.8	5.0 vs. 1.8	*Leuctra nigra*	3.25	2.3 vs. 12.4
Coniferous - Moorland	Simuliidae	4.6	21.2 vs. 36.3	*Serratella ignita*	4.7	9.5 vs. 46.8	*Serratella ignita*	4.05	16.3 vs. 75.4
	Hydropsyche instabilis	3.7	6.3 vs. 0.2	*Rhithrogena spp.*	4.0	4.3 vs. 5.6	*Leuctra hippopus*	3.16	3.2 vs. 12.0
	Serratella ignita	3.6	6.8 vs. 24.0	*Chloroperla tripunctata*	3.9	3.8 vs. 0	Simuliidae	3.15	23.2 vs. 45.7
	Baetis spp.	3.3	95.5 vs. 145.8	*Gammarus pulex*	3.5	22.0 vs. 14.4	*Chloroperla tripunctata*	3.13	4.6 vs. 0
	Hydraena gracilis	3.2	2.8 vs. 0.3	*Caenis rivulorum*	3.4	1.3 vs. 3.4	*Hydropsyche instabilis*	2.90	6.8 vs. 0.2
Deciduous – Moorland	*Gammarus pulex*	5.8	109.0 vs. 6.7	*Leuctra nigra*	5.3	11.2 vs. 0	*Gammarus pulex*	4.24	193.2 vs. 21.0
	Leuctra inermis	3.9	1.8 vs. 22.3	*Gammarus pulex*	4.6	84.2 vs. 13.0	*Leuctra nigra*	4.15	12.4 vs. 0
	Philopotamus montanus	3.8	11.0 vs. 0	*Electrogena lateralis*	3.9	14.4 vs. 26.8	*Serratella ignita*	3.52	6.4 vs. 75.4
	Hydropsyche instabilis	3.7	7.8 vs. 0.2	*Leuctra inermis*	3.8	1.8 vs. 7.6	*Leuctra inermis*	3.47	3.6 vs. 31.0
	Electrogena lateralis	3.6	0.6 vs. 13.7	*Serratella ignita*	3.7	4.0 vs. 46.8	*Electrogena lateralis*	3.17	15.0 vs. 39.0

Table 3: Effects of land use on macroinvertebrate abundance, diversity and proportional functional group representation using General Linear Models. P values < 0.05 are highlighted in bold. See Table S2 for functional group composition data.

	Sample Type								
	Riffle			Margin			Combined		
Dependent	Df	F	P	df	F	P	df	F	P
Total Abundance	3, 19	0.79	0.52	3, 18	0.88	0.47	3, 18	0.49	0.69
Diversity (Shannon Index)	3, 19	0.23	0.87	3, 18	0.94	0.44	3, 18	0.36	0.79
Proportion Collector Gatherer	3, 19	1.29	0.31	3, 17	3.48	**0.04**	3, 18	1.49	0.25
Proportion Filterer	3, 18	0.89	0.47	3, 16	1.97	0.16	3, 18	0.27	0.85
Proportion Grazer	3, 19	0.21	0.89	3, 18	3.38	**0.04**	3, 18	1.56	0.22
Proportion Predator	3, 19	0.78	0.52	3, 18	4.10	**0.02**	3, 17	0.43	0.74
Proportion Shredder	3, 19	6.98	**0.002**	3, 18	6.12	**0.004**	3, 18	6.85	**0.002**

Table 4: Biomass (mg m^{-2}: mean ± 1 SE) of each Functional Feeding Group (FFG), along with totals, across all sampling periods at the repeatedly sampled sites. Shared letters within each FFG denote land use type site-pairs where FFG biomass did not differ significantly (Tukey's *post-hoc* comparisons following GLMM: $P > 0.05$).

Functional Feeding Group	Buffer	Coniferous	Deciduous	Moorland
Collector-Gatherer	106.29 ± 25.41 a	87.77 ± 28.70 b	92.12 ± 18.82 a	99.03 ± 15.75 a
Filterer †	16.74 ± 3.99 a	2.55 ± 1.28 b	35.72 ± 7.48 c	8.23 ± 3.30 a
Grazer †	70.96 ± 12.97 ab	58.26 ± 9.91 a	107.02 ± 15.68 b	61.30 ± 8.07 ab
Predator	116.2 ± 40.59 ab	29.56 ± 7.56 a	88.68 ± 24.87 ab	87.51 ± 15.73 b
Shredder	15.24 ± 4.71 a	19.66 ± 9.81 a	182.66 ± 52.01 b	7.93 ± 2.91 a
Total†	325.49 ± 61.60 a	197.80 ± 40.09 b	506.21 ± 71.49 c	264.01 ± 26.36 a

† Interaction terms indicated significant temporal variation in the direction of the difference between land use type site-pairs.

Table 5: Relationships between Coarse Particulate Organic Matter (CPOM) biomass, and biomass and proportional representation of each Functional Feeding Group (FFG) on a sample-by-sample basis. P values < 0.05 are highlighted in bold.

	FFG Biomass vs. CPOM Biomass		Proportion FFG vs. CPOM Biomass	
Functional Feeding Group	$F_{1,\ 189}$	P	$F_{1,\ 189}$	P
Collector-Gatherer	0.964	0.328	0.734	0.393
Filterer	0.138	0.711	0.044	0.834
Grazer	2.590	0.109	1.787	0.183
Predator	0.726	0.395	2.320	0.129
Shredder	7.632	**0.006**	17.218	**0.001**

Figure Legends

Figure 1: NMDS ordinations of macroinvertebrate communities (after 4th root transformation) collected from South Wales streams in a.) riffles; b.) marginal habitats; c.) combined samples: points indicate Buffer (solid lines; ■), Coniferous (dashed lines; ▲), Deciduous (dotted lines; ●) and Moorland (dot-dash lines; ◆) sites.

Figure 2: CPOM biomass (mg m^{-2}: mean ± 1SE) dynamics across land use types and sampling periods. (a) Site-specific values averaged across all sampling periods, (b) Yearly values averaged across all sites, (c) Monthly values averaged across sites in 2011 and (d) Monthly values averaged across sites in 2012. Land use categories: CB = Coniferous, DE = Deciduous, GB = Buffer, MO = Moorland. Y-axis scales differ between graphs.

Figure 3: Macroinvertebrate biomass (mg m^{-2}: mean ± 1 SE) over two years (2011 and 2012) at eight streams in South Wales draining different land use: CB = Coniferous, DE = Deciduous, GB = Buffer, MO = Moorland. Shared letters denote land use type site-pairs that did not differ significantly within each sampling period (Tukey's *post-hoc* comparisons following GLMM: $P > 0.05$).

Figure 4: Relationships between log transformed CPOM biomass and (a) total macroinvertebrate biomass, (b) total macroinvertebrate density. Solid lines indicate best fit as predicted by Linear Mixed Effects models, dashed lines represent predicted standard errors around the mean.

Figure 5: Estimated proportional terrestrial resource use in each of four macroinvertebrate functional groups collected for stable isotope analysis in streams in South Wales, across land use types on two sampling occasions: (a) filtering taxa, (b) grazing taxa, (c) predatory taxa and (d) shredding taxa. Values presented are mean proportional terrestrial resource use ± 1 SE derived from SIAR.

Figure 1:

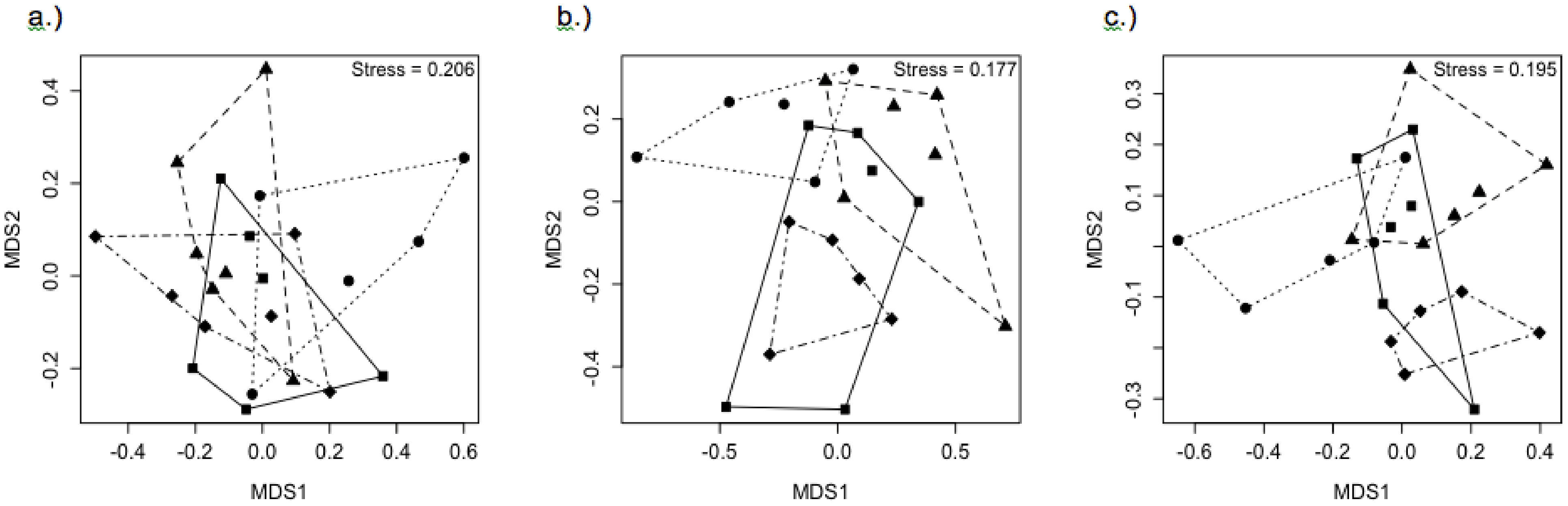

a.)
Stress = 0.206
0.4
0.2
0.0
-0.2
MDS2
-0.4
-0.2
0.0
0.2
0.4
0.6
MDS1
b.)
Stress = 0.177
0.2
0.0
-0.2
-0.4
MDS2
-0.5
0.0
0.5
MDS1
c.)
Stress = 0.195
0.3
0.2
0.1
-0.1
-0.3
MDS2
-0.6
-0.4
-0.2
0.0
0.2
0.4
MDS1

Fig 2:

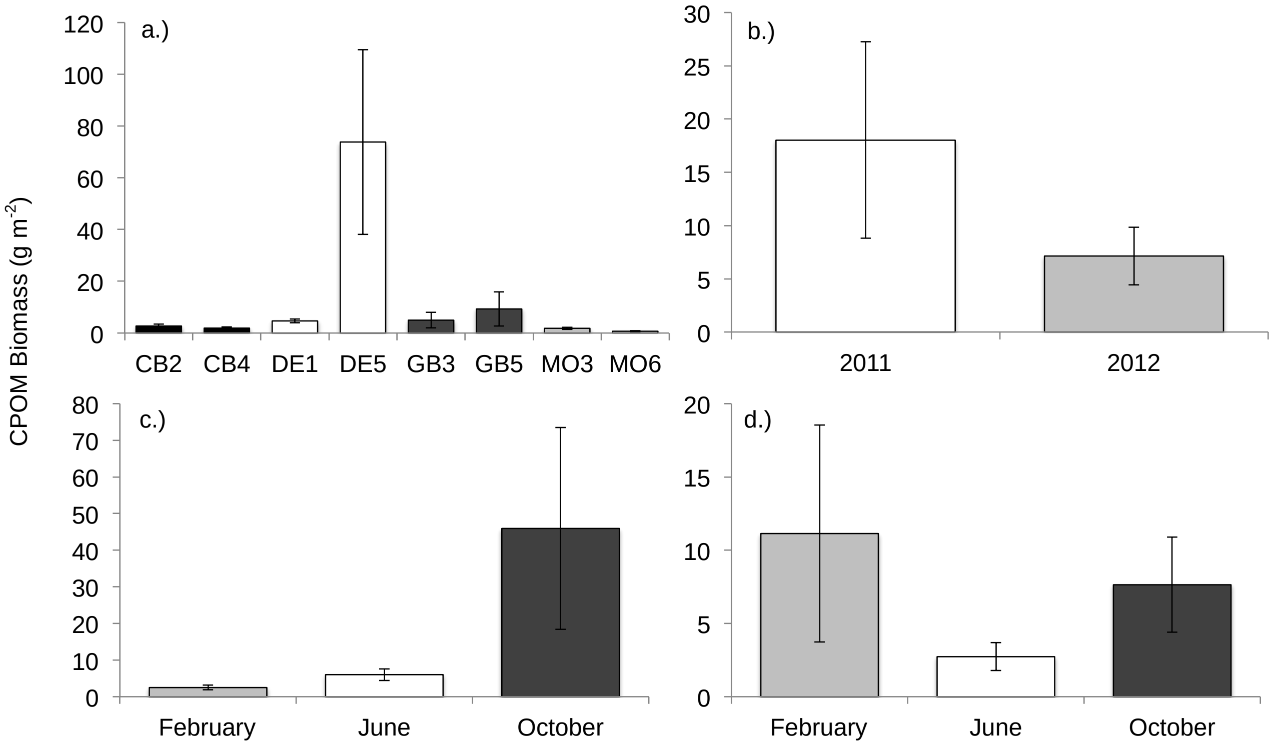
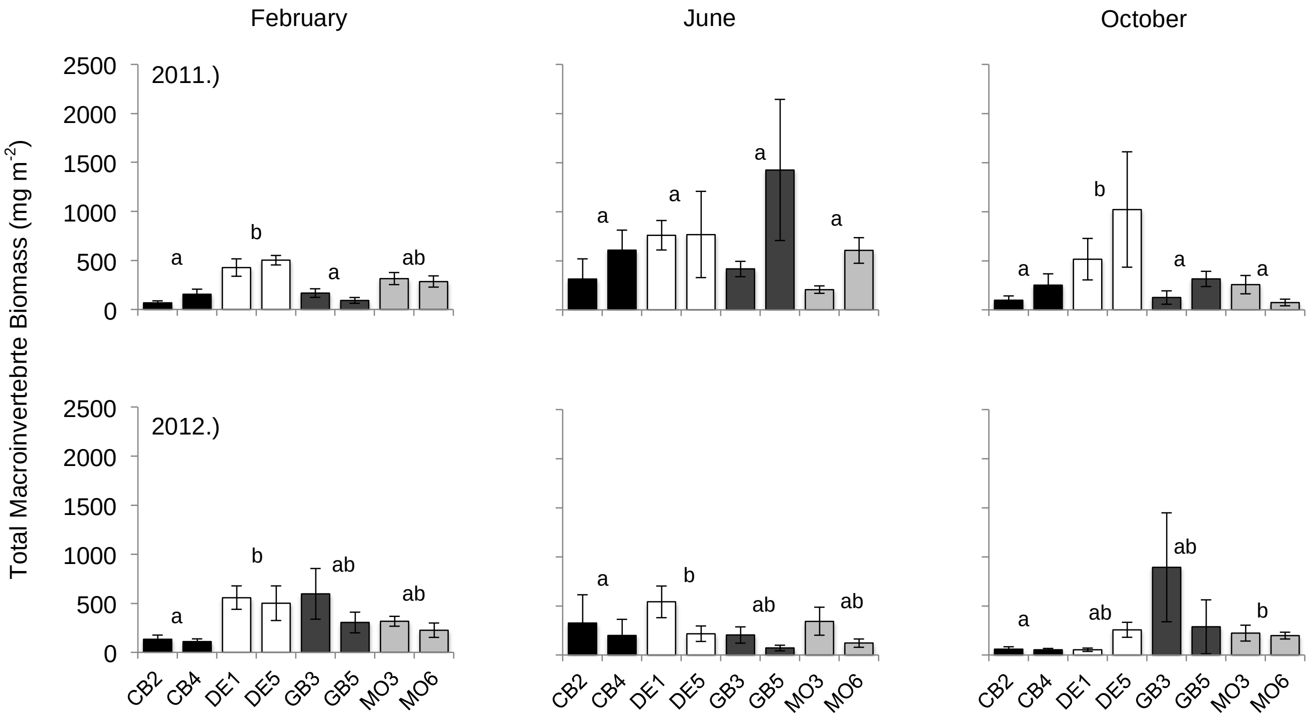
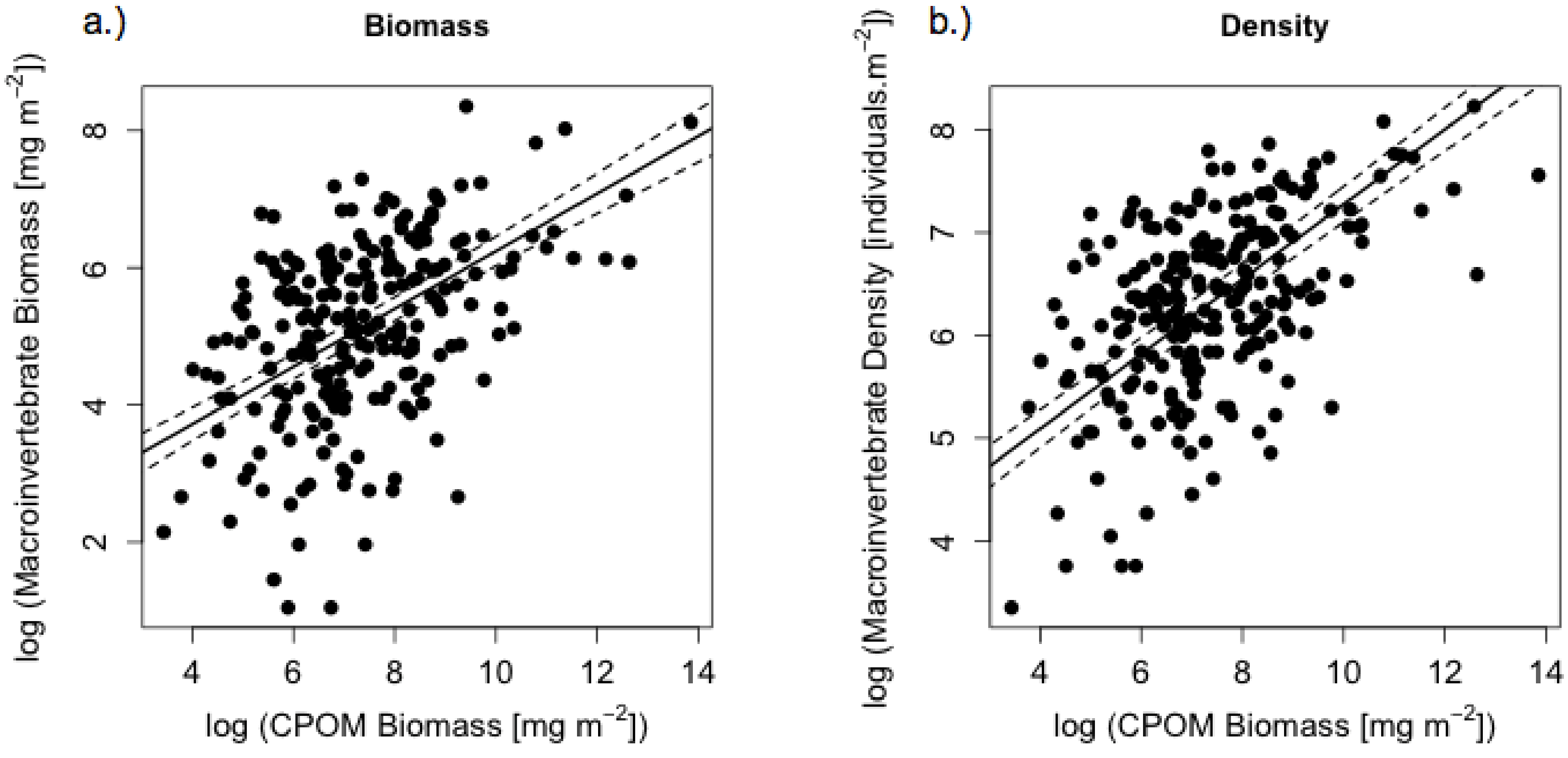

a.)
120
100
80
60
40
20
0
CB2
CB4
DE1
DE5
GB3
GB5
MO3
MO6
b.)
30
25
20
15
10
5
0
2011
2012
CPOM Biomass (g m-2)
c.)
80
70
60
50
40
30
20
10
0
February
June
October
d.)
20
15
10
5
0
February
June
October

Figure 3:



February
June
October
2011.)
2012.)
Total Macroinvertebrte Biomass (mg m-2)
2500
2000
1500
1000
500
0
a
b
a
ab
a
a
a
a
a
b
a
a
a
b
ab
ab
a
b
ab
ab
a
ab
ab
b
CB2
CB4
DE1
DE5
GB3
GB5
MO3
MO6

Figure 4:


a.)
Biomass
log (Macroinvertebrate Biomass [mg m^{-2}])
2
4
6
8
4
6
8
10
12
14
log (CPOM Biomass [mg m^{-2}])
b.)
Density
log (Macroinvertebrate Density [individuals.m^{-2}])
4
5
6
7
8
4
6
8
10
12
14
log (CPOM Biomass [mg m^{-2}])

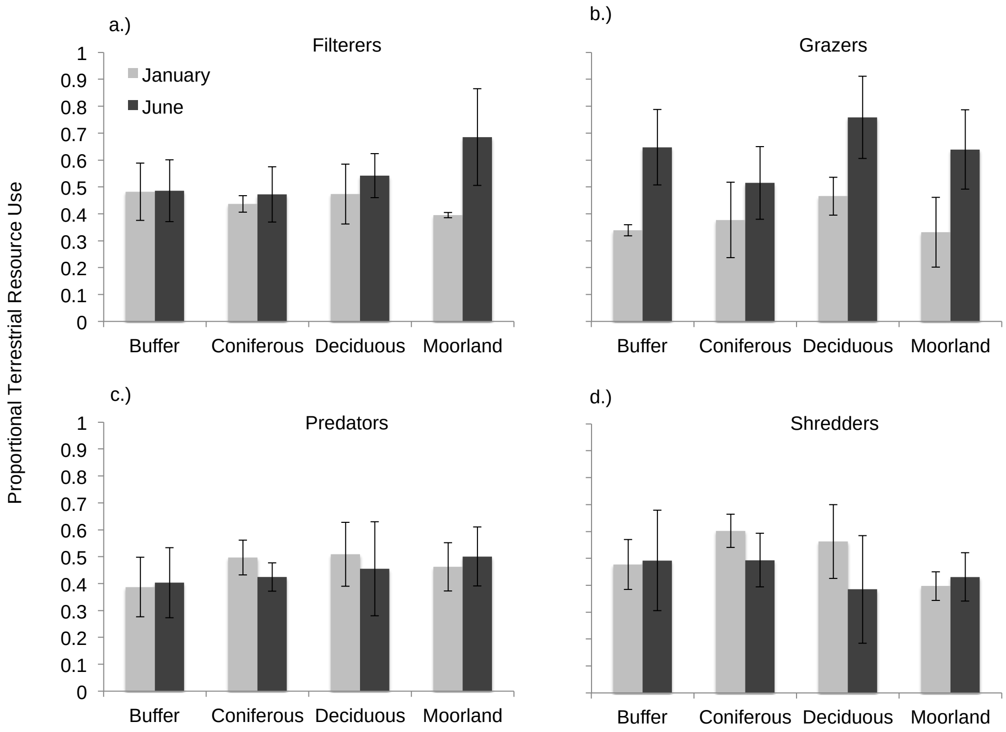

a.)
Filterers
b.)
Grazers
c.)
Predators
d.)
Shredders
Proportional Terrestrial Resource Use
January
June
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Buffer
Coniferous
Deciduous
Moorland

Figure 5