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

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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

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; Ca^{2+}: ~5 − 40 mg l^{-1};

12 NO_3-: ~1 − 10 mg l^{-1}; PO_4^{3-}: ~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

7

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 m^2 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 m^2 of streambed.

18 CPOM, defined as all nonwoody vascular plant material > 1 mm^2 (Cummins, 1974), was

19 rinsed from each sample into a 1 mm sieve, and also dried, weighed and converted to m^2

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 ºC 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 Simullidae (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 ^{13}C 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 DH_2O and any non-target materials

21 removed using forceps before freeze-drying at -60 ºC 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^{13}C and δ^{15}N 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 δ^{15}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 ordinates 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 $^{13}C/^{12}C$ and $^{15}N/^{14}N$, 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 $\delta\ ^{13}C$ and $\delta\ ^{15}N$ 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 ± 1 ‰ and 6.46 ± 2 ‰ 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 % 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. Conifererous 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,

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,

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*

18　*al*., 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 allocthony 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 stochiometry 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 autochthnous 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 shad 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

26

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

14

15

16 **References**

17

18 Abelho M (2001). From litterfall to breakdown in streams: a review. The Scientific World

19 Journal, **1**, 656-680.

20

21 Allan D, Erickson D & Fay J (1997). The influence of catchment land use on stream integrity

22 across multiple spatial scales. Freshwater Biology, **37**, 149-161.

23

24 Anderson MJ (2001). A new method for non-parametric multivariate analysis of variance.

25 Austral Ecology, **26**, 32–46.

1

2   Anderson MJ (2006) Distance-based tests for homogeneity of multivariate dispersions.

3   Biometrics, **62**, 245–253.

4

5   Battin J, Wiley MW, Ruckelshaus MH, Palmer RN, Korb E, Bartz KK & Imaki H (2007).

6   Projected impacts of climate change on salmon habitat restoration. Proceedings of the

7   National Academy of Sciences, **104**, 6720-6725.

8

9   Bradley DC & Ormerod SJ (2002). Evaluating the precision of kick-sampling in upland

10   streams for assessments of long-term change: the effects of sampling effort, habitat and

11   rarity. Archiv für Hydrobiologie, **155**, 199-221.

12

13   Broadmeadow S & Nisbet TR (2004). The effects of riparian forest management on the

14   freshwater environment: a literature review of best management practice. Hydrology and

15   Earth System Sciences Discussions, **8**, 286-305.

16

17   Broadmeadow SB, Jones JG, Langford TEL, Shaw PJ & Nisbet TR. (2011). The influence of

18   riparian shade on lowland stream water temperatures in southern England and their viability

19   for brown trout. River Research and Applications, **27**, 226-237.

20

21   Clarke KR (1993). Non-parametric multivariate analyses of changes in community structure.

22   Australian Journal of Ecology, **18**, 117-143.

23

24   Clarke KR & Warwick RM (2001). *Changes in Marine Communities: an Approach to*

25   *Statistical Analysis and Interpretation.* Second edition. PRIMER-E, Plymouth, UK.

1

2   Clews E, Vaughan IP, Ormerod SJ (2010) Evaluating the effects of riparian restoration on a

3   temperate river-system using standardized habitat survey. Aquatic Conservation: Marine and

4   Freshwater Ecosystems, 20 (S1), S96-S104.

5

6   Countryside Council for Wales (2004). Phase 1 habitat survey.

7

8   Crowther TW, Glick HB, Covey KR et al (2015) Mapping tree density at a global scale.

9   Nature, 525, 201-205.

10

11 Cummins KW (1974). Structure and function of stream ecosystems. BioScience, **24**, 631-

12 641.

13

14 Cummins KW & Klug MJ (1979). Feeding ecology of stream invertebrates. Annual Review

15 of Ecology and Systematics, **10**, 147-172.

16

17 Dangles O (2002). Functional plasticity of benthic macroinvertebrates: implications for

18 trophic dynamics in acid streams. Canadian Journal of Fisheries and Aquatic Sciences, **59**,

19 1563-1573.

20

21 Dobson M & Hildrew AG (1992). A test of resource limitation among shredding detritivores

22 in low order streams in southern England. Journal of Animal Ecology, **61**, 69-77.

23

1   Doucett RR, Barton DR, Guiguer KR, Power G, Drimmie RJ (1996) Comment: critical

2   examination of stable isotope analysis as a means for tracing carbon pathways in stream

3   ecosystems. Canadian Journal of Fisheries and Aquatic Sciences, 53, 1913-1915.

4

5   Dudgeon D, Arthington AH, Gessner MO *et al*. 2006. Freshwater biodiversity: importance,

6   threats, status and conservation challenges. Biological Reviews, **81**, 163–182.

7

8   Durance I & Ormerod SJ (2007). Climate change effects on upland stream

9   macroinvertebrates over a 25-year period. Global Change Biology, **13**, 942-957.

10

11   Durance I, Ormerod SJ (2009) Trends in water quality and discharge confound long-term

12   warming effects on river macroinvertebrates. Freshwater Biology, 54, 388-405.

13

14   Durance I, Ormerod SJ (2010) Evidence for the role of climate in the local extinction of a

15   cool-water triclad. Journal of the North American Benthological Society, 29, 1367-1378.

16

17   Eggert SL, Wallace JB, Meyer JL & Webster J. R. (2012) Storage and export of organic

18   matter in a headwater stream: responses to long-term detrital manipulations. Ecosphere, **3**,

19   Article UNSP 75.

20

1 England LE & Rosemond AD (2004). Small reductions in forest cover weaken terrestrial-

2 aquatic linkages in headwater streams. Freshwater Biology, **49**, 721-734.

3

4 Environment Agency (2011) Keeping Rivers Cool: Getting ready for climate change by

5 creating riparian shade. Environment Agency, Bristol .

6 Everall NC, Farmer A, Heath AF, Jac,lin TE, Wilby RL (2012) Ecological benefits of

7 creating messy rivers. Area, 44, 470-478.

8

9 Flores L, Díez JR, Larrañaga A, Pascoal C & Elosegi A (2013). Effects of retention site on

10 breakdown of organic matter in a mountain stream. Freshwater Biology, **58**, 1267 -1278

11

12 France RL (1996). Carbon-13 conundrums: limitations and cautions in the use of stable

13 isotope analysis in stream ecotonal research. Canadian Journal of Fisheries and Aquatic

14 Sciences, **53**, 1916-1919.

15

16 Goodwin CN, Hawkins CP & Kershner JL (1997). Riparian restoration in the western United

17 States: overview and perspective. Restoration Ecology, **5**, 4-14.

18

19 Graham CT & Harrod C (2009). Implications of climate change for the fishes of the British

20 Isles. Journal of Fish Biology, **74**, 1143-1205.

21

22 Hamilton SK, Sippel SJ & Bunn SE (2005). Separation of algae from detritus for stable

23 isotope or ecological stoichiometry studies using density fractionation in colloidal silica.

24 Limnology and Oceanography: Methods, **3**, 149-157.

Harding JS, Claassen K & Evers N (2006). Can forest fragments reset physical and water quality conditions in agricultural catchments and act as refugia for forest stream invertebrates? Hydrobiologia, **568**, 391-402.

Hauer FR & Lamberti GA (2006). *Methods in Stream Ecology*. Academic Press.

Hax CL & Golladay SW (1993). Macroinvertebrate colonization and biofilm development on leaves and wood in a boreal river. Freshwater Biology, **29**, 79-87.

Hess AD (1941). New limnological sampling equipment. Limnological Society of America. Special Publication 6, 1 – 5.

Hill WR, Ryon MG & Schilling EM (1995). Light limitation in a stream ecosystem: responses by primary producers and consumers. Ecology, **76**, 1297-1309.

Hladyz S, Gessner MO, Giller PS, Pozo J & Woodward G. (2009). Resource quality and stoichiometric constraints on stream ecosystem functioning. Freshwater Biology, **54**, 957-970.

Holmlund CM & Hammer M (1999). Ecosystem services generated by fish populations. Ecological Economics, **29**, 253-268.

Hulme PE (2005). Adapting to climate change: is there scope for ecological management in the face of a global threat? Journal of Applied Ecology, **42**, 784-794.

1

2 IPCC, 2014: Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global

3 and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of

4 the Intergovernmental Panel on Climate Change [Field CB, Barros VR, Dokken DJ *et al.*

5 (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA,

6 1132 pp.

7

8 Ishikawa NF, Doi H & Finlay JC (2012). Global meta-analysis for controlling factors on

9 carbon stable isotope ratios of lotic periphyton. Oecologia, **170**, 541-549.

10

11 Jonsson B & Jonsson N (2009). A review of the likely effects of climate change on

12 anadromous Atlantic salmon Salmo salar and brown trout Salmo trutta, with particular

13 reference to water temperature and flow. Journal of Fish Biology, **75**, 2381-2447.

14

15 Kauffman JB, Beschta RL, Otting N & Lytjen D (1997). An ecological perspective of

16 riparian and stream restoration in the western United States. Fisheries, **22**, 12-24.

17

18 Kiffney PM, Richardson JS & Bull JP (2003). Responses of periphyton and insects to

19 experimental manipulation of riparian buffer width along forest streams. Journal of Applied

20 Ecology, **40**, 1060-1076.

21

22 Kiffney PM, Richardson JS & Bull JP (2004). Establishing light as a causal mechanism

23 structuring stream communities in response to experimental manipulation of riparian buffer

24 width. Journal of the North American Benthological Society, **23**, 542-555.

25

1   Kowalik RA, Cooper DM, Evans CD, Ormerod SJ (2007) Acidic episodes retard the

2   biological recovery of upland British streams from chronic acidificaiton. Global Change

3   Biology, 13, 2439-2452.

4

5   Kruskal JB (1964). Nonmetric multidimensional scaling: a numerical method.

6   Psychometrika, **29**, 115-129.

7

8   Larsen S, Vaughan IP, Ormerod SJ (2009) Scale-dependent effects of fine sediments on

9   temperate headwater invertebrates. Freshwater Biology, 54, 203-219.

10

11   Layman CA, Araujo MS, Boucek R *et al.* (2012). Applying stable isotopes to examine food-

12   web structure: an overview of analytical tools. Biological Reviews, **87**, 545-562.

13

14   Leberfinger K, Bohman I & Herrmann J (2011). The importance of terrestrial resource

15   subsidies for shredders in open-canopy streams revealed by stable isotope analysis.

16   Freshwater Biology, **56**, 470-480.

17

18   Macgregor, N. & van Dijk, AN (2014) Adaptation in Practice: How Managers of Nature

19   Conservation Areas in Eastern England are Responding to Climate Change. Environmental

20   Management, **54**, 700-719.

21

22   Malmqvist B (2002). Aquatic invertebrates in riverine landscapes. Freshwater Biology, **47**,

23   679-694.

24

1   Mawdsley JR, O'Malley R & Ojima DS (2009) A Review of Climate-Change Adaptation

2   Strategies for Wildlife Management and Biodiversity Conservation. Conservation Biology,

3   **23**, 1080-1089

4   Menninger HL & Palmer MA (2007) Herbs and grasses as an allochthonous resource in

5   open-canopy headwater streams. Freshwater Biology, **52**, 1689-1699

6   Merritt RW & Cummins KW (Eds.) (1996). *An Introduction to the Aquatic Insects of North*

7   *America*. Kendall Hunt.

8

9   Moog O (Ed.) (1995). *Fauna Aquatica Austriaca*. Wasser-Wirtschafts-Kataster,

10   Bundesministerium für Land-und Forstwirtschaft.

11

12   Moore JC, Deruiter PC & Hunt HW (1993) Influence of productivity on the stability of real

13   and model ecosystems. Science, **261**, 906-908.

14   Muotka T & Laasonen P (2002) Ecosystem recovery in restored headwater streams: the role

15   of enhanced leaf retention. Journal of Applied Ecology, **39**, 145-156

16   Murphy JM, Sexton DMH, Jenkins GJ et al (2009) UK Climate Projections Science Report:

17   Climate Change Projections. Meteorological Office Hadley Centre, Exeter, UK.

18

19   Naiman RJ, Alldredge JR, Beauchamp DA *et al.* (2012). Developing a broader scientific

20   foundation for river restoration: Columbia River food webs. Proceedings of the National

21   Academy of Sciences, **109**, 21201-21207.

22

1   Nakano S & Murakami M (2001). Reciprocal subsidies: dynamic interdependence between

2   terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences, **98**, 166-

3   170.

4

5   Oksanen J, Blanchet FG, Kindt R *et al.* (2012) vegan: Community Ecology Package. *R*

6   *package version*, 2.0-5.

7

8   Ormerod SJ (2009). Climate change, river conservation and the adaptation challenge. *Aquatic*

9   *Conservation: Marine and Freshwater Ecosystems*, **19**, 609-613.

10

11   Ormerod SJ, Durance I (2009) Restoration and recovery from acidification in upland Welsh

12   streams over 25 years. Journal of Applied Ecology, 46, 164-174.

13

14   Ormerod SJ, Weatherly NS, Varallo PV, Whitehead PG (1988) Preliminary empirical models

15   of the historical and future impact of acidification on the ecology of Welsh streams.

16   Freshwater Biology, 20, 127-140.

17

18   Ormerod SJ, Rundle SD, Lloyd EC, Douglas AA (1993) The influence of riparian

19   management on the habitat structure and macroinvertebrate communities of upland streams

20   draining plantation forests. Journal of Applied Ecology, 30, 13-24.

21

22   Ormerod SJ, Dobson M, Hildrew AG & Townsend CR (2010). Multiple stressors in

23   freshwater ecosystems. Freshwater Biology, *55*(s1), 1-4.

24

1 Osborne LL, Kovacic DA (1993) Riparian vegetated buffer strips in water-quality restoration

2 and stream management. Freshwater Biology, 29, 243-258.

3

4 Palmer MA, Lettenmaier DP, Poff NL, Postel SL, Richter B & Warner R (2009). Climate

5 change and river ecosystems: protection and adaptation options. Environmental Management,

6 **44**, 1053-1068.

7

8 Parnell AC, Inger R, Bearhop S & Jackson AL (2010). Source partitioning using stable

9 isotopes: coping with too much variation. PLOS ONE, **5**, e9672.

10

11 Pautasso M, Aas G, Queloz V, Holdenrieder O (2013) European ash (*Fraxinus excelsior*)

12 dieback - a conservation biology challenge. Biological Conservation, 158, 37-49.

13

14 Perry J (2015) Climate change adaptation in the world's best places: a wicked problem in

15 need of immediate attention. Landscape and Urban Planning, 133, 1-11

16

17 Penheiro J, Bates D, DebRoy S, Sarkar D (2013). R Development Core Team (2012) nlme:

18 linear and nonlinear mixed effects models. R package version 3.1-103. R Foundation for

19 Statistical Computing, Vienna.

20

21 Post DM (2002). Using stable isotopes to estimate trophic position: models, methods, and

22 assumptions. Ecology, **83**, 703-718.

23

1 R Core Team (2012). R: A language and environment for statistical computing. R Foundation

2 for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL: http://www.R-

3 project.org/.

4

5 Riley WD, Pawson MG, Quayle V & Ives MJ (2009). The effects of stream canopy

6 management on macroinvertebrate communities and juvenile salmonid production in a chalk

7 stream. Fisheries Management and Ecology, **16**, 100-111.

8

9 Rybczynski SM, Walters DM, Fritz KM, Johnson BR (2008) Comparing trophic position of

10 stream fishes using stable isotope and gut contents analyses. Ecology of Freshwater Fish, 17,

11 199-206.

12

13 Seavy NE, Gardali T, Golet GH *et al.* (2009). Why climate change makes riparian restoration

14 more important than ever: recommendations for practice and research. Ecological

15 Restoration, **27**, 330-338.

16

17 Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. WH Freeman and Company, New York, NY.

18

19 Sweeney BW, Bott TL, Jackson JK *et al.* (2004). Riparian deforestation, stream narrowing,

20 and loss of stream ecosystem services. Proceedings of the National Academy of Sciences,

21 **101**, 14132-14137.

22

23 Tanentzap AJ, Szkokan-Emilson EJ, Kielstra BW, Arts MT, Yan ND & Gunn JM (2014)

24 Forests fuel fish growth in freshwater deltas. Nature Communications, **5**, Article Number:

25 4077.

1   Thomas SM & Crowther TW (2015). Predicting rates of isotopic turnover across the animal

2   kingdom: a synthesis of existing data. *Journal of Animal Ecology*, in press.

3   DOI: 10.1111/1365-2656.12326

4   Thomas SM, Griffiths SW & Ormerod SJ (2015). Adapting streams for climate change using

5   riparian broadleaf trees and its consequences for stream salmonids. Freshwater Biology, **60**,

6   64–77.

7

8   Vannote RL, Minshall GW, Cummins KW, Sedell JR & Cushing CE (1980). The river

9   continuum concept. Canadian Journal of Fisheries and Aquatic Sciences, **37**, 130-137.

10

11   Wahl CM, Neils A & Hooper D (2013). Impacts of land use at the catchment scale constrain

12   the habitat benefits of stream riparian buffers. Freshwater Biology, **58**, 2310–2324.

13

14   Wallace JB, Eggert SL, Meyer JL & Webster JR (1997). Multiple trophic levels of a forest

15   stream linked to terrestrial litter inputs. Science, **277**, 102-104.

16

17   Wallace JB, Whiles MR, Eggert S, Cuffney TF, Lugthart GJ & Chung K (1995). Long-term

18   dynamics of coarse particulate organic matter in three Appalachian Mountain streams.

19   Journal of the North American Benthological Society, **14**, 217-232.

20

21   Warton DI & Hui FK (2011). The arcsine is asinine: the analysis of proportions in ecology.

22   Ecology, **92**, 3-10.

23

1   Weatherly NS, Ormerod SJ (1990) Forests and the temperature of upland streams: a

2   modelling study of the biological consequences. Freshwater Biology, 24, 109-122.

3

4   Wilson MA & Carpenter SR (1999). Economic valuation of freshwater ecosystem services in

5   the United States: 1971-1997. Ecological Applications, **9**, 772-783.

6

7   Wipfli MS (2005). Trophic linkages between headwater forests and downstream fish habitats:

8   implications for forest and fish management. Landscape and Urban Planning, **72**, 205-213.

9

10   Zoellick BW (2004). Density and biomass of redband trout relative to stream shading and

11   temperature in southwestern Idaho. Western North American Naturalist, **64**, 18–26.

12

13   Zuur AF, Ieno EN & Smith GM (2007). *Analysing Ecological Data*. Springer.

14

15

16

17

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.
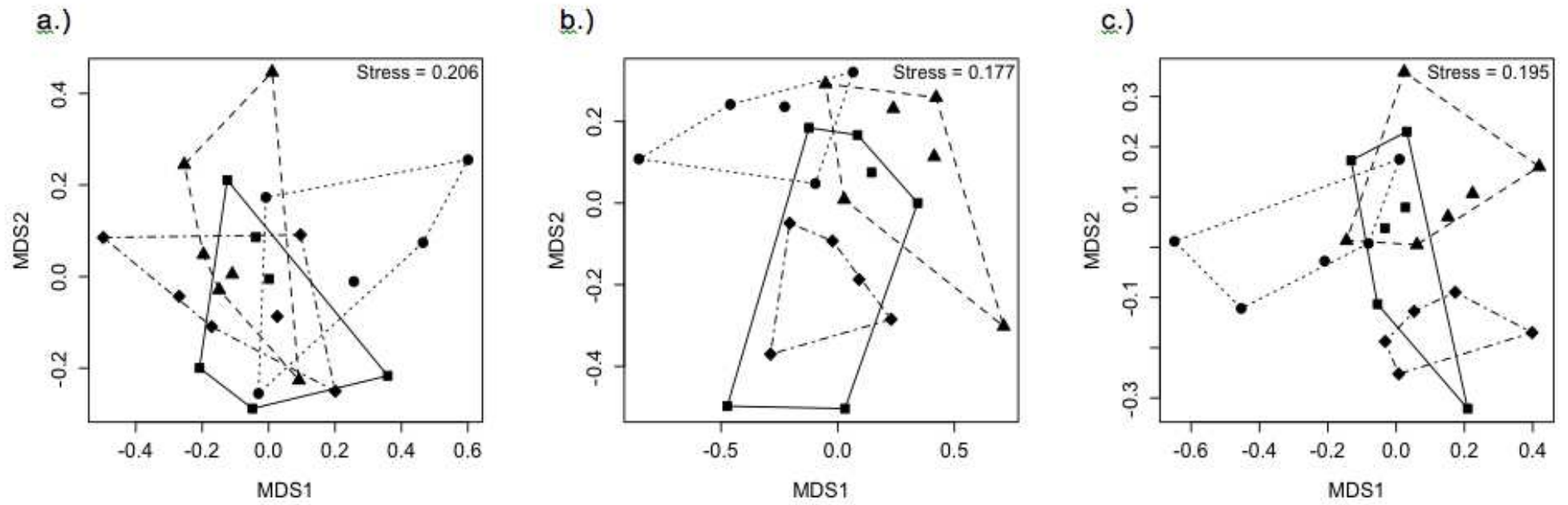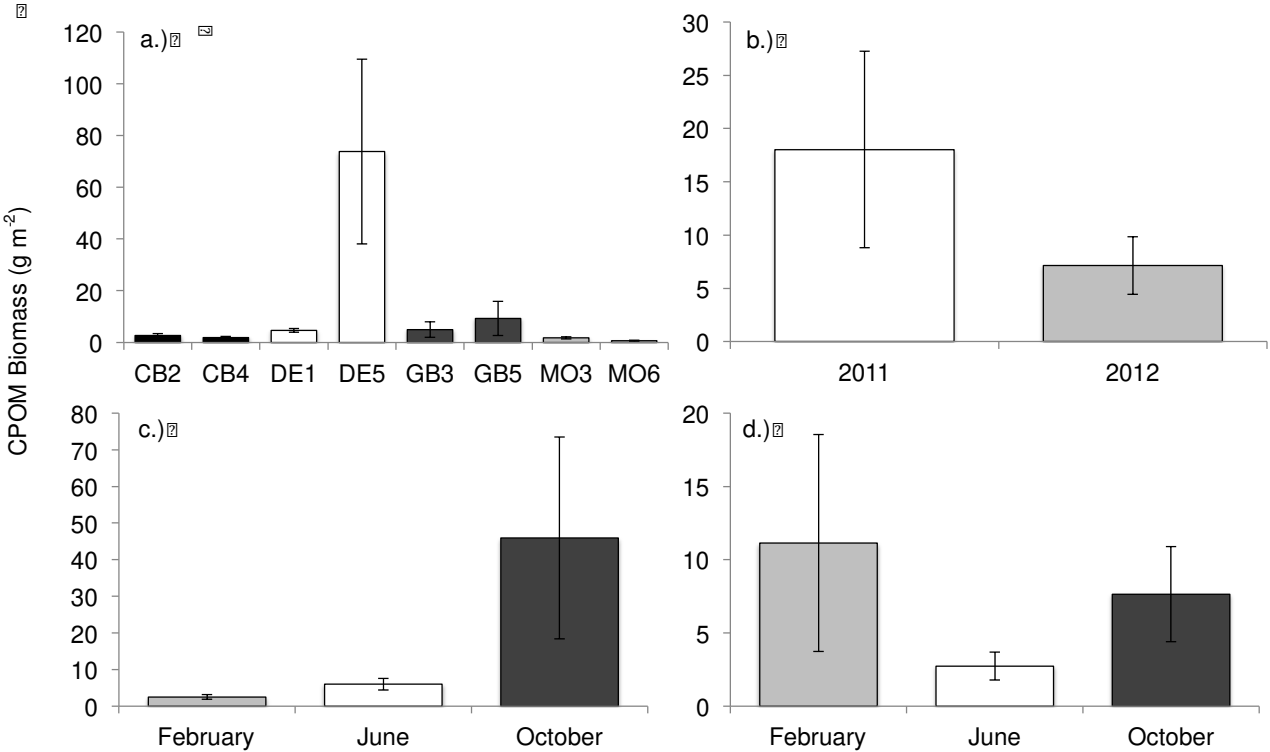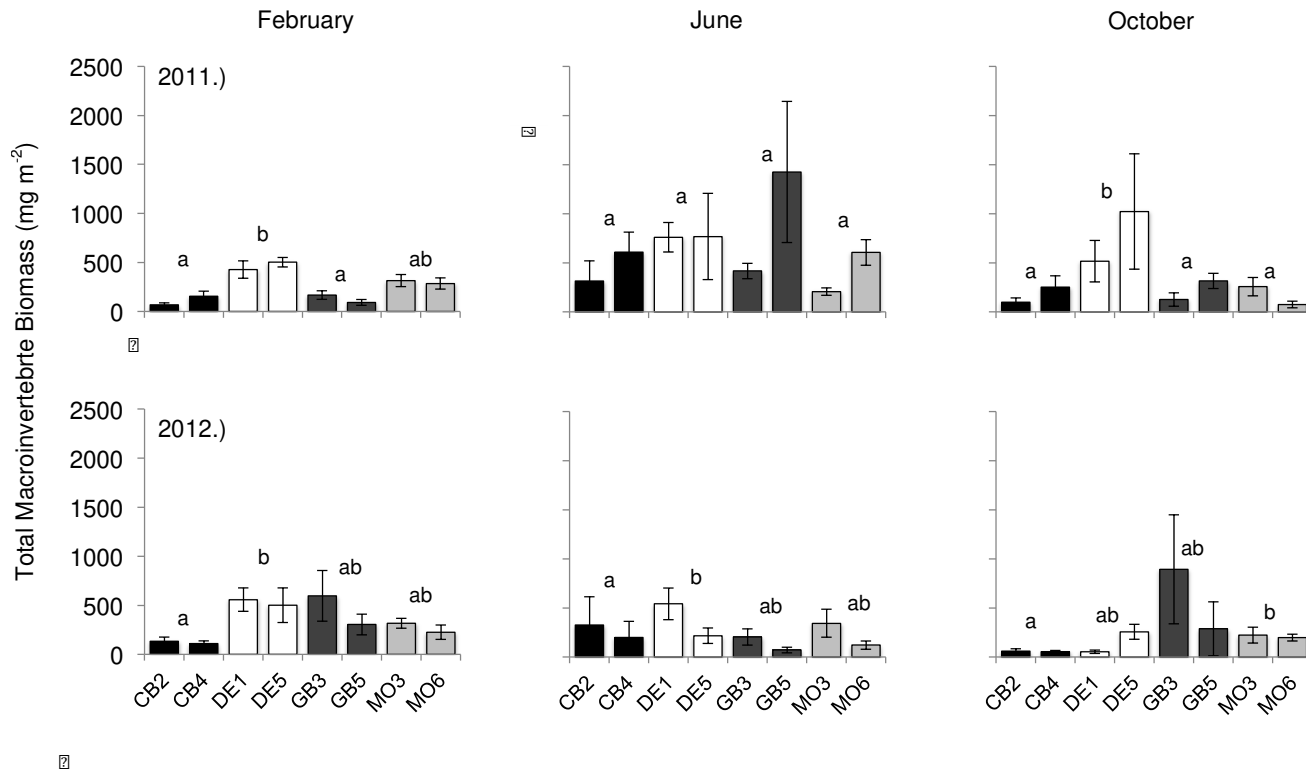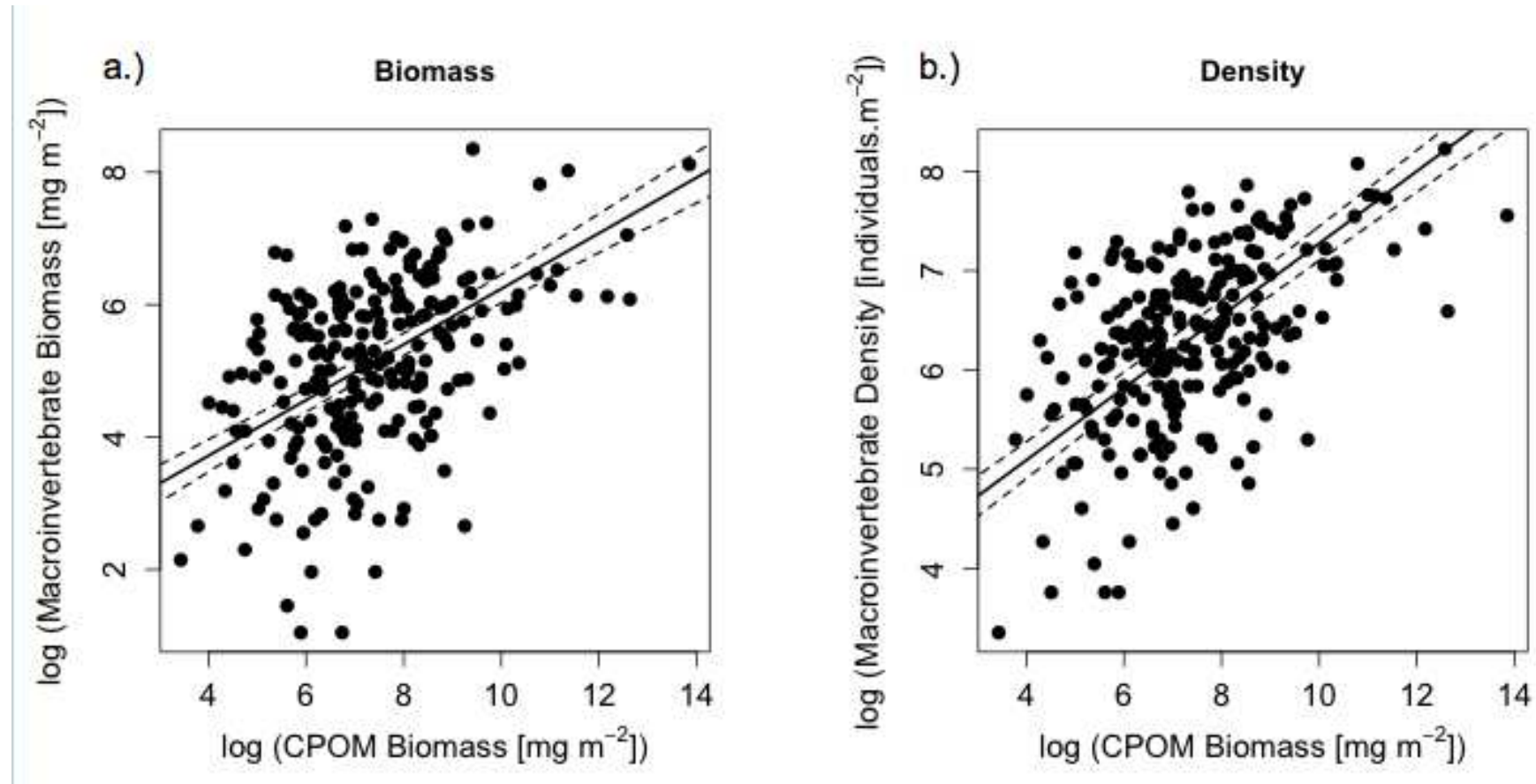
Figure 1:

Fig 2:

Figure 3:

Figure 4:

Figure 5