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

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Running head: Riparian woodlands and climate change adaptation

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1 **Abstract**

2

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

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

3
4

5 **Introduction**

6

7 Although reducing greenhouse gas emissions is fundamental to mitigating future climate
8 change, there is growing expectation that further increase in global temperature cannot now
9 be avoided (IPCC, 2014). Interest is growing, therefore, in strategies for climate change
10 adaptation that might minimize the worst effects on key resources (Perry, 2015). These
11 include organisms, ecosystems and the many services that they provide, and as a result
12 ecologists have been among the strongest advocates for climate change adaptation (Hulme,
13 2005; Dudgeon *et al.*, 2006; Seavy *et al.*, 2009). The broad aims involve predicting the
14 effects on vulnerable species or habitats, increasing their resilience, maintaining sensitive
15 species or assemblages, restoring lost connectivity, reducing the stressors with which climate
16 change interacts, and providing security for critical ecosystems (Hulme, 2005; Ormerod,
17 2009; Palmer *et al.* 2009; Seavy *et al.*, 2009). So far, however, there are few specific
18 examples where approaches advocated in theory have been evaluated in practice (Mawdsley
19 *et al.*, 2009; Macgregor & van Dijk, 2014). This is an important knowledge gap given the
20 extent of actions likely to be required to adapt ecosystems to climate change, and because of
21 the potentially far-reaching effects on the risks, benefits and services that might arise.

22

23 Stream and river ecosystems have figured strongly in the adaptation debate for two major
24 reasons. First, they have major global value to human life support, for example through
25 water supply, flood regulation, pollutant disposal, support for major biogeochemical cycles,

1 and critical roles in fisheries (Holmlund & Hammer, 1999; Wilson & Carpenter, 1999;
2 Ormerod, 2009). Secondly, streams and rivers are among the most sensitive of all
3 ecosystems to climate change because they are coupled directly to the global hydrological
4 cycle, linked closely to atmospheric thermal regimes, and at risk from interactions between
5 climate change and existing anthropogenic stressors (Dudgeon *et al.*, 2006; Durance &
6 Ormerod, 2007; Ormerod *et al.*, 2010). Moreover, because the majority of riverine organisms
7 are poikilothermic, they are affected metabolically both by direct temperature change and by
8 interactions between water temperature and oxygen solubility (Graham & Harrod, 2009;
9 Jonsson & Jonsson, 2009). Many freshwater ecosystems are also coupled tightly to the
10 surrounding riparian zones, floodplains and catchments through lateral or longitudinal fluxes
11 of energy that are under strong climatic influence (Nakano & Murakami, 2001; Wipfli,
12 2005). This includes the delivery, processing and downstream transport of detrital carbon
13 from terrestrial litter-fall that then acts as an important basis of production throughout whole
14 river systems (Vannote *et al.*, 1980; Malmqvist, 2002).

15

16 Broad suggestions for adapting rivers to climate change are the same as for other ecosystems
17 and include enhancing resilience, connectivity and legal protection while reducing stressors
18 such as water quality impairment (Durance & Ormerod, 2009; Ormerod, 2009; Palmer *et al.*,
19 2009). However, some proposed adaptation strategies are specific to rivers such as reducing
20 abstraction (ie the active removal of water for human usage) and using riparian forest to
21 buffer rivers against temperature gain to protect sensitive organisms (Ormerod, 2009;
22 Broadmeadow *et al.*, 2011). Enhancing or restoring riparian tree cover is advocated
23 particularly in temperate regions where much native forest has been removed for agriculture
24 (Battin *et al.*, 2007; Palmer *et al.*, 2009; Seavy *et al.*, 2009). Already, the value of such
25 “buffer strips” in moderating stream temperature is well supported by evidence (Zoellick,

1 2004; Battin *et al.*, 2007; Broadmeadow *et al.*, 2011), some of it from our own study region
2 (Weatherley & Ormerod, 1990; Clews *et al.*, 2010).

3
4 In addition to moderating thermal conditions in rivers, riparian woodlands might aid climate
5 change adaptation through effects on ecological processes, for example by soil
6 denitrification, nutrient flux and sediment delivery from agricultural land (Osbourne &
7 Kovacic, 1993; Broadmeadow & Nisbet, 2004; Larsen *et al.*, 2009). More generally, riparian
8 trees might affect important aspects of stream and river energetics by two major pathways.
9 First, shading along streams is likely to reduce autotrophic productivity potentially limiting
10 resources for some consumers (Hill *et al.*, 1995; Kiffney *et al.*, 2003; 2004; Riley *et al.*,
11 2009). Secondly, increased inputs of terrestrial organic matter from trees might provide
12 important subsidies for consumers linked to allochthony either in the form of abscised leaf
13 litter (Wallace *et al.*, 1997; Abelho, 2001) or terrestrial invertebrates (Nakano & Murakami,
14 2001). Understanding any such collateral effects on important river organisms such as
15 macroinvertebrates could aid decisions on where and when to use of riparian trees for shade
16 and thermal damping. Additionally, allochthonous energetic subsidies might increase stream
17 ecosystem resilience to global change by increasing in-stream biomass (Moore *et al.*, 1993;
18 Wallace *et al.*, 1997; Muotka & Laasonen, 2002). There is a need to assess whether smaller
19 riparian ‘buffers’ of native woodland could provide such benefits when used as climate
20 change adaptation in the riparian zones of catchments managed for agriculture or production
21 forestry in an attempt to mimic more extensive woodland (Broadmeadow & Nisbet, 2004;
22 Wahl *et al.*, 2013).

23
24 A major difficulty in assessing the effects of riparian woodlands in climate change adaptation
25 is that several decades of tree growth are required between implementation of the concept

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

16

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

1

2 **Materials and Methods**

3

4 *Study sites*

5

6 Sites were located in and around the Brecon Beacons National Park, South Wales, UK (51°
7 51' 46" N, 3° 22' 41" W Fig SM1) and the area has been described previously (Thomas *et al.*,
8 2015). Briefly, the region is temperate (1.1 °C - 19.1 °C mean min to mean max temperature;
9 mean annual rainfall is 1433 mm), with brown earth, gleys and occasionally peaty soils that
10 mostly overlay Devonian Old Red Sandstone drained by unpolluted, circumneutral and
11 oligotrophic headwaters (pH: ~6.5 – 7.5; conductivity: ~20 – 400 µS; Ca²⁺: ~5 – 40 mg l⁻¹;
12 NO₃⁻: ~1 – 10 mg l⁻¹; PO₄³⁻: ~0 mg l⁻¹). Temperate deciduous woodlands would form the
13 climax vegetation, but most land is now used for rough sheep grazing and commercial
14 forestry with non-native conifers. As such, the area is generally representative of upland land
15 use patterns throughout the UK and western Europe more generally. Moreover, such habitats
16 represent ideal candidates for management adaptations, as they are predicted to experience
17 summer temperature increases of around 4-5 °C by 2080s (compared to historical averages)
18 as a direct result of climate change (UKCP09 medium emissions scenario; Murphy *et al.*,
19 2009). Warming effects are already apparent in the region, with increases in mean
20 temperatures of 1.4-1.7 °C over the 25 years between 1980 and 2005 (Durance & Ormerod,
21 2007), leading to local species extinction (Durance & Ormerod, 2010).

22

23 Twenty-four second-to-third-order streams at elevations of ~150 to 450 m were selected
24 (Table S1; Fig. S1) to represent four land uses across the region: open moorland (hereafter
25 Moorland; MO; n = 6); grassland with deciduous buffer (Buffer; GB; n = 6), where moorland

1 catchments had buffers (~15 – 60 m) of mature deciduous alder *Alnus glutinosa*, birch *Betula*
2 *pendula*, ash *Fraxinus excelsior* and oak *Quercus* spp.; deciduous woodland (Deciduous; DE;
3 n = 6), where catchments still had relatively extensive areas of deciduous woodland in the
4 riparian zone (width ~ 75–220 m) with grassland/moorland beyond; coniferous buffer
5 (Coniferous; CB; n = 6), where catchments were dominated by exotic conifer plantations of
6 mostly sitka spruce *Picea sitchensis*, with deciduous trees in the riparian zone (~ 15 – 65 m).
7 Eight of these 24 sites (two in each land use; Table S1) were involved in an in-depth
8 quantitative study of variations within streams.

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

17

18 *Water chemistry and habitat physiography*

19

20 In May-June 2010, stream widths and depths were measured at four 10 m intervals along
21 each sampling reach and water samples collected during base-flow to assess a) cations after
22 filtration at 0.45 μm and acid fixation (inductively coupled plasma mass spectrometry;
23 Thermo Elemental X-Series ICP-MS: Thermo Fisher Scientific, Waltham, MA, USA) and b)
24 anions by ion chromatography (Dionex DX-80 Ion Analyser; Thermo Fisher Scientific, Inc.).
25 Conductivity, pH and total dissolved solids (ppm) were assessed immediately following a

1 storm event in October 2011, as these values are typically at their most extreme during high
2 flow (Kowalik et al., 2007). Three replicate readings were taken at each 10m interval within
3 each study reach using a Hanna HI 98129 low-range pH/Conductivity/TDS Tester (Hanna
4 Instruments, Woonsocket, RI, USA).

5

6 *Regional macroinvertebrate communities*

7

8 During May-June 2010, benthic macroinvertebrates were collected from a 30 m reach at all
9 24 sites by separate kick-sample (D-frame kick net: net mesh 1 mm) respectively, in riffles
10 (2-min sampling duration) and marginal habitats (i.e. slow-flowing depositional areas within
11 1 m of the stream bank; 1-min sampling duration), and preserved in 70% ethanol. This
12 standardized procedure collects around 70% of species present at any one site and sufficient
13 to detect differences among similar hillstreams (Bradley & Ormerod, 2002). Separating riffle
14 and marginal samples provide a more representative species pool while also recording
15 communities in contrastingly eroding/depositing environments where coarse particulate
16 organic matter (CPOM) might accumulate (Bradley & Ormerod, 2002).

17

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

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

7

8 *Macroinvertebrate and CPOM within streams*

9

10 In February, June and October of 2011 and 2012 (i.e. six occasions), macroinvertebrates and
11 CPOM standing stock were collected from fast-flowing riffles at the smaller sub-set of eight
12 of the 24 sites in 5 x 0.07 m² quantitative Hess samplers (Hess, 1941; upstream net: 1mm
13 mesh; downstream net: 500µm mesh; EFE-UK and GB Nets Lostwithiel, UK). Samples were
14 immediately preserved in 70 % Industrial Methylated Spirits (IMS: Fisher Scientific,
15 Loughborough, UK). Following treatment as above for kick samples, all macroinvertebrate
16 individuals from each taxon and sample were transferred to glass vials for drying at 60 °C for
17 48 h and weighing to the nearest 0.1 mg. Biomass data were expressed per m² of streambed.
18 CPOM, defined as all nonwoody vascular plant material > 1 mm² (Cummins, 1974), was
19 rinsed from each sample into a 1 mm sieve, and also dried, weighed and converted to m²
20 estimates of standing stock.

21

22 *Stable isotopes*

23

24 Samples for stable isotope analysis were collected from all 24 study sites twice over the
25 annual cycle in May - June 2010 and again during January 2011. Benthic macroinvertebrates

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

19

20 All samples for stable isotope analysis were rinsed with DH₂O and any non-target materials
21 removed using forceps before freeze-drying at -60 °C for 48 h in glass vials. Dried samples
22 were homogenized and quantities for analysis (1 ± 0.2 mg for invertebrate tissue, 3 ± 0.2 mg
23 for autotrophic material) were packaged within tin capsules for transport to the University of
24 California, Davis Stable Isotope Facility. Dual δ ¹³C and δ ¹⁵N analysis was performed using a
25 PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20–20 isotope ratio

1 mass spectrometer (Sercon Ltd., Cheshire, U.K.). Values are reported in delta (δ) notation, as
2 parts per thousand (‰) deviation from international standards (Vienna Pee Dee Belemnite for
3 carbon and atmospheric air for nitrogen). Epilithic $\delta^{15}\text{N}$ from DE4 was anomalously enriched
4 (> 13 ‰ versus a mean of 1.42 ‰ at all other sites), probably reflecting local drainage, and
5 was excluded from analyses.

6

7 *Statistical analysis*

8

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

16

17 *Regional macroinvertebrate communities*

18

19 Variations in community composition among land uses were initially plotted using Non-
20 Metric Multidimensional Scaling (NMDS; Kruskal, 1964) using the metaMDS function
21 within R's vegan package (version 2.0-5), based on 500 iterations (Oksanen *et al.*, 2012).
22 NMDS is a robust and well-known method that ordines samples on overall dissimilarity
23 (Kruskal, 1964; Clarke & Warwick, 2001; Zuur *et al.*, 2007), and was here used in
24 conjunction with the Bray-Curtis index, due to the ability of this metric to accommodate
25 zero-skewed composition data (Clarke & Warwick, 2001). All values were fourth root

1 transformed prior to calculation to down-weight the influence of the most abundant taxa
2 (Clarke & Warwick, 2001). Permutational Multivariate Analysis of Variance (*PERMANOVA*;
3 Anderson, 2001) was subsequently used to assess whether variations in community
4 composition between land use types were significant. This non-parametric alternative to
5 MANOVA compares groups in multivariate space based on dissimilarities and generates p
6 values via a permutation procedure. *PERMANOVA* makes few major assumptions about the
7 data set, and does not require multivariate normality (Anderson, 2001). To rule out
8 potentially confounding effects of differential dispersion, *PERMANOVAs* were followed by
9 betadisper tests (Anderson, 2006), a multivariate analogue of Levene's test for homogeneity
10 of variances. Following an overall *PERMANOVA* to assess whether land use affected
11 community composition, we appraised group-by-group pair-wise differences using the *adonis*
12 function within *vegan* based on 4999 permutations (Oksanen *et al.*, 2012) following 4th root
13 transformation. Where *PERMANOVAs* indicated significant differences among land uses,
14 Similarity Percentage analysis (*SIMPER*; Clarke, 1993) assessed which taxa were principally
15 responsible.

16

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

1 included as covariates in each GLM carried out to test for differences between land use
2 categories.

3

4 *Macroinvertebrate and CPOM within streams*

5

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

17

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

1 proportions, FFG representation data were arcsine square root transformed (Sokal & Rohlf,
2 1995).

3

4 *Stable isotopes*

5

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

14

15 Dual stable isotopic assessments of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was used here in conjunction with *R*'s
16 SIAR (*Stable Isotope Analysis in R; version 4.1.3*; R Core Team, 2012) mixing model
17 (Parnell *et al.*, 2010) with the *SIARsolomcmcV4* function to estimate proportional contribution
18 from terrestrial and in-stream production to consumer diets individually by site, functional
19 feeding group and season. Mixing models were fitted for 14 sites where basal resources were
20 isotopically distinct (GB, $n = 3$; CB, $n = 4$; DE, $n = 3$; MO, $n = 4$), but 10 sites were excluded
21 where basal resource signatures overlapped or where consumer measurements fell outside the
22 mixing polygons implied by basal signatures. All SIAR models were based on 500,000
23 iterations, with the first 50,000 discarded (Parnell *et al.*, 2010). Trophic enrichment factors
24 (TEFs) of 0.5 ± 0.5 ‰ for ^{13}C and 3.23 ± 1 ‰ for ^{15}N were assumed for primary consumers
25 (Filterers, Grazers, Shredders) based on calculated mean difference between primary

1 consumers and basal resources. An additional trophic level of enrichment was added for
2 Predators (i.e. TEFs of $1 \pm 1 \text{ ‰}$ and $6.46 \pm 2 \text{ ‰}$ were used for ^{13}C and ^{15}N , respectively).
3
4 Variations in mean proportional contributions of terrestrial organic matter to consumer
5 production estimated by SIAR (hereafter, ‘terrestrial resource use’) were analysed using a
6 General Linear Mixed Model (GLMM). Riparian land use, month of sampling and Functional
7 Feeding Group, along with all possible interactions between these factors, were included as
8 fixed effects. Site was included as a random term to account for potential non-independence
9 due to repeated measures at each site through time. As analysis of all proportion data resulted
10 in normally distributed, homoscedastic residuals, no transformations were applied (Warton &
11 Hui, 2011).

12

13 **Results**

14

15 *Regional macroinvertebrate communities*

16

17 Macroinvertebrate communities at the 24 regional sites varied among land uses in riffle ($F_{3,22}$
18 = 1.7442, $p = 0.004$), marginal ($F_{3,21} = 2.1634$, $p > 0.001$) and combined samples ($F_{3,21} =$
19 2.116, $p > 0.001$), with contrasts greatest between Moorland vs. Deciduous, Coniferous vs.
20 Moorland and Coniferous vs. Deciduous sites (Table 1; Fig. 1). Buffer sites were generally
21 intermediate, although communities in their marginal habitats differed from Deciduous sites
22 (Table 1 and 2). SIMPER showed that differences in community composition were mostly
23 due to overall changes in abundance: no single taxon contributed $> 7 \text{ ‰}$ of the difference
24 between any two land use categories and those responsible represented a relatively small
25 proportion of the total species pool (Table 2). For example, differences between Deciduous

1 sites and other land uses were principally caused by increased abundance of the amphipod
2 *Gammarus pulex*, decreases in the grazing mayfly *Electrogena lateralis* and variations
3 among *Leuctra* stoneflies. Coniferous sites differed from others mostly because of
4 increased abundances of leuctrid and nemourid stoneflies, notably *Amphinemura sulcicollis*.
5 *Betadisper* tests confirmed that differences between land uses were not due to unequal
6 dispersion between groups (Riffle: $F_{3, 19} = 0.140$, $p = 0.935$; Margin: $F_{3, 18} = 0.326$, $p = 0.807$;
7 Combined: $F_{3, 18} = 0.049$, $p = 0.985$).

8
9 Functional group representation varied more strongly among land uses (Tables 3 and S2), and
10 shredders contributed more to communities at Deciduous sites than any other land use in
11 riffle, margin and combined samples (Tukey's HSD for Riffle: Deciduous v Buffer $P =$
12 0.008 , Coniferous $P = 0.006$, Moorland $P = 0.005$; Margin: Deciduous v Buffer $P = 0.030$,
13 Coniferous $P = 0.005$, Moorland $P = 0.013$; Combined: Deciduous v Buffer $P = 0.011$,
14 Coniferous, $P = 0.004$, Moorland $P = 0.008$). Other effects were weaker: Coniferous sites
15 contained a higher proportion of Grazers ($P = 0.025$) and Predators ($P = 0.022$) than at
16 Deciduous sites, and a lower proportion of Collector-Gatherers ($P = 0.024$) than at Moorland
17 sites.

18
19 *Macroinvertebrate and CPOM within streams*

20
21 At the eight sites sampled repeatedly, benthic CPOM in Hess samples varied significantly
22 among riparian land uses ($F_{3, 213} = 43.41$, $P < 0.001$) with amounts greater at Deciduous sites
23 than in any other site type (Tukey's HSD: $P < 0.001$ in all cases), and lowest in Moorland
24 (Fig. 2). Standing stocks at Coniferous and Buffer sites were intermediate, and did not differ
25 significantly from each other ($P = 0.557$). These differences were maintained throughout the

1 study, and did not depend on sampling year ($F_{3, 213} = 1.04$, $P > 0.377$) or month ($F_{6, 213} = 1.15$,
2 $P > 0.337$) despite some seasonal variations (Fig. 2).
3
4 Consistent with the variations in CPOM, total macroinvertebrate biomass ($F_{3, 213} = 14.57$, $P <$
5 0.001) and density ($F_{3, 213} = 15.84$, $P < 0.001$) were both greater at Deciduous sites and lower
6 at Coniferous sites (Tukey's HSD: $P < 0.01$ in all cases) than in any other land use ($P < 0.05$
7 in all cases) when averaged across all sampling periods (Table 4; Fig. 3). Moorland and
8 Buffer sites had intermediate biomass, and did not differ significantly from each other ($P =$
9 0.971). Again, these effects occurred irrespective of variations in biomass and density among
10 seasons and years (see Supplementary Material Appendix S2).
11
12 Biomass values in each FFG also varied among land uses when averaged across sampling
13 periods (Table 4). Shredder biomass was higher in Deciduous streams than in all other land
14 uses ($P < 0.05$ in all cases), which did not differ significantly from one another ($P > 0.05$ in
15 all cases). Collector-Gatherers and Filterers had their lowest biomass in Coniferous streams
16 (Tukey's HSD: $P < 0.05$ in all cases), while Grazer biomass was also significantly lower in
17 Coniferous than Deciduous streams ($P = 0.03$). Predator biomass was higher in Moorland
18 than Coniferous sites ($P = 0.002$), but otherwise did not differ among land uses ($P > 0.05$ in
19 all cases). Land use effects on FFG biomass were consistent among months, years and
20 individual sampling periods for Collector-Gatherers (Month: $F_{6, 213} = 0.90$, $P = 0.498$; Year:
21 $F_{3, 213} = 1.04$, $P = 0.377$; Sampling Period: $F_{6, 213} = 1.26$, $P = 0.277$), Predators (Month: $F_{6, 213}$
22 $= 0.50$, $P = 0.810$; Year: $F_{3, 213} = 2.54$, $P = 0.058$; Sampling Period: $F_{6, 213} = 2.24$, $P = 0.051$)
23 and Shredders (Month: $F_{6, 213} = 1.10$, $P = 0.365$; Year: $F_{3, 213} = 1.42$, $P = 0.238$; Sampling
24 Period: $F_{6, 213} = 1.26$, $P = 0.276$). Variations among land uses for Filterer ($F_{6, 213} = 2.18$, $P =$
25 0.047) and Grazer biomass ($F_{6, 213} = 4.31$, $P < 0.001$) were more transient, and both differed

1 among sampling months. The biomass of several functional feeding groups also varied
2 seasonally when averaged across land use types (see Supplementary material Appendix S2).
3 In general, similar patterns were confirmed by proportionate variations among FFGs, and in
4 particular Deciduous sites had a greater proportion of Shredder taxa than all other land use
5 types ($P < 0.001$ in all cases) while Coniferous sites supported a lower proportion of
6 Collector-Gatherer taxa and greater proportion of Grazers (Tukey's HSD: $P < 0.05$ in all
7 cases) (See Appendix S3).

8
9 Supporting a likely effect of CPOM on macroinvertebrates across land uses, total
10 macroinvertebrate biomass ($F_{1, 189} = 94.96$, $P < 0.001$) and density ($F_{1, 189} = 138.63$, $P <$
11 0.001) both increased significantly in samples with greater standing stocks of CPOM (Fig. 4;
12 Table 5). These relationships were independent of land use type (Biomass: $F_{3, 189} = 2.49$, $P =$
13 0.062 ; Density: $F_{3, 189} = 0.53$, $P = 0.661$), month (Biomass: $F_{2, 189} = 0.41$, $P = 0.665$; Density:
14 $F_{2, 189} = 2.12$, $P = 0.122$) or year (Biomass: $F_{1, 189} = 0.74$, $P = 0.393$; Density: $F_{1, 189} = 0.02$, P
15 $= 0.888$). Within individual guilds, Shredder biomass also increased with CPOM biomass
16 across samples ($F_{1, 189} = 7.63$, $P = 0.006$), though the relationship varied seasonally ($F_{2, 189} =$
17 5.85 , $P = 0.003$). Similarly, the proportion of total macroinvertebrate biomass composed of
18 Shredders was significantly positively related to CPOM biomass ($F_{1, 189} = 17.22$, $P < 0.001$),
19 but the relationship varied between months ($F_{1, 189} = 4.52$, $P = 0.012$) and years of sampling
20 ($F_{1, 189} = 9.93$, $P = 0.002$). The biomass or proportional representation of all other functional
21 feeding groups was not significantly related to CPOM biomass.

22

23 *Stable isotopes*

24

25 Contrary to prediction (ii) and unexpectedly given the apparent relationship between land
26 use, CPOM and macroinvertebrate biomass, terrestrial resource use by macroinvertebrates, as

1 revealed by isotopic data, did not vary significantly among riparian land use types ($F_{3, 95} =$
2 0.416, $P = 0.742$; Fig. 5) even when variations between months ($F_{3, 93} = 0.923$, $P = 0.433$) or
3 FFGs ($F_{8, 87} = 0.620$, $P = 0.759$) were considered. Across all land use categories in both
4 months, roughly 50% (range: 33.1-75.8 %) of resources assimilated by all macroinvertebrate
5 functional groups were of terrestrial origin (Fig. 5). When all land use categories were
6 pooled, terrestrial resource use varied between functional feeding groups in ways that
7 differed between months ($F_{3, 95} = 3.890$, $P = 0.012$), but this effect occurred only as
8 significantly increased terrestrial contributions to Grazer tissues in June ($P = 0.002$; Fig. S 3).

9

10 **Discussion**

11

12 Despite increasing concern about climate change, practical evidence about the effectiveness
13 of management adaptations that could reduce adverse effects on ecosystems is still
14 remarkably scarce. To our knowledge this study, combined with an associated article
15 (Thomas *et al.*, 2015), is the first to appraise collateral ecological effects of using riparian
16 trees to create shade - one of the most widely advocated adaptation measures for rivers
17 (Ormerod 2009; Palmer *et al.*, 2009; Clews *et al.*, 2010). Of the three predictions we
18 examined, only one was supported unequivocally: streams draining deciduous woodland
19 differed clearly from others in having substantially enhanced standing stocks of CPOM as
20 well as a greater density and biomass of macroinvertebrates, particularly Shredders. In
21 contrast, there were no variations across land uses in functional group reliance on terrestrial
22 resources (prediction ii), and nor were the effects of riparian buffers of 15-60m width
23 sufficient to mimic the effects of more extensive riparian woodlands (prediction iii). These
24 outcomes provide some support for the hypothesis that climate change adaptation using
25 broadleaves might alter macroinvertebrate communities functionally and compositionally,

1 also enhancing stocks of CPOM as an important basal resource. However, on our evidence
2 this effect is likely only where broadleaf restoration or planting is extensive, and large step-
3 changes from autochthony to allochthony may not be a major feature. Interestingly, the data
4 support previous suggestions that narrow riparian buffer zones may be insufficient to offset
5 some of the influences of wider catchment land use on stream communities and ecosystem
6 functioning (Allan *et al.*, 1997; Kauffman *et al.*, 1997; Harding *et al.*, 2006; Wahl *et al.*,
7 2013).

8
9 Before discussing more general ramifications of this study, two important caveats must be
10 noted. First, as with other cross-sectional investigations using space-for-time substitution, our
11 site categories were created neither by experimental manipulation nor random allocation to
12 treatments. Our interpretation must, therefore, rely on correlative techniques that are at risk
13 from possible confounding effects. The land use categories differed marginally on
14 physicochemistry, with, for example, treeless moorland streams at higher elevations than
15 other land use types (Supplementary material). However, the range over which these
16 variables differed appeared to be insufficient to influence community composition: moorland
17 (MO) and buffer strip (GB) sites differed on physical criteria but supported similar
18 communities. Similarly, buffer strip (GB) sites and those draining larger areas of deciduous
19 woodland (DE) differed with respect to water chemistry, but not in overall macroinvertebrate
20 community composition and the principal results were consistent across the two scales of the
21 investigation. In other fields, such as freshwater acidification, early evidence based on space-
22 for-time substitution (Ormerod *et al.*, 1988) has since been validated using long-term data
23 (Ormerod & Durance 2009) and coupled with studies of processes (Kowalik *et al.*, 2007) to
24 provide important insights into global change effects. A second caveat is that the study was
25 intended to appraise the effects of riparian management as an adaptation to climate change,

1 yet could only be carried out under current climatic conditions. While there is already
2 evidence of warming effects on streams in the study region (Durance & Ormerod 2007, 2010;
3 Clews *et al.*, 2010), any extrapolation requires the assumption that patterns detected here will
4 persist under the higher temperatures, more variable rainfall and potentially extreme
5 discharge expected in NW Europe. Interestingly, future climates could also affect streamside
6 woodlands as well as in-stream conditions – for example through altered disease effects on
7 tree species such as European Ash (*Fraxinus excelsior*) (Pautasso *et al.*, 2013).
8 Notwithstanding these concerns, we suggest that comparative studies like ours provide a
9 useful basis for predicting how temperate upland streams might respond to the restoration of
10 catchment tree cover, thereby increasing understanding of the resultant ecological changes
11 (Naiman *et al.*, 2012). Decades would be required for the experimental development of
12 riparian tree cover, yet evidence to inform decision about climate change adaptation are
13 required now.

14

15 The clearest overall trends we detected of increased CPOM stocks, enhanced shredder
16 density and increased macroinvertebrate biomass in extensive deciduous woodlands are
17 generally well known (Wallace *et al.*, 1997). Interestingly, these effects occurred in both
18 riffles and margins, but were stronger in the latter, where leaf litter and other terrestrial
19 organic material often accumulate in ‘softer’ habitats of woody debris, roots and vegetated
20 features (Ormerod *et al.*, 1993; Flores *et al.*, 2013). Such marginal features that increase
21 riparian shore-length and increase litter retention could be as important in increasing CPOM
22 stocks as the adjacent canopy is in providing inputs (Muotka & Laasonen, 2002). Deciduous
23 woodlands would form the principal climax vegetation communities over large parts of the
24 temperate zone and, where riparian zones are intact, the resulting litter input to headwaters is
25 a key component of energy flux through food webs (Vannote *et al.*, 1980). Where subsidies

1 of CPOM are large enough to offset climatically mediated export, riparian woodlands might
2 also increase the resilience of macroinvertebrate populations by increasing basal resources
3 (Moore *et al.*, 1993; Wallace *et al.*, 1995; Eggert *et al.*, 2012). Understanding future
4 interactions between litter subsidies, uptake into food webs, secondary production and
5 climate change is likely to be a key area of interest: land use in the riparian zone is important
6 in that it mediates both climatic effects and riparian subsidies (Wallace *et al.*, 1995;
7 Broadmeadow *et al.*, 2011).

8

9 Despite apparently changing CPOM and invertebrate abundance across the study streams,
10 however, land use did not affect the relative use of terrestrial and aquatic resource use by
11 macroinvertebrates in any functional feeding group. Thus, while shredders apparently
12 intercepted the terrestrial subsidy at deciduous sites and converted it into increased
13 invertebrate biomass, they still depended in part on autotrophic production. This contrasts
14 with the resource-use patterns typically assigned to this group (Cummins & Klug, 1979).
15 Such effects would arise where shredding taxa ingested and assimilating algal production
16 attached to leaf litter (Hax & Golladay, 1993). In the same way, grazing taxa can supplement
17 their diets with fine terrestrial organic matter captured within epilithic biofilms (Hamilton *et al.*,
18 2005). Thus, even at open moorland sites where greater autotrophic production would be
19 expected, roughly 50% of animal production in all FFGs originated from terrestrial sources.
20 These results are contrary to the expectation that relative allochthony versus autochthony
21 should differ among deciduous woodland, grassland and conifer sites (Abehlo, 2001; Kiffney
22 *et al.*, 2003, 2004).

23

24 Such unexpected effects might be explained either by intrinsic biological processes or by
25 extrinsic, contextual factors alone or combination. For example, autotrophic food webs

1 persist even in streams in woodland environments prior to seasonal canopy closure or where
2 primary production is maintained in habitats such as mosses (Wallace *et al.*, 1997). Equally,
3 allochthonous resources still occur in moorland catchments, and Menninger & Palmer (2007)
4 illustrated how herbs and grasses provided significant inputs of litter to open-canopy
5 piedmont streams. Leberfinger *et al.* (2011) used stable isotope analysis to show that such
6 terrestrial organic resources were important to shredding macroinvertebrates in grassland
7 streams despite the availability of autotrophic production. Resource-use patterns might also
8 be mediated directly and locally by invertebrate consumers: despite varying amounts of
9 terrestrial organic matter in different land uses, use and uptake can be constrained by the
10 capacity for feeding plasticity in consumer taxa (e.g. morphological adaptations for rock
11 scraping vs. leaf shredding vs. filter feeding) (Cummins & Klug, 1979; Dangles, 2002).
12 Variations in resource quality between terrestrial and in-stream production might also
13 constrain feeding choices, with CPOM typically less rich in macronutrients than benthic
14 epilithon: macroinvertebrates often require elemental stoichiometry with their food sources,
15 and CPOM alone may be insufficient to support growth and metabolism (Hladyz *et al.*,
16 2009). More extrinsically, wider catchment effects or downstream export might mask local
17 riparian effects from land use: there is evidence to indicate that even small reductions in
18 catchment tree cover (~10 % deforestation in otherwise totally afforested catchments)
19 weakens terrestrial-aquatic linkages (England & Rosemond, 2004). Resource use patterns
20 may therefore reflect whole catchment land use rather than those just in the riparian zone,
21 even where wider riparian land uses are extensive: in woodland catchments, large areas of
22 lateral tree cover may be needed to offset downstream subsidy export, particularly transport
23 during high flow events (Wallace *et al.* 1995; Eggert *et al.*, 2012). Finally, measurement or
24 modelling artefacts with stable isotopes cannot be excluded. For instance, in some riverine
25 systems it may be difficult to fully discern in-stream production using isotopic signals alone,

1 as there can be substantial overlap in ^{13}C concentrations between autochthonous and
2 allochthonous material (France, 1996). However, care was taken to exclude data from sites
3 where assumptions of isotopic mixing models were violated, and repeated sampling at each
4 site improved robustness by minimizing the effects of temporal variability. Additionally,
5 potential error in the estimation resource isotopic composition was of explicitly incorporated
6 into the Bayesian models used here (Parnell *et al.*, 2010).

7

8 *Implications for climate change adaptation*

9

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

21

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

1 (Moore *et al.*, 1993; Wallace *et al.*, 1997; Sweeney *et al.*, 2004). Our data extend
2 understanding this technique by illustrating how riparian broadleaves used in climate change
3 adaptation would be likely to enhance CPOM stocks, Shredder densities and overall
4 macroinvertebrate biomass, but only where woodland is extensive. In this respect the
5 management implications are clear. First, where narrow woodland buffers are used solely to
6 moderate thermal regimes, large energetic benefits or effects on CPOM dynamics would, on
7 our evidence, be unlikely. In contrast, more extensive woodland restoration would have
8 additional further benefits beyond cooling through enhanced litter subsidies and retention in
9 marginal habitats. Both of these effects could be enhanced by encouraging planting or natural
10 regeneration of native riparian vegetation, for example through agri-environment schemes or
11 as part of wider global reforestation efforts (Crowther *et al.*, 2015), and by protecting
12 retentive features such as marginal vegetation or woody debris during river management
13 (Muotka & Laasonen, 2002; Sweeney *et al.*, 2004; Flores *et al.* 2013). Such techniques could
14 either be implemented alone, or in combination with other adaptation strategies which could
15 act to enhance local shade and cooling (e.g. Everall *et al.*, 2012). The ecological benefits
16 locally within headwaters might include improved conservation of woodland stream
17 organisms, restored linkage between headwaters and riparian zones, restoration of natural
18 stream function and potentially increased resilience through enhanced basal resources
19 (Moore *et al.*, 1993; Goodwin *et al.*, 1997; Muotka & Laasonen, 2002). More extensive
20 benefits from litter processing and export to ecosystems downstream are possible, but require
21 fuller appraisal in more extensively wooded landscapes (Wipfli, 2005; Tanentzap *et al.*,
22 2014).

23

24 More generally, our study illustrates a possible approach to appraising the potential
25 effectiveness of climate change adaptation – through studies of ecological processes

1 combined with a survey of locations assumed to mimic future land cover options. With
2 current practical knowledge of climate change adaptation in most ecosystems still
3 rudimentary, we suggest that this subject needs greater research attention given the urgency
4 for action and the time required to develop, implement and fully realize change at the
5 landscape scales necessary.

6

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8

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14

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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.

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

| Dependent | Sample Type | | | | | | | | |
|-------------------------------|-------------|--------|--------------|-------|--------|--------------|-------|----------|--------------|
| | Df | Riffle | | | Margin | | | Combined | |
| | | 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 \pm 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 \pm 25.41 a | 87.77 \pm 28.70 b | 92.12 \pm 18.82 a | 99.03 \pm 15.75 a |
| Filterer † | 16.74 \pm 3.99 a | 2.55 \pm 1.28 b | 35.72 \pm 7.48 c | 8.23 \pm 3.30 a |
| Grazer † | 70.96 \pm 12.97 ab | 58.26 \pm 9.91 a | 107.02 \pm 15.68 b | 61.30 \pm 8.07 ab |
| Predator | 116.2 \pm 40.59 ab | 29.56 \pm 7.56 a | 88.68 \pm 24.87 ab | 87.51 \pm 15.73 b |
| Shredder | 15.24 \pm 4.71 a | 19.66 \pm 9.81 a | 182.66 \pm 52.01 b | 7.93 \pm 2.91 a |
| Total† | 325.49 \pm 61.60 a | 197.80 \pm 40.09 b | 506.21 \pm 71.49 c | 264.01 \pm 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.

| Functional Feeding Group | FFG Biomass vs. CPOM Biomass | | Proportion FFG vs. CPOM Biomass | |
|--------------------------|------------------------------|--------------|---------------------------------|--------------|
| | 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 \pm 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 \pm 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:

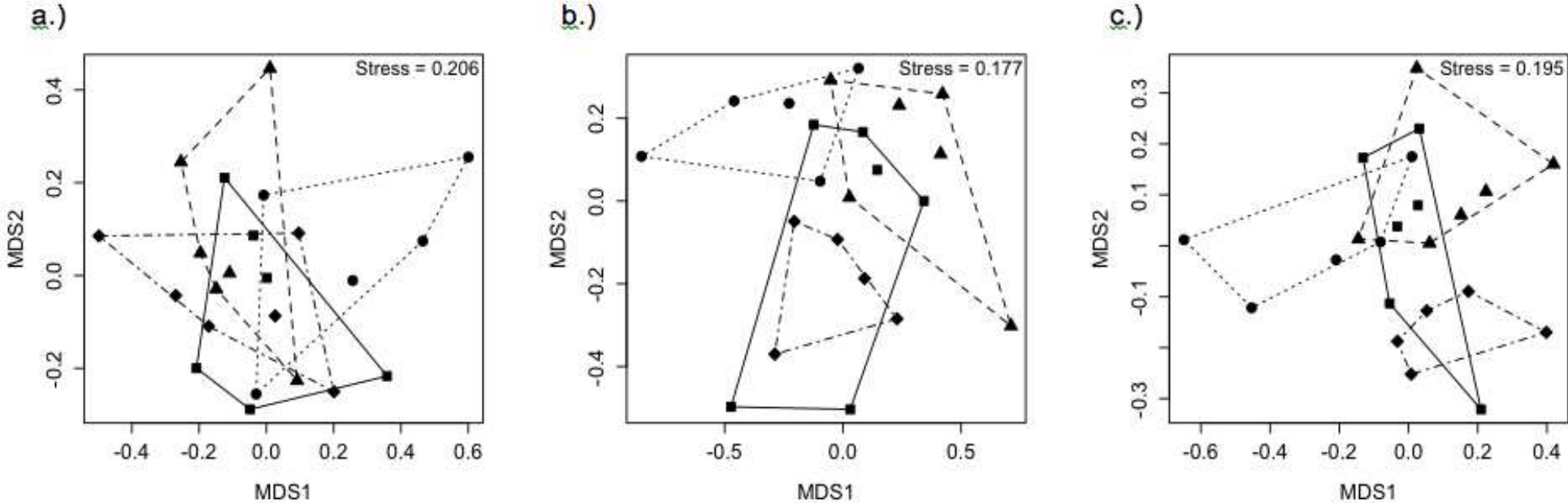


Fig 2:

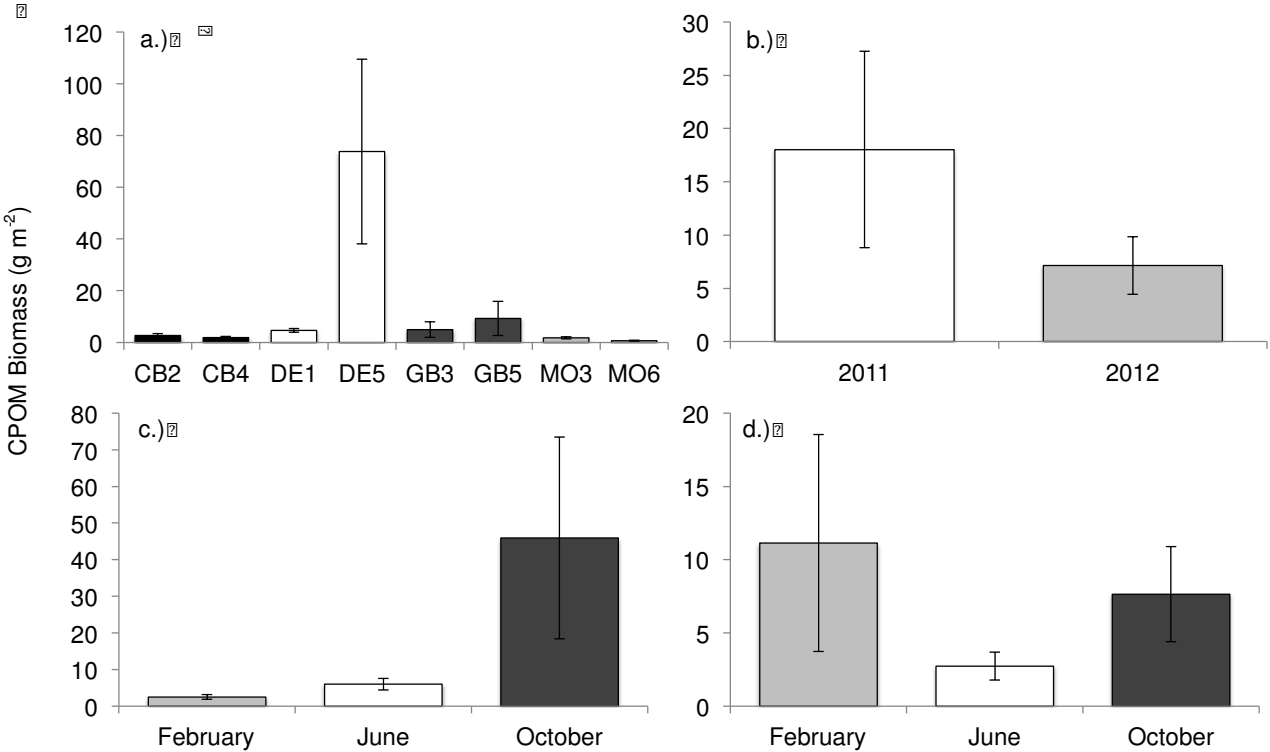


Figure 3:

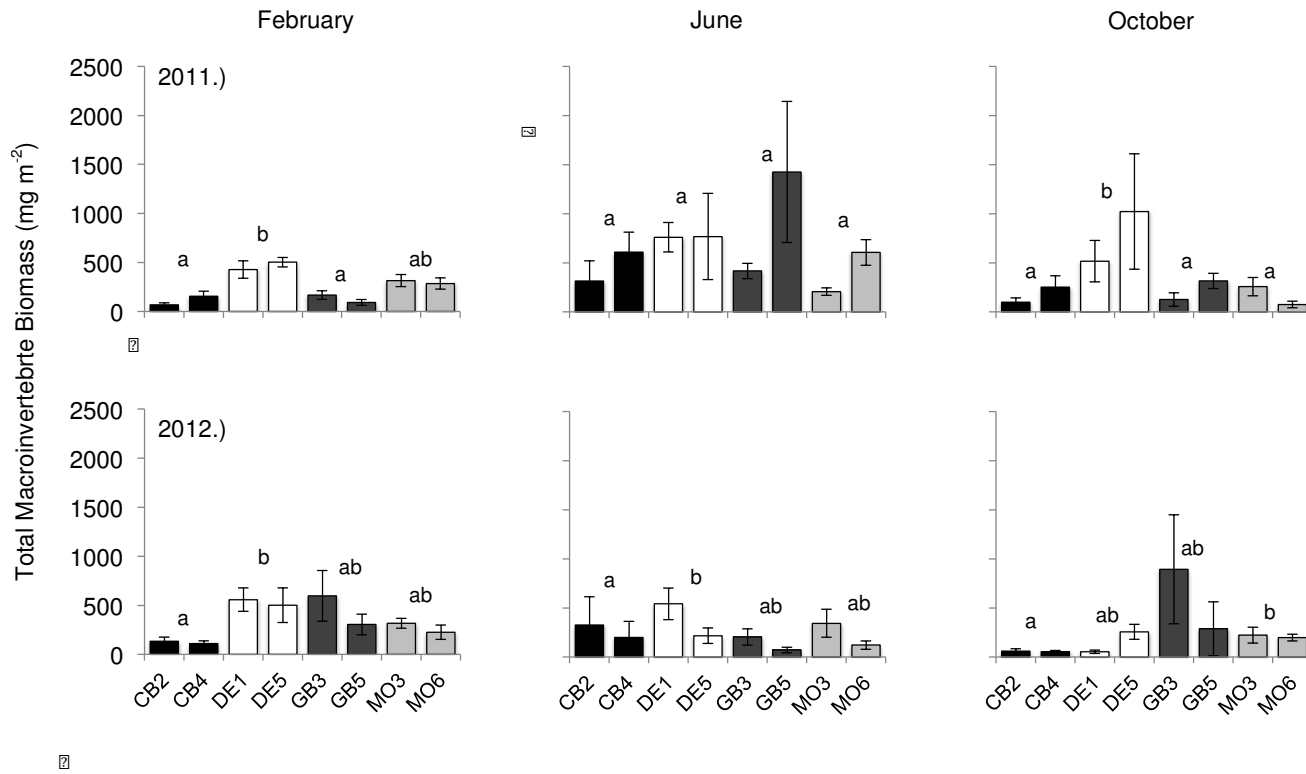
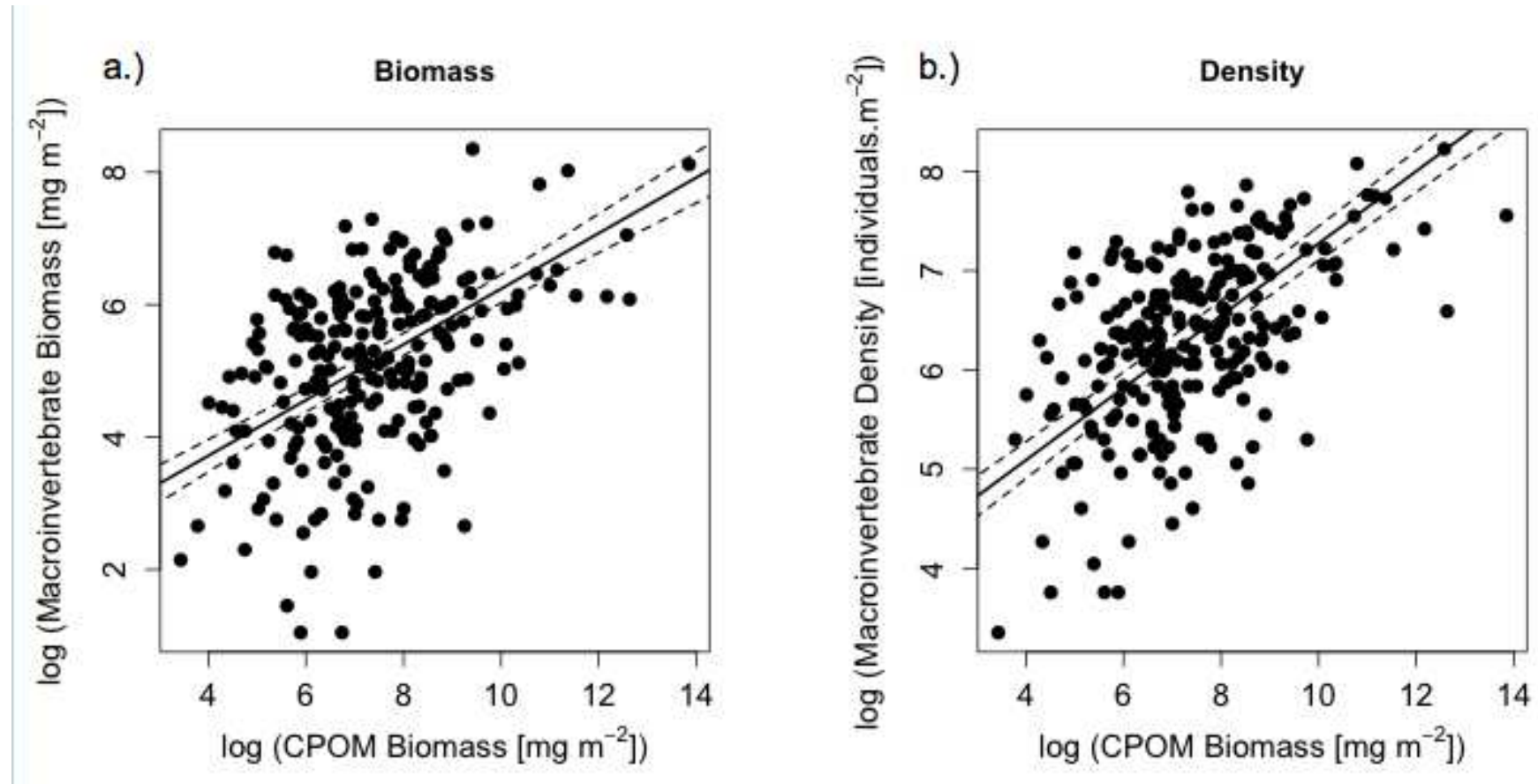


Figure 4:



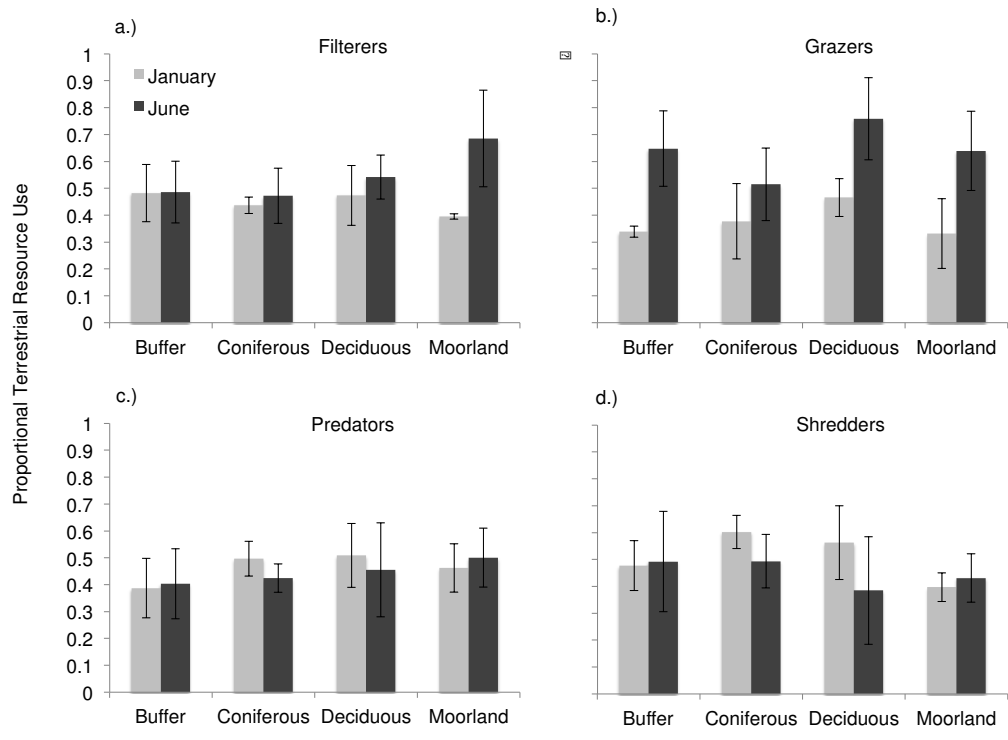


Figure 5