Consequences of riparian land use for macroinvertebrate communities and brown trout in upland streams

Thesis submitted for the degree of Doctor of Philosophy

by

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Summary

1. Freshwaters ecosystems are sensitive to climate change due to their position in the hydrological cycle, thermal links to the atmosphere and dominance by poikilothermic organisms. Such changes threaten freshwater biodiversity and ecosystems services, and adaptation schemes to limit impacts are therefore widely advocated. One management action recommended widely for rivers is the adaptive restoration of "buffer strips" of riparian tree cover to lower stream temperatures and protect thermally sensitive species, including salmonid fish.

2. Despite thermal consequences being well-quantified, responses to adaptive riparian restoration among stream invertebrate and fishes are poorly understood, and there is only limited evidence from which to predict restoration outcomes and inform management for these organisms.

3. Using surveys and experiments on 24 upland streams, this thesis assessed the effects of contrasting catchment tree cover on terrestrial resource subsidies to stream food webs, macroinvertebrate community composition and salmonid biomass and density.

4. Several lines of evidence indicated that extensive catchment tree cover affected the functional composition of stream communities by mediating availability of terrestrial resources. However, woodland buffer strips did not have the same effects, and supported communities that were functionally

indistinguishable from streams draining unafforested moorland. Catchment broadleaf cover did not affect salmonid populations.

5. These results extend the understanding of land use effects on stream communities and their use in river management in two ways. First, when woodland buffer strips are restored to shade streams, benefit to fish populations should arise without negative effects on prey availability. Second, re-establishing woodland stream communities of invertebrates will require more extensive broadleaf planting.

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Chapter 1: Literature Review, Aims, Hypotheses and Study Area

1.0: Summary

1. This review outlines the shifts in global climate predicted during the 21st Century, and the potential ecological consequences of such change. Riverine ecosystems appear disproportionately at risk due to habitat-specific factors, including generally low thermal buffering capacity, dependence on discharge and predominantly poikilothermic fauna.

2. Potential risks for ecosystem services provision by such habitats include threats to economically important inland fisheries. Wide-ranging salmonid species (Family: Salmonidae) are vulnerable, due to physiological and life-history traits. Probable consequences for salmonid populations in UK rivers include reductions in growth and production, particularly if water temperatures regularly exceed current conditions by around 3 °C during summer; such increases are expected by the mid-to-late 21st Century.

3. Despite suggestions that increased riparian tree cover might moderate thermal regimes in temperate streams at risk from warming, uncertainties remain in this approach. One of the major knowledge gaps is the potential change that riparian tree cover effects in stream food web structure and energetics, as a result of shifts in resource availability.

4. This chapter also introduces the approach used in this thesis, in which surveys and experiments were used in combination to test the overarching hypothesis that animal communities in streams with increased catchment tree cover are relatively more dependent on terrestrial resources than those in treeless catchments, due to increased allochthonous inputs. Differential resource availability is predicted to alter community composition, functional group representation and energetics in macroinvertebrate communities, favouring taxa adapted to process terrestrial detrital material. These shifts are hypothesised to affect salmonid populations, which are reliant on secondary invertebrate production.

1.1: Literature Review

1.1.1: Preamble

Global climate has changed significantly since the mid-20th Century: the years 1995 to 2007 included 12 of the 13 warmest years on record, and this period was marked by concurrent shifts in global precipitation patterns (IPCC, 2007). Change was principally driven by anthropogenic emissions of various greenhouse gasses, with CO_2 the major contributor to this warming effect (IPCC, 2007). Emissions are likely to accelerate throughout much of the 21st Century, with mean global air temperatures predicted to increase 1.8 – 4 ºC by 2100 as a result (IPCC, 2007). The ecological consequences are likely to be profound, affecting organisms at all levels of biological organisation, jeopardizing both global biodiversity and the supply of ecosystem services to human populations worldwide (Thomas *et al*., 2004; Parmesan, 2006; Pörtner and Farell, 2008).

Freshwaters are vulnerable to such change, with riverine ecosystems particularly at risk: these environments are marked both by low capacity to buffer temperature increases, and an inherent dependence on catchment precipitation and evapotranspiration (Arnell, 1998; Nijssen *et al*., 2001; Cassie, 2006). Moreover, freshwater organisms are often thermally sensitive, as evidenced by a wide range of ecological responses to recent climate change in many freshwater ecosystems globally (O'Reilly *et al*., 2003; Winder and Schindler, 2004; Daufresne and Boët, 2007; Durance and Ormerod, 2007). Freshwaters are disproportionately biologically diverse, however, and supply a wide range of ecosystem services, notably drinking water, irrigation, flood protection and inland fisheries (Ficke *et al*., 2007; Vörösmarty *et al*., 2010), while providing a host of additional cultural and recreational services (Costanza *et al*., 1997; Dudgeon *et al.,* 2006). Climate change impacts in river systems could therefore have major consequences for global economies and nature conservation.

Despite the large-scale, global nature of likely impacts, there is considerable scope for management practices that may be able to minimize or offset many of the negative consequences associated with climate change. Human populations may act to mitigate emissions to minimize magnitude of future climatic change, for instance, or adapt agricultural and natural systems to increase their inherent resilience (Hulme, 2005; IPCC, 2007). Alternatively, no specific action might be taken, though this 'do nothing' option would likely result in widespread negative impacts globally. As such, mitigation practices, including emissions reductions and carbon sequestration schemes, are underway in many countries worldwide (IPCC, 2007). However, models predict that even if CO_2 concentrations remained constant at their 2000 level, considerable changes in average climate would still be expected during the 21st Century, due to a lag between CO_2 and temperature increases. This phenomenon, coupled with the fact that emissions are in reality predicted to continue or even accelerate during the 21st Century, suggests that adaptation schemes may play a key role in limiting climate change impacts on both human populations and natural systems. Adaptation schemes likely to be most effective are those that can increase the inherent resilience of communities, often by minimising or offsetting negative impacts of present day anthropogenic activities (Hulme, 2005; IPCC, 2007). Evidence is, however, needed to support the efficacy of such adaptation schemes. Specifically, the capacity of these measures to offset direct climatic impacts effects needs to be assessed, along with potential indirect consequences for wider ecosystem dynamics.

Restoration of riparian tree cover in historically deforested catchments is among the major adaptation strategies advocated for river systems (Battin *et al*., 2007; Ormerod, 2009; Seavy *et al*., 2009; Palmer *et al*. 2008; 2009). A range of empirical and modeling evidence has demonstrated the capacity of tree cover to offset thermal impacts, particularly in temperate ecosystems (Zoellick, 2004; Battin *et al*., 2007; Broadmeadow *et al*., 2011). This adaptation method may be able to protect ecosystem service provision and biodiversity in river habitats; this includes economically important fisheries based on thermally-sensitive salmonid species (Family: Salmonidae). However, the wider ecosystem consequences of differential catchment tree cover remain largely unexplored: reforestation of riparian zones could lead to large-scale changes in relative resource availability, shifting the autotrophic-heterotrophic balance of adjacent streams and rivers, by reducing in-stream primary production whilst increasing inputs of terrestrial subsidies (Hill *et al*., 1995; Kiffney *et al*., 2003; 2004).

This thesis will evaluate the possible value of differential riparian management for invertebrate and salmonid communities in temperate upland river systems, to inform such management and adaptation practices. This chapter reviews likely consequences of climate change for temperate river systems and the salmonid fisheries that they support. The utility of riparian restoration for offsetting thermal change is assessed, though uncertainties currently associated with this adaptation method are also highlighted. Finally, probable community-wide changes resulting from differential tree cover are described, and hypotheses allowing these predictions to be tested are outlined.

1.1.2: Ecological consequences of climate change

Considerable changes in average global climate occurred during the 20th Century, with mean air temperatures increasing by approximately 0.75 ºC during this period (IPCC, 2007). Change was particularly marked during the second half of the century, with observed warming of approximately 0.13 ºC occurring per decade between 1956 and 2005 (IPCC, 2007). It is likely that this trend will continue, with an accelerating rate of warming also predicted: increases in mean global air temperatures of 1.8 – 4 ºC compared to current averages are forecast by the end of the 21st Century (IPCC, 2007). Concurrent changes in global precipitation patterns are also probable, with higher latitudes likely to experience increases in average annual rainfall, while many subtropical and equatorial regions will become drier (IPCC, 2007). An increased regularity in the occurrence of extremes climatic events, including heat waves and storms, is also deemed very likely (IPCC, 2007).

The ecological consequences of such change may be profound, affecting populations, species, interspecific interactions and ecosystem processes; potentially 20 – 30 % of animal and plant species worldwide may be at risk of extinction (Thomas *et al*., 2004). Effects of increasing temperatures may manifest themselves at multiple levels of biological organisation, potentially inducing physiological changes within individual organisms, shifting the distribution and population dynamics of many species, and ultimately mediating species interactions and ecosystem processes (Thomas *et al*., 2004; Parmesan, 2006). Inherent thermal thresholds may lead to shifts in species' ranges and the timing of climatically-cued developmental events (Walther *et al*., 2002; Parmesan, 2006), cause reversals in the outcome of competitive interactions (Taniguchi and Nakano, 2000) and ultimately even changes in trophic structure of whole communities (Winder and Schindler, 2004). Disruptions to some facets of ecological functioning, such as decreases in productivity, are already being linked to shifts in local climate (O'Reilly *et al*., 2003). Complex interactions between varying climate and other sources of anthropogenic disturbance, including land use change and introduction of non-native species, are also widely predicted, with these acting in synchrony to determine the fate of individual species and populations (Thomas *et al*. 2004; Sharma *et al*., 2011). Such potentially large-scale, widespread impacts may have far-reaching implications for the provision of goods and services by ecosystems worldwide. In 1997, it was estimated that the total value of such services was US $33 trillion, a figure exceeding the total global Gross National Product (Costanza *et al*., 1997). As such, impacts are likely lead to major economic, as well as ecological consequences.

1.1.3: Climate change and fresh waters

Freshwater ecosystems may be among those most affected by global climate change, experiencing increasing temperature and change in precipitation regimes particularly acutely (Carpenter *et al*., 1992; Meyer *et al*., 1999). The increased regularity of heat waves and storms will likely manifest in inland waters as droughts and flood events, negatively impacting in many freshwater organisms (Humphries and Baldwin, 2003; Pörtner and Farrell, 2008). A majority of freshwater species may be particularly sensitive due to their predominantly ectothermic nature, with elevated temperatures likely leading to direct physiological costs in these organisms (Pörtner and Farell, 2008). Moreover, ecological changes ultimately manifested in these environments may be greater than could be predicted from known thermal and hydrological tolerances of individual species alone, with non-linear responses deemed likely, as thresholds are crossed in many systems (Burkett *et al*. 2005).

Likely species losses in freshwater ecosystems induced by climate change will have major implications for wider global biodiversity, with these habitats being disproportionately diverse: despite covering only 0.8 % of the Earth's surface, it has been estimated that rivers, lakes and wetlands, combined, contain around 6 % of all currently described species (Dudgeon *et al*., 2006). These ecosystems also provide a wealth of goods and services to human populations, including provision of inland fisheries (Ficke *et al*., 2007) and drinking water (Vörösmarty *et al*., 2010). This suggests there may be appreciable economic costs associated with diminished functioning of these habitats. Conflicts between biodiversity conservation and ecosystem service provision may ultimately arise, with global freshwater resources likely to be further stressed due to increasing demand for water needed to sustain growing human populations in a changing climate (Jackson *et al*., 2001; Vörösmarty *et al*., 2010).

Shifts in the structure and function of many freshwater ecosystems are already attributable to climatic changes that have occurred since the mid-20th Century. Decreases in primary productivity (O'Reilly *et al*., 2003) and uncoupling of trophic linkages in lake ecosystems (Winder and Schindler, 2004), along with shifts in the composition of riverine communities (Daufresne and Boët, 2007; Durance and Ormerod, 2007), have already been observed. Predicted future changes include increased prevalence of various aquatic disease organisms (Marcogliese, 2001; Harvell *et al*., 2002), and the facilitation of the invasion of non-native species due to the geographical expansion of their favoured climatic envelopes (Rahel and Olden, 2008; Sharma *et al*., 2011). The extent of such impacts may, however, be habitat-specific, affecting some aquatic environments disproportionately.

1.1.4: Vulnerability of global river systems

Among freshwater environments, rivers and streams are particularly susceptible to climate change (Meyer *et al*., 1999; Dudgeon *et al*., 2006). Water temperatures in river bodies closely track local air temperature, due to the limited thermal buffering capacity of these low volume environments (Cassie, 2006). Temperature increases in rivers and streams are likely to be comparable in magnitude to those experienced by terrestrial ecosystems, though moderated by the higher specific heat capacity of water in comparison with air (Cassie, 2006). Significant changes in the thermal regimes of many streams and rivers are already documented, with increases in mean temperatures of as much as 1.4 – 1.7 ˚C occurring over as short a period as 25 years in several upland UK streams (Durance and Ormerod, 2007). Such trends appear consistent in river systems across the Northern Hemisphere, with similar significant linear warming trends apparent across much of the USA (Kaushal *et al*., 2010).

Hydrological regimes in many catchments could also be perturbed as a result of changing precipitation patterns; reduced flows during summer, increased flows during winter and less reliable water supply are all predicted to occur in many temperate river systems worldwide (Arnell, 1998; Nijssen *et al*., 2001). Decreased flow and increased temperature are likely to act simultaneously to reduce dissolved oxygen availability and increase ionic concentrations, particularly during summer (Arnell, 1998; Nijssen *et al*., 2001). Such effects would negatively impact riverine ecosystems: poikilothermic organisms (whose body temperature varies with that of their environment), such as fish and invertebrate fauna, may prove particularly sensitive to such changes. These organisms may experience metabolic costs associated with both elevated temperature and decreased dissolved oxygen availability (Ficke *et al*., 2007; Pörtner and Farell, 2008). Increased ionic concentrations during low flow periods may act to intensify current stressors, such as acidification and eutrophication, potentially affecting species sooner than if either occurred in isolation (Dudgeon *et al*., 2006; Ormerod *et al*., 2010). As such, it is likely that climate-change effects on global river systems will interact with existing catchment-scale degradation, such as land use change, water abstraction and pollutant inputs (Dudgeon *et al*., 2006), with this likely to reduce the inherent capacity for resilience in these ecosystems (Ormerod *et al*., 2010).

1.1.5: Consequences for ecosystem service provision in freshwater habitats

The provision of fisheries is one of the major ecosystem services provided by aquatic ecosystems worldwide, and negative consequences for global fish production as a result of climate change are widely predicted (Schindler, 2001; Graham and Harrod, 2009; Lassalle and Rochard, 2009; Pörtner and Peck, 2010). Freshwater fish species are a major global human food resource, with inland capture fisheries accounting for approximately 12 % of total annual fish consumption (Johnson *et al*., 2001). Recreational fisheries in inland waters are also of importance to the economy of many countries: it has been estimated, for example, that an approximate 2.9 million anglers contribute as much as £2.4 billion per annum to the UK economy (Lyons *et al*., 2002). Furthermore, fish populations, along with wider freshwater biodiversity, offer a range of intrinsically valuable recreational and cultural services to human populations (Costanza *et al*., 1997; Dudgeon *et al*., 2006), which may ultimately be eroded due to climate change.

Small temperature increases may be beneficial for some commercial and recreational fisheries, particularly those at higher latitudes (Mantua *et al*., 1997; Brander, 2007; Graham and Harrod, 2009). However, models predict that warming of the magnitude expected by the second half of the 21st Century is likely to have deleterious effects on many fish populations (Xenopoulos *et al*., 2005; Lassalle and Rochard, 2009). Aside from the direct effects of increasing temperature, a range of indirect processes associated with climate change may also negatively impact fish populations. Increases in diseases and parasitism are widely predicted (Marcogliese, 2001; Harvell *et al*., 2002), along with increased competition from both native species with higher thermal tolerances (Graham and Harrod, 2009) and newly establishing invasive species (Rahel and Olden, 2008; Sharma *et al*., 2011). Climate impacts may also manifest themselves as ecosystem-level changes in food webs of which fish form a part (Pörtner and Peck, 2010). Impacts of climate change on fish populations are already being documented, and include range shifts in species that inhabit marine environments (Perry *et al*., 2005) and changes in abundance and community composition of riverine species (Daufresne and Boët, 2007).

The effects of climate change upon migratory fish species may be particularly pronounced, with populations having to contend with physiological and ecological shifts in both marine and freshwater environments (Jonsson and Jonsson, 2009; Lassalle and Rochard, 2009). Climatic changes in these environments will probably be uneven, with greater warming forecasted for inland freshwaters than for the oceanic systems (IPCC, 2007). This may lead to possible asynchronies between developmental processes and key ecological events, for instance, and may potentially expose migrating individuals to more distinct thermal gradients (Jonsson and Jonsson, 2009), likely increasing mortality amongst transitioning juveniles in some species (Kennedy and Crozier, 2010).

1.1.6: Implications of climate change for salmonid production

Salmonid species (Family: Salmonidae) are the dominant anadromous fishes across much of the Northern Hemisphere. This family includes species of widespread genera such as *Salmo* and *Oncorhynchus*, which are ecologically important in many ecosystems (Power, 1990; Wipfli *et al*., 1998), and support extensive commercial and recreational fisheries across much of their range (Ficke *et al*., 2007). Salmonid production, particularly that of well-studied populations of North American *Oncorhynchus* species, closely tracks past climatic oscillations (Mantua *et al*. 1997): during the late 20th Century, warmer, wetter phases of the Pacific Decadal Oscillation were assocaiated with a large reduction in reported catches in mid-latitude North America, whilst production increased in more northerly areas, such as Alaska, while the converse was true during colder, drier phases. There is strong evidence to suggest that salmonid species will respond to further directional climate change predicted to occur throughout the 21st Century: physiological costs of increasing temperature may be particularly acute for these species, many of which are cold water adapted (Ficke *et al*., 2007; Elliot and Elliot, 2010) and sensitive to temperature change at many levels of biological organisation and throughout all life-history stages (Jonsson and Jonsson, 2009; Elliot and Elliot, 2010). Since climate models predict that the degree of warming will be greater over land than over the oceans (IPCC, 2007), it is likely that anadromous salmonids will experience the most negative effects of climate change during their residence in running waters, a stage which coincides with their most thermally-sensitive developmental stages (Ojanguren *et al*., 1999; Ojanguren and Braña, 2003). Populations in streams and rivers may also experience the effects of changing precipitation patterns directly through more variable flow regimes (Jonsson and Jonsson, 2009).

Although recent studies suggest that salmonid populations may be able to adapt to some aspects of climate change via behavioural shifts, such as use of thermal refugia (Goniea *et al*., 2006) or changes in the timing of migratory or developmental events (Taylor, 2008), it is unlikely that these will be able to account for the rate and extent of the expected changes in temperature and stream flow. For example, little evidence exists of appreciable physiological thermal adaptation in populations of *Salmo* species existing at the edges of their respective ranges (Elliot and Elliot, 2010), suggesting that scope for rapid evolutionary increases in thermal tolerance in these species may be limited. The anticipated consequences for salmonids in many areas of the world are therefore negative. Models predict that range contractions of as much as 30% are probable for European populations of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) by 2100, for instance, with major losses in abundance or even total disappearance of these species likely in many Southern European catchments (Lassalle and Rochard, 2009).

There is evidence to suggest that many UK salmonid populations may also be at risk from increasing temperature: thermal tolerance limits of *Salmo* species have been accurately established, with optimal growth occurring at around 16 ºC and temperature-induced feeding cessation occurring at 22 ºC in juvenile *Salmo salar* (Elliot and Elliot, 2010). Certain life history stages may be considerably more vulnerable, however, with eggs and larval fish notably sensitive to elevated temperature (Ojanguren *et al*., 1999; Ojanguren and Braña, 2003). Mean summer water temperatures at un-shaded streams in Southern England are already as high as 19 ºC (Broadmeadow *et al*. 2011), however, and such streams are predicted to experience temperature increases of around 4 – 5 °C by 2100 as a result of climate change (UKCIP02 HadRM3 scenario; Hulme *et al*., 2002). *Salmo* species may therefore already be approaching the upper range of their preferred thermal tolerances in many UK river systems.

Moreover, climate change may cause current UK salmonid habitats to exceed such thresholds regularly in the future, potentially leading to local extinctions or decreases in fish production. These data concur with conclusions of past in-depth reviews of salmonid thermal requirements; salmonids may experience negative consequences for growth and survival if UK river water temperatures exceed current averages by around 3 ºC (Elliot and Elliot, 2010). Such increases are likely to have occurred by the mid-21st Century (Hulme *et al.,* 2002).

The stream food webs supporting salmonid populations are likely to be directly affected by climate change; this may suggest a potential indirect mechanism by which production of salmonid species may also be reduced, particularly where fish populations are currently food-limited. Aquatic macroinvertebrates typically compose the main dietary component for salmonids during their residence in fresh water (Elliot, 1973), for instance, though terrestrial invertebrate subsidies are also seasonally important (Kawaguchi and Nakano, 2001). Past work has demonstrated that macroinvertebrate prey populations in headwater streams respond strongly to both climatic oscillations and directional climate change (Daufresne *et al*., 2004; Durance and Ormerod, 2007). Future warming is anticipated to influence assemblage composition in UK headwater streams, with 5 – 12 % of local species potentially at risk of extinction under current climate projections (Durance and Ormerod, 2007). Moreover, experimental manipulations of stream thermal regimes, in line with those anticipated by the end of the 21st Century, suggest that increased temperature may act to reduce total macroinvertebrate densities in such habitats (Hogg and Williams, 1996). However, macroinvertebrate communities provide a crucial intermediate link between primary production, detritus pools and higher trophic levels within such streams, and are as such key for supporting fish production and wider nutrient cycling (Malmqvist, 2002). Losses in secondary production in such communities may therefore negatively impact fish production in these environments.

Declines in salmonid production as a result of such direct or indirect processes would likely have considerable local ecological and economic implications globally; salmonid rod-fishing licenses in the UK alone are worth around £128 million per year, while recreational fisheries based on these species comprise a large proportion of the total £2.4 billion UK annual angling expenditure (Lyons *et al*., 2002; Aprahamian *et al*., 2010). Salmonid fish are also often keystone species in many ecosystems worldwide, structuring stream communities via top-down control (Power, 1990), providing resource subsidies to riparian organisms via deposition of carcasses following spawning (Wipfli *et al*., 1998; Williams *et al*., 2009), and supporting a range of terrestrial and semi-aquatic vertebrate predators (Durbin, 1997; Carter *et al*., 2001). Population declines as a result of climate change could therefore result in negative consequences for many local economies, along with a range of wider ecological impacts that may ultimately limit the provision of other ecosystem services by riverine habitats. As such, there may be significant imperative for implementing adaptation schemes, where such measures are feasible.

1.1.7: Climate change adaptation in rivers - riparian protection and restoration

Though ecosystems globally are likely to be adversely affected by climate change, there is evidence to suggest that timely and properly implemented management strategies may be able to offset some of the more severe impacts (Hulme, 2005). The adaptation schemes often deemed most effective are those which are able to increase the inherent resilience of communities, often by minimising negative impacts of present day anthropogenic activities

(Hulme, 2005; IPCC, 2007). Whilst running waters are predicted to be amongst the environments most affected by changing climate, they may also be amongst the systems with the greatest scope for adaptation (Ormerod, 2009; Seavy *et al*., 2009; Palmer *et al*. 2008; 2009; Wilby and Dessai, 2010).

Although some ecological effects attributable to directional climatic change are beginning to be documented in running waters, the most marked changes are likely to become evident by the mid-21st Century; by this time, critical thermal and hydrological thresholds of many species may be regularly exceeded (Malmqvist and Rundle, 2002; Palmer *et al*., 2008; Elliot and Elliot, 2010). Several researchers have suggested that there may be potential for adaptation measures to offset climate change impacts prior to this, particularly in river catchments that are currently degraded due to human activity. The major adaptation strategy currently advocated is the restoration of near-stream broadleaf tree cover in historically deforested catchments (Battin *et al*., 2007; Ormerod, 2009; Seavy *et al*., 2009; Palmer *et al*. 2008; 2009). The benefits of such “restorative adaptation” measures are likely to be multifaceted, buffering against extremes and large fluctuations in water temperature (Broadmeadow *et al*., 2011), improving water quality (Broadmeadow and Nisbet, 2004), and increasing terrestrial resource subsidies to in-stream consumers (Kawaguchi and Nakano, 2001; Baxter *et al*. 2005). River systems currently supporting salmonid fisheries may present suitable cases for such adaptive management strategies; many facets of the ecology and population dynamics of these species have been extensively investigated, and thermal tolerance thresholds have been firmly established for all of their respective life history stages (Elliot and Elliot, 2010). Once major physicochemical and biological effects of various restoration strategies are fully understood, it may be possible to predict how such factors are likely to influence survival and production in these focal species, allowing for targeted adaptation measures to be designed and implemented.

As a management strategy, the restoration of broadleaf "buffer strips" in deforested riparian zones has the potential advantages of both minimising direct effects of climatic change (Broadmeadow *et al*., 2011) whilst also increasing the resilience of restored river systems by reducing the impacts of other anthropogenic stressors, and as such may be particularly effective (Hulme, 2005; IPCC, 2007; Ormerod, 2009; Palmer *et al*., 2008; 2009). Restored riparian forest may act to limit the impact of extreme climatic events within streams and rivers by, for example, stabilising stream flows, reducing the severity of flood events (Bosch and Hewlett, 1982; Bradshaw *et al*. 2007) and significantly limiting maximum water temperatures during summer heat waves (Broadmeadow *et al*., 2011). The major benefit of riparian restoration appears to be alterations in average thermal regimes within streams: mean water temperatures can be 0.6 – 4.5 ºC lower in shaded streams, in comparison with adjacent sites without riparian cover (Weatherley and Ormerod, 1990; Opperman and Merenlender, 2004; Zoellick, 2004; Broadmeadow *et al*., 2011). Riparian shading also decreases daily thermal maxima, with one study recording a 5.5 ºC temperature reduction when compared to a similar open reach (Broadmeadow *et al*., 2011). The same study also found that riparian vegetation acts a buffer against daily and inter-annual temperature variation, limiting the range of both (Broadmeadow *et al*., 2011). The magnitude of such thermal buffering may be sufficient to offset temperature impacts associated with climate change in such streams, and may be useful for protecting thermally sensitive salmonid populations.

Aside from their potential ability to negate some of the more severe effects of climate change likely to affect streams and rivers, buffer strips may also confer a range of ancillary benefits to local aquatic and terrestrial riparian biota. Forested riparian zones are able to improve water quality, via both the interception of contaminated run off (Broadmeadow and Nisbet, 2004), and the increased in-stream processing of nutrients that occurs in wooded streams (Sweeney *et al*., 2004). Riparian trees may also enhance facets of in-stream habitat quality: inputs of large woody debris can lead to increases in pool formation (Gurnell *et al*., 2002), whilst bank stabilisation conferred by root systems can result in wider streams, increasing the area of stream habitat available per unit length of stream (Sweeney *et al*., 2004). Broadleaf buffers are also likely to moderate the strength of terrestrial-aquatic trophic linkages, by increasing cross boundary resource subsidies and facilitating retention of terrestrial organic matter in streams, increasing available food resources to consumers in both terrestrial and aquatic habitats (Wallace *et al*., 1997; Kawaguchi and Nakano, 2001; Baxter *et al*., 2005). This may act to offset the increased metabolic costs incurred by poikilothermic aquatic organisms inhabiting rivers and stream, potentially increasing their resilience in the face of temperature increases. Furthermore, mature riparian corridors provide habitat for many terrestrial species, often contributing significantly to local biodiversity (Naiman *et al*., 1993; Olson *et al*., 2007). Such corridors also function as conduits for dispersal and migration for many species, a facility that may prove particularly valuable in a changing climate, potentially allowing populations to move in order to track climatic optima (Naiman *et al*., 1993; Seavy *et al*., 2009).

1.1.8: Current uncertainties associated with restoration of riparian tree cover

Despite many benefits that broadleaf buffer strips may confer to stream ecosystems, there are still many uncertainties associated with their usage, particularly in climate change adaptation. Changes in canopy cover can alter the amount of direct solar radiation being received by the streambed (Kjeldsen, 1996), with light limitation likely to influence in-stream primary productivity, with consequences for aquatic consumers reliant on autotrophic basal resources (Behmer and Hawkins, 1986; Hill *et al.*, 1995; Quinn *et al.*, 1997; Kiffney *et al.*, 2003, 2004; Riley *et al.*, 2009). The biomass of both epilithic biofilms and macroinvertebrates often respond positively to decreased shading, suggesting that reduced light levels resulting from restoration of riparian tree cover may negatively influence secondary production by stream communities (Kiffney *et al.*, 2003; 2004). Inputs of terrestrial resource subsidies to aquatic ecosystems generally positively co-vary with tree cover (Wallace *et al.*, 1997; Kawaguchi and Nakano, 2001; Baxter *et al.*, 2005; Earl and Semlitsch, 2013), however, suggesting these may be able to offset decreases in autotrophic production, where the extent of such subsidies are large enough. Large-scale changes in basal resource availability may cause compositional and functional shifts in macroinvertebrate communities, however, with morphological constraints typically limiting resource acquisition in consumer taxa (Cummins and Klug, 1979; Moog, 1995). Increased terrestrial resource subsidies may therefore favour "shredding" taxa adapted to process detrital material, at the expense of "Grazers" that typically feed on autotrophic biofilms. Such changes would likely affect the trophic pathways supporting fish populations in restored streams, shifting food webs away from autotrophic production, towards greater heterotrophic dependence, though the ultimate consequences of such change for stream fish production remain largely unexplored.

Despite relatively limited knowledge of the processes underlying effects of riparian tree cover on food webs supporting fish, much empirical evidence exists to suggest that populations may respond directly to varying riparian land uses: for example, streams with intact riparian forest typically support a more abundant and diverse fish community than those that have been clear-felled (Jones *et al.*, 1999; Burcher *et al*, 2008). Effects upon salmonid species appear equivocal, however. Riley *et al*. (2009) report that both the density and individual size of *S. salar* and *S. trutta* populations in lowland UK streams with dense canopy cover were significantly lower than those of adjacent open canopy sites. Several other authors have observed increased salmonid biomass in shaded reaches throughout a range of temperate streams (Kawaguchi and Nakano, 2001; Opperman and Merenlender, 2004; Zoelick, 2004). Past work has, however, highlighted the need to consider explicitly catchment-wide influences in effects of land use on river systems (Allan *et al*., 1997; Kauffman *et al*. 1997). This factor may therefore play a key role in explaining outcomes of previous investigations, with effects of the extent of catchment forest cover likely influencing the magnitude of terrestrial resource subsidies supplied to communities in restored streams: larger areas of deciduous woodland in riparian zones may input energy and nutrients to streams in quantities great enough to offset decreases in autotrophic production, whilst narrow buffer strips may be unable to confer similar benefits (Abelho, 2001). Such effects may therefore lead to overall reductions in secondary production. The underlying causes of such ambiguities may be resolved by developing an improved mechanistic understanding of changes in community composition and trophic process likely to accompany riparian restoration (Goodwin *et al*., 1997; Naiman *et al*., 2012), whilst explicitly considering the influence of wider catchment land use on such factors. This understanding may help establish the ultimate efficacy of such measures for protecting and improving fish habitat, which is often the key economic impetus for riverine habitat restoration (Battin *et al*., 2007).

Establishing likely ecological changes elicited within stream communities in response to modifications of riparian land use may prove crucial for assessing their ultimate utility as an adaptive management strategy. Riparian buffer strips may act to reduce in-stream secondary production, food supply to fish, and ultimately fish production; if this is the case, adaptation schemes may only be valuable in streams where salmonid populations would otherwise be greatly reduced or completely expatriated as a result of climate change. If increased terrestrial resource subsidies supplied to streams are, however, able to offset decreases in autotrophic production, or even increase food supply to fish in restored streams, they may have a much wider utility. Such measures may then be able to limit both thermal and metabolic costs to salmonid populations, and the food webs of which they form a part. Though time constraints negate the ability to implement and monitor the consequences of various adaptation schemes in real time, surrogates for a range of potential restoration outcomes exist in many catchments worldwide, due to differential management of stream riparian zones within individual sub-catchments. The research described in this thesis aimed to utilise such surrogates to investigate likely community and trophic consequences of differential catchment tree cover, and whether such changes had resultant impacts on salmonid production.

1.2 Aims and Hypotheses

The overall aim of the research presented in this thesis was to assess potential compositional, functional and trophic changes in stream communities likely to accompany variations in riparian tree cover in upland catchments. Theory and empirical evidence predicts that increased riparian tree cover should reduce the quantity of solar radiation available at the streambed, reducing primary production by in-stream autotrophs, and potentially limiting secondary production by aquatic consumers. The supply of terrestrial resource subsidies typically co-varies with catchment tree cover, and therefore has the potential to offset these decreases. Such changes would likely modify stream community structure and energetics, however, switching food webs currently based predominantly on autotrophic production to ones heavily reliant on heterotrophic subsidies. Using catchments with differential tree cover, this series of studies tested the overarching hypothesis that animal communities in streams with increased catchment forest cover are relatively more dependent on terrestrial resources than those in treeless catchments, due to increased allochthonous inputs. This investigation sought to establish whether such changes were evident, and, if so, whether they were dependent on wider catchment land use influences. Ultimately, the research aimed to assess if differences in catchment tree cover acted to alter salmonid density and biomass in stream habitats, as a result of community-wide changes in food webs supporting these species:

Chapter 2 investigates the role of riparian land use in influencing stream macroinvertebrate community composition and terrestrial subsidy dependence. Using 24 streams representing four distinct land use types, this chapter tests the specific predictions that (i) streams draining deciduous woodland would be characterised by increased abundances of leaf-shredding invertebrates; (ii) resource use in invertebrates in deciduous woodland streams would reflect terrestrial production more than in grassland streams; and (iii) riparian deciduous 'buffers' would approximate the effects on invertebrate composition and resource reliance of more extensive catchment woodland.

Work presented in Chapter 3 used a subset of the study streams to assess how catchment tree cover affected Coarse Particulate Organic Matter (CPOM) availability and macroinvertebrate biomass dynamics. Testing the overall hypothesis that streams draining contrasting land use support functionally and compositionally different macroinvertebrates communities linked to different energetic pathways, three specific predictions were evaluated: (i) total macroinvertebrate biomass and density should be increased in streams draining more extensive deciduous woodland, largely determined by increased contributions by functional groups linked to detrital processing (Filterers and Shredders); (ii) enhanced macroinvertebrate biomass should be driven by terrestrially-derived resources in the form of benthic CPOM; and (iii) streams with riparian buffer zones of deciduous trees would have macroinvertebrate biomass, density and CPOM standing stock levels intermediate between streams in more extensive deciduous woodland and open moorland.

Chapter 4 reports a study that aim to simulate subsidy inputs likely to accompany increasing tree cover in restored streams. Using Before-After-Control-Impact pairs, the effects of supplying reaches in treeless moorland catchments with quantities of leaf litter equivalent to those entering forested streams during autumn and winter were assessed. Here, predictions were that increasing inputs of such subsidies in these stream would (i) increase biomass and density of macroinvertebrate consumers, (ii) alter community functional composition, favouring taxa adapted to process and assimilate detrital leaf material, and (iii) increase incorporation of terrestrially derived organic matter into tissues of taxa representing various functional groups.

Chapter 5 aims to integrate themes of the previous chapters in the context of consequences of riparian land use for fish production, using surveys based on quantitative electrofishing. This study tested the hypothesis that increasing broadleaf cover in the riparian zone affects salmonid production, with effects mediated by food availability, in the form of stream macroinvertebrates (Chapter 3). Specific predictions were that (i) salmonid biomass, density and individual size would reflect available stream macroinvertebrate biomass, being greatest in deciduous woodland, lowest in conifer, and intermediate in moorland and buffer strip streams (Chapter 3); (ii) the use of terrestrial of terrestrially-fixed organic matter by *Salmo trutta* populations would be increased at streams with deciduous cover, compared to those draining moorland; and (iii) the use of terrestrial production by *Salmo trutta* populations would track that of local macroinvertebrate communities - to which trout should be trophically connected.

Finally, in Chapter 6 the general implications of the evidence presented in the thesis for understanding and applying climate adaptation strategies focused on riparian zone management is considered.

1.3: Study Area - The Brecon Beacons National Park

The research was carried out in streams located in and around the Brecon Beacons National Park, South Wales, UK (51° 51' 46”' N, 3° 22' 41" W). Climate in the area is typical of Northwest Europe, with relatively high rainfall and mild temperatures, due to maritime influences. Met Office data for Wales report mean minimum temperatures in February (coldest month) of 1.1 °C and mean maximum temperatures in July (warmest month) of 19.1 °C for the 30 year period 1971 - 2000. Mean annual rainfall for the same period was 1,433 mm, though high ground may receive up to 2,500 mm of rainfall per year (Thomas and Williams, 2002). The underlying geology is relatively homogeneous and consists of Devonian Old Red Sandstone (Barclay *et al*. 2005), though this gives way to Carboniferous limestone and millstone grit in some areas (George, 1970). This geology, combined with brown earth, gleys and occasional peat soils, ultimately produce a radial drainage of mostly unpolluted headwaters that are circumneutral (pH: ~6.5 – 7.5; conductivity: ~20 – 400 µS; Ca^{2+}: ~5 – 40 mg l^{-1}) and mainly oligotrophic (NO_3-: ~1 – 10 mg l^{-1}; PO_4^{3-}: ~0 mg l^{-1}). Due to the uniform geology, much of the topography is undulating: the high point is 886 m, while over half the area is above 300 m (Thomas and Williams, 2002).

The area is largely rural; the dominant land uses are agriculture and commercial forestry. Agricultural land comprises expanses of rough moorland, used for sheep grazing, and smaller areas of enclosed improved pasture, typical of land use practices in upland habitats throughout the UK. Commercial forestry covers slightly less than 10 % of the total area of the National Park, around 12,000 ha, and consists of non-native conifer species, principally Sitka spruce (*Picea sitchensis*), Norway spruce (*Picea abies*) and Japanese (*Larix kaempferi*), and hybrid (*Larix x marschlinsii*) larch (Thomas and Williams, 2002). Native deciduous woodland once formed the climax vegetation up to an elevation of 600 m, though this is now represented by remnant forest fragments (comprised principally of oak *Quercus* spp., alder *Alnus glutinosa*, birch *Betula pendula*, and ash *Fraxinus excelsior*) totaling around 5000 ha, less than 4 % of the total land area (Thomas and Williams, 2002).

The study area contains the headwaters of the majority of the major South East Wales river systems, including those of the Taff and Usk, with upper tributaries of the Tawe and Neath also draining Western areas. The wider catchments of these river systems have been greatly modified from their original state over timescales ranging from hundreds (e.g. urbanization and heavy industry: Learner *et al*., 1971; Scullion and Edwards, 1980; Thornton and Walsh, 2001) to thousands of years (e.g. deforestation and land use change: Thomas and Williams, 2002; Williams and Duigan, 2009). As a result of such extensive change, particularly industrial impacts during the 19th and 20th Centuries, it was estimated that by the early 1970s around 60 % of the rivers within urbanized downstream areas were "grossly polluted or of doubtful or poor quality" (Scullion and Edwards, 1980). Signs of ecological recovery are now evident, however, following industrial decline from the mid-20th Century onwards (Thornton and Walsh, 2001). Such streams present a case study for temperate headwater stream restoration in similarly industrially degraded catchments.

The area described above was specifically chosen for use in this study based on its high number of low-order streams with varying catchment land use, allowing hypotheses to be tested using stream-level replication. The area contains streams draining treeless moorland catchments, those supporting narrow "buffer strips" of riparian broadleaf cover, and others with larger areas of remnant deciduous woodland. Land use patterns also allowed for investigation of the influence of catchment conifer cover, which is likely to be an important factor affecting streams and rivers ecosystems across much of upland Britain: it is estimated that > 20 % of all the land in Wales above 200 m is currently afforested with exotic conifers, and that around 10 % of Welsh rivers have plantations within their catchment (Williams and Duigan, 2009). As such, these streams offer a model for potential restoration outcomes that could be instigated in similar upland areas across much of Britain and Western Europe. Due to homogeneous geology, streams within the area allow for investigation of these land use effects largely free from other potentially confounding factors such as differential pollution or acidification: underlying sandstones and limestones act to buffer streams against effects of acid deposition, a factor affecting many other upland areas across Wales (Weatherly and Ormerod, 1987; Kowalik *et al*., 2007).

The chosen river systems historically supported salmonid populations, including both resident brown trout and anadromous sea trout (*S. trutta*), along with anadromous Atlantic salmon (*S. salar*). Low-order upland streams in the area are of particular importance due to their use as spawning grounds by these species (Turnpenny and Williams, 1980). Additionally, rivers upstream from major pollutant inputs within the area are biologically diverse, particularly with regard to mayfly (Order: Ephemeroptera), stonefly (Order: Plecoptera) and caddisfly (Order: Trichoptera) taxa (Learner *et al*., 1971), and, as such, may be inherently worthy of conservation. Resident brown trout are currently present within most headwater streams across the area, though, due to extensive downstream barriers to migration, anadromous populations are now typically absent from most catchments (Wu *et al*., 1996; Russell *et al*., 1998). Whilst measures are in place to re-instate salmonid access to these streams, climate change presents an additional future threat to such re-establishing populations. Recent work has demonstrated that impacts of increased temperature are already beginning to manifest in similar streams: the Llyn Brianne experimental catchments, which lie approximately 30 km Northwest of the Brecon Beacons, and at a similar altitude, have seen mean temperature increases of between 1.4 – 1.7 °C over the last 25 years (Durance and Ormerod, 2007). Concurrent ecological impacts in these streams have also been documented, with macroinvertebrate communities responding strongly to climatic conditions during winter. Such streams could therefore take precedence for conservation in light of climate change; they may be among the first within the UK to experience negative consequences as a result of changing thermal and hydrological regimes. Adaptation measures within such streams therefore merit priority, due to the potential vulnerability of such environments, and their current provision of a wealth of economically important ecosystem services to downstream catchments, including fish production and drinking water supply.

All investigations carried out as part of this research used 24 mainly second to third order streams (Figure 1.1) or a smaller subset of these sites (see Table 2.1 for geographical and land use data for all sites). Study streams represented four distinct land use categories (each with n = 6 replicates) of contrasting riparian and wider catchment tree cover: treeless moorland sites with no broadleaf cover in their riparian zones or wider catchment (Moorland; MO); streams in moorland/grassland with narrow (mean upstream width: ~15 – 60 m) riparian broadleaf "buffer strips" (Buffer; GB); catchments with wider (mean upstream width: ~ 75 – 220 m) remnant deciduous woodland cover (Deciduous; DE); and catchments dominated by exotic conifer plantations, though with riparian broadleaf buffer strips (Coniferous; CB) .

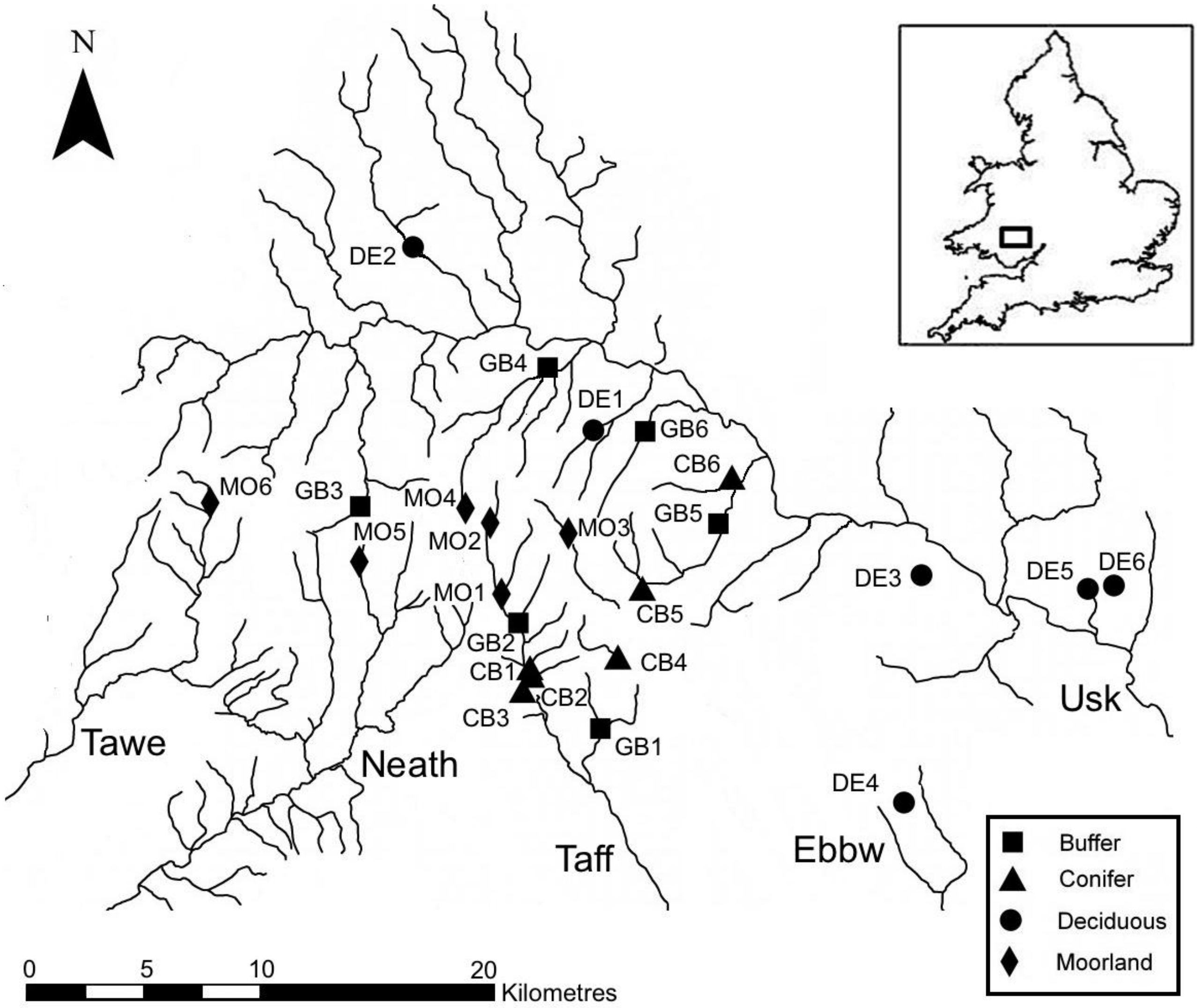

Figure 1.1: Map showing the geographical distribution of the 24 upland South Wales streams sampled as part of this study (some study sites were located on smaller side-tributaries, which are not displayed at this scale). Major river systems are labelled. The location of the study area within England and Wales is indicated (inset).

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Chapter 2: Effects of riparian land use on macroinvertebrate community structure and function in temperate, upland streams

2.0: Summary

1. Climate change is predicted to affect temperate, upland streams ecosystems by altering thermal regimes and discharge. Adaptation is widely advocated, particularly restoration of riparian tree cover, but functional effects on stream communities are still poorly quantified.

2. To test three hypotheses about variations in community composition, functional group representation and resource use in relation to riparian land use, macroinvertebrates were collected from 24 streams in the Brecon Beacons (Wales, UK) draining (i) open moorland; (ii) moorland/grassland with deciduous riparian zones; (iii) deciduous woodland and (iv) conifer forest with deciduous riparian zones. In addition to taxonomic identity, samples were assessed for variations in C and N stable isotopes to appraise variations in terrestrial resource use across land uses.

3. Invertebrate composition did not vary between streams in moorland with or without deciduous riparian zones. However, streams draining more extensive deciduous woodland had significantly greater numbers of "shredding" detritivore taxa, primarily the amphipod crustacean *Gammarus pulex*. Streams in conifer plantations had a greater proportion of grazing taxa and predatory Plecoptera than most other land use types. Communities in marginal habitats were more widely affected by land use than those in fast-flowing riffles.

4. Despite apparently affecting functional guild composition by increasing relative Shredder abundance, stable isotope analysis revealed that terrestrial resource use by all functional guilds was mostly split evenly between terrestrial and aquatic sources. Roughly 50% of resources assimilated by all macroinvertebrate functional groups and across all land uses were of terrestrial origin.

5. These results confirm that riparian deciduous trees can modify invertebrate assemblages and function in temperate, upland headwaters, but only where cover is extensive. Moreover, riparian land-use had no effects on the balance between allochthonous and autochthonous resource use by any functional groups. This implies that either allochthonous sources are underestimated in moorland catchments and overestimated in deciduous catchments, or that local riparian subsidies in upland streams are swamped by wider catchment effects or downstream export.

2.1: Introduction

Rivers worldwide are among the most sensitive of all ecosystems to climate change, due to their dependence on the hydrological cycle and atmospheric thermal regimes, and the potential for interactions between climatic factors and existing anthropogenic stressors (Dudgeon *et al*, 2006; Ormerod *et al.*, 2010). Upland streams are particularly liable to increasing temperatures due to their low thermal mass (Cassie, 2006) with impacts likely upon their predominantly cool-water organisms (Durance and Ormerod, 2007). Climate change effects on these systems also pose risks to the ecosystem services provided by rivers. For example, upland streams often support spawning by economically important fishes and subsidise food webs both downstream and in the riparian zone (Vannote *et al.*, 1980; Nakano and Murakami, 2001; Wipfli, 2005). Upland stream macroinvertebrates also form an important pathway linking primary production and detrital breakdown to higher trophic levels, with consequences for nutrient cycling and fish production (Malmqvist, 2002). These examples involve fluxes of matter and macronutrients, but the effects of catchment land use on these ecological processes are less well understood than those involving thermal regimes or run-off (Broadmeadow and Nisbet, 2004; Broadmeadow *et al.*, 2011).

Concerns about the sensitivity of streams and rivers to climate change have prompted consideration of adaptation measures to minimize adverse effects. For example, in temperate catchments where native forest has been removed, restoration of riparian tree cover is increasingly advocated (Battin *et al.*, 2007; Ormerod, 2009; Palmer *et al.*, 2009; Seavy *et al.*, 2009). Empirical and modeling evidence has demonstrated the capacity of "buffer strips" of riparian tree cover to moderate stream temperature (Zoellick, 2004; Battin *et al.*, 2007; Broadmeadow *et al.*, 2011), whilst offsetting negative effects of some catchment land use practices (Osbourne and Kovacic, 1993; Broadmeadow and Nisbet, 2004). If successful, the restoration and protection of riparian trees could therefore increase resilience to climate change (Hulme, 2005; Ormerod, 2009).

Although the effects of riparian tree cover on water temperature and diffuse pollutants have been investigated extensively, there is less information on potential energetic consequences for in-stream organisms and their trophic ecology. Shading induced by dense canopy cover in streams is likely to reduce autotrophic productivity by epilithic algae and aquatic macrophytes (Hill *et al.*, 1995; Kiffney *et al.*, 2003; 2004; Riley *et al.*, 2009), potentially limiting quantities of food resources for some consumer organisms. Conversely, increased inputs of terrestrial organic matter, primarily in the form of abscised leaf litter (Wallace *et al.*, 1997; Abelho, 2001) or terrestrial invertebrates (Nakano and Murakami, 2001), may subsidise other stream fauna. Any such shifts in available resources are likely to affect macroinvertebrate community structure, for example mediating changes between those taxa adapted to process terrestrial detrital material and those adapted to graze autotrophic epilithic biofilms. Understanding how such functional changes might manifest would not only provide important information on energetic links between land use and stream ecosystems, but could also guide the restoration of riparian zones in climate change adaptation (Naiman *et al.*, 2012). Potentially more important, there is a need to understand how smaller scale riparian ‘buffer’ zones of native woodland can mimic the effects of more extensive woodland cover in catchments managed for other purposes such as livestock grazing or production forest (Broadmeadow and Nisbet, 2004; Wahl *et al.*, 2013).

Assessments of the functional and compositional structure of macroinvertebrate assemblages in upland streams may indicate the major energetic pathways supporting communities in catchments of contrasting land use. Moreover, the stable isotopic composition of consumer tissues, particularly ratios of $^{12}C/^{13}C$ and $^{14}N/^{15}N$, can indicate community-wide dependence on isotopically distinct food resources from different origins (Post, 2002; Layman *et al*, 2012). When applied to different taxa within a food web, isotopic methods can therefore infer energy flow and trophic pathways (Layman *et al*, 2012). In streams and rivers, this includes tracing energy sources supporting macroinvertebrate consumers to their terrestrial (allochthonous) or in-stream (autochthonous) origins, as these are often isotopically distinct (Ishikawa *et al*., 2012). So far, however, such techniques have not been widely used in appraising possible energetic effects of contrasting riparian zones and their role in climate-change adaptation.

This study tests the hypothesis that streams in contrasting land use support functionally and compositionally different macroinvertebrate communities linked to different energetic pathways. Specific predictions were that (i) streams draining deciduous woodland would be characterised by increased abundances of leaf-shredding invertebrates and (ii) resource use in invertebrates in deciduous woodland streams would reflect terrestrial production more than in grassland streams and (iii) riparian deciduous ‘buffers’ would approximate the effects on invertebrate composition and resource reliance of more extensive catchment woodland. The work described here involved a field survey, with findings followed up with process studies and experimentation in Chapters 3 and 4, and potential consequences for salmonids in Chapter 5.

2.2: Materials and Methods

2.2.1: Study sites

Study sites were located in and around the Brecon Beacons National Park, South Wales, UK (51° 51' 46”" N, 3° 22' 41" W). Climate in the area is typical of Northwest Europe, with relatively high rainfall and mild temperatures, due to maritime influences: Met Office data for Wales as a whole show mean minimum temperatures in February (coldest month) of 1.1 °C and mean maximum temperatures in July (warmest month) of 19.1 °C. Mean annual rainfall is 1433 mm (Met Office, 1971-2000 averages). The underlying geology is relatively homogeneous and consists of Devonian Old Red Sandstone (Barclay *et al.* 2005), though this gives way to Carboniferous limestone and millstone grit in some areas (George, 1970). This geology, combined with brown earth, gleys and occasional peat soils ultimately produce a radial drainage of mostly unpolluted headwaters that are circumneutral (pH: ~6.5 – 7.5; conductivity: ~20 – 400 μS; Ca^{2+}: ~5 – 40 mg l^{-1}) and mainly oligotrophic (NO_3-: ~1 – 10 mg l^{-1}; PO_4^{3-}: ~0 mg l^{-1}). While temperate deciduous woodlands would have once formed the climax vegetation, the principal land uses are now rough sheep grazing and commercial forestry using non-native conifers.

Twenty-four mostly second to third order streams at elevations ranging from ~150 to 450 m were selected (Table 2.1) to represent four land uses: open moorland (hereafter Moorland; MO; n = 6); grassland with deciduous buffer (Buffer; GB; n = 6), where moorland catchments had narrow (~15 – 60 m) riparian strips of native deciduous woodlands mostly of alder *Alnus glutinosa*, birch *Betula pendula*, ash *Fraxinus excelsior* and oak *Quercus* spp.; deciduous woodland (Deciduous; DE; n = 6), where catchments still had relatively extensive areas of remnant deciduous woodland in the riparian zone (width ~ 75 – 220 m), though with grassland/moorland beyond; coniferous buffer (Coniferous; CB; n = 6), where catchments were dominated by exotic conifer plantations of mostly sitka spruce *Picea sitchensis*, with deciduous trees in the riparian zone (~ 15 – 65 m).

2.2.2: Catchment and reach-scale land use

Catchment land use data were obtained using ArcGIS (version 9.2; ESRI, 2009). The *Arc Hydrtools* package (version 9; Center for Research in Water Resources, University of Texas, TX, USA) was used to determine catchment area, which was then combined with the Countryside Council for Wales' habitat land-cover map (Countryside Council for Wales, 2004) to apportion land use by percentage cover. Riparian buffer lengths and widths were estimated at 100m intervals along each stream using Google Earth (Version 5.2; Google, Inc., 2012), which was also used to determine site elevations and distance from source data.

2.2.3: Water chemistry and habitat physiography

Fieldwork began in May-June 2010: stream widths and depths were measured at four 10m intervals centred on the sampling reach (Table 2.1). To assess potential differences in water chemistry among land uses, water samples were collected by grab sampling during base-flow in June. Ionic composition was quantified and analysed respectively using (a) inductively coupled plasma mass spectrometry (Thermo Elemental X-Series ICP-MS; Thermo Fisher Scientific, Inc.) for cations, after filtration at 0.45 μm and acid fixation, and (b) ion chromatography for anions (Dionex DX-80 Ion Analyser; Thermo Fisher Scientific, Inc.). In addition, pH, conductivity and total dissolved solids (ppm) were assessed at each site immediately following a storm event in October 2011 using a Hanna HI 98129 low-range pH/Conductivity/TDS Tester (Hanna Instruments, Ltd.) on three replicate samples per site. Values of pH are likely to be at their most extreme during high flow following periods of increased precipitation, and any associated acid episodes can influence acid sensitive taxa (Soulsby, 1995; Kowalik, 2007).

2.2.4: Macroinvertebrate community and functional group composition

During May-June 2010, benthic macroinvertebrates were collected from a 30 m reach at each site by two separate kick-sample (D-frame kick net: net mesh 1 mm), one each in riffles (2 minutes duration) and marginal habitats (1 minute duration). This standardised procedure is likely to collect around 70 % of species present at any one site and sufficient to detect difference among similar hillstreams (Bradley and Ormerod, 2002). Separate riffle and marginal samples allowed for collection of a more representative species pool at each site, as well as revealing any differences in communities in these contrastingly eroding/depositing environments where CPOM might accumulate (Bradley and Ormerod, 2002). Samples were preserved in 70 % ethanol, and returned to the laboratory for processing. Each sample was sieved though a 500 μm mesh and transferred to a sorting tray, where all macroinvertebrates were removed. Collected invertebrates were then sorted and identified as far as was practically feasible: most taxa were identified to species or genus, except Diptera (Athericidae, Ceratopogonidae, Chironomidae, Pedicidae, Simuliidae, Tabanidae, Tipulidae) and selected Coleoptera (Dytiscidae, Gyrindiae, Scirtidae), which were identified to family, and Annelida, which were identified to subclass. Ephemeroptera samples collected from marginal areas at site MO2 deteriorated during storage and could not be accurately identified, and this site was excluded from some analyses.

Following identification, taxa were assigned to one of five functional feeding groups, according to the classification of Cummins and Klug (1979): “Shredders” are adapted to process coarse particulate organic matter (CPOM: principally decaying leaf litter and riparian grasses); “Grazers” are primarily dependent on in-stream primary production, predominantly epilithic algae; “Collector-Gatherers”, referred to as detritivores under some classifications (Moog, 1995), utilise benthic fine particulate organic matter (FPOM); “Filterers” obtain suspended materials from the water column; “Predators” capture and consume other animal taxa. Moog (1995) provides a database recording the predominant feeding strategy in most European stream invertebrates; this reference base was used here, supplemented by information from Meritt and Cummins (1996), and Hauer and Lamberti (2006).

2.2.5: Stable isotope sampling and sample processing

Dual stable isotopic assessments of $\delta\,^{13}C$ and $\delta\,^{15}N$ in macroinvertebrate tissue were used to assess variations in terrestrial/aquatic resource use in each macroinvertebrate functional group, across different riparian land use categories in combination with Bayesian mixing models. These models provide estimates of the relative importance of terrestrial versus in-stream organic matter to macroinvertebrate diets, where these two resources are isotopically distinct. Such information can therefore help elucidate resource use patterns in stream taxa, and allow for the flow of terrestrial organic matter through these ecosystems to be traced.

Samples for stable isotope analysis were collected twice from each study site in May - June 2010 and again during January 2011, respectively. These periods were expected to reveal any variations in relative terrestrial versus aquatic resource use in the study streams over the annual cycle, due to large-scale terrestrial subsidy inputs during autumnal leaf-fall. Benthic macroinvertebrates for isotopic analysis were collected from a 30m reach at each site using kick samples (net mesh 1 mm) that were sorted on the bankside, and dominant macroinvertebrate taxa removed. Larger, later-instar individuals were preferentially collected, to minimise any effect of ontogenic diet shifts in sampled taxa (Dobson and Hildrew, 1992). All samples were transferred to screw-top plastic vials and frozen at -18 ºC within 8 hours of collection and stored until processing began. Aggregate samples of Coarse Particulate Organic Matter (CPOM), mostly decaying broadleaf litter or riparian grasses, representing terrestrial production, were collected from the streambed at each site using kick sampling. In-stream primary production was similarly represented by benthic epilithic algae (hereafter, epilithon), which was scraped from rocks within the sampling reach using a knife. Samples were frozen as above.

Following thawing, macroinvertebrate samples were rinsed with DH_2O and transferred to a sorting tray. Each invertebrate was then assigned to a Functional Feeding Group (FFG) using the scoring system outlined in Moog (1995), as above. The dominant Collector-Gather taxa collected at the study streams, *Baetis spp*. ephemeroptera and *Leuctra spp*. plecoptera, were also assigned equally to another functional group (Grazers for *Baetis* and Shredders for *Leuctra*; Moog, 1995). As these resource acquisition methods were likely to be more pronounced in the larger individuals collected for isotopic analysis (Dobson and Hildrew, 1992), this grouping was split, resulting in four major guilds being used in subsequent isotopic analyses: Grazers were therefore represented in the study streams by Heptageniidae and Baetidae ephemeropterans, Shredders were represented by Leuctridae and Nemouridae plecopterans, along with the amphipod crustacean *Gammarus pulex*; Filterers were represented by Hydropsychidae (Trichoptera) and Simullidae (Diptera); Predators were represented by Perlidae and Chloroperlidae (Plecoptera), and Rhyacophilidae (Trichoptera).

Samples of CPOM and riparian vegetation were rinsed with DH_2O and non-target materials such as macroinvertebrates were removed using forceps. All consumer and basal resource samples were then transferred to glass vials and freeze-dried at -60 ºC for 48 h. Dried samples were ground until homogenized and weights required for analysis (1 ± 0.2 mg for invertebrate tissue, 3 ± 0.2 mg for autotrophic material) were packaged within tin capsules. All samples were then submitted to the University of California, Davis Stable Isotope Facility for dual $\delta\ ^{13}C$ and $\delta\ ^{15}N$ analysis using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, U.K.) Where reported, stable isotope values are given in delta (δ) notation, where quantities of each isotope are expressed as parts per thousand (‰) deviation from international standards (Vienna Pee Dee Belemnite for carbon and atmospheric air for nitrogen).

Preliminary analyses of data from site DE4 revealed that epilithic $\delta\ ^{15}N$ values were anomalously enriched (> 13 ‰ versus a mean value of 1.42 ‰ at all other sites), probably reflecting local drainage from land-fill, and excluded from all final analyses.

2.2.6: Physicochemistry and land use

All statistical analyses were conducted in R Version 2.15.2 (R Development Core Team, 2012). Prior to further analysis, sites were ordinated on physicochemistry and land use using Principal Component Analysis (PCA) respectively of (i) water chemistry (pH, conductivity, anion and cation concentrations); (ii) stream physical character (elevation, mean depth and width, catchment area and distance from source); and (iii) land use (percentage broadleaf deciduous, coniferous and grassland cover, upstream buffer strip length and mean buffer strip width). Differences among land use categories on PC1 and PC2 scores from each ordination were then assessed using one-way ANOVAs.

2.2.7: Macroinvertebrate community composition

Differences in community composition between land use categories were visualised using Non-Metric Multidimensional Scaling (NMDS; Kruskal, 1964). NMDS is a robust ordination method that iteratively assigns samples to locations in low dimensional space according to their overall dissimilarity, based on a distance metric. Inter-point distances in the final ordination then reflect the ranked dissimilarity of the original samples (Kruskal, 1964; Clarke and Warwick, 2001). The goodness of fit between distances apparent in the generated plot and the ranked dissimilarities are assessed via a "stress" score, a lower value of which indicates better agreement between the two, and hence more reliable graphical interpretability: values > 0.3 are generally deemed problematic (Zuur *et al*. 2007). The required dissimilarity matrices were constructed using the Bray-Curtis index, due to the ability of this metric to accommodate zero-skewed species composition data (Clarke and Warwick, 2001). As there was a large range of abundances (0 > 400) in the data sets, all values were fourth root transformed prior to calculation of Bray-Curtis values, to down-weight the influence of the most abundant taxa and gain a truer, community-wide evaluation of site-to-site differences (Clarke and Warwick, 2001). Riffle and marginal invertebrate communities were first analysed separately to assess any potential differences arising from marginal habitat structure between land use categories, and were then combined to investigate total dissimilarity. All NMDS ordinations were carried out using the *metaMDS* function within R's *vegan* package (version 2.0-5) and were based on 500 iterations (Oksanen *et al*., 2012).

Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson, 2001) was used to assess whether differences in community composition between land use types were statistically significant. This non-parametric alternative to MANOVA compares groups in multivariate space based on dissimilarities (here Bray-Curtis) and generates *p* values via a permutation procedure. PERMANOVA makes few major assumptions about the data set, and does not require multivariate normality (Anderson, 2001). PERMANOVA is sensitive to unequal variance (dispersion) between treatments, however, and this may confound significant differences in multivariate means (centroids) between groups. In order to rule out potentially confounding effects of differential dispersion, PERMANOVAs were followed by *betadisper* tests (Anderson, 2006), a multivariate analogue of Levene's test for homogeneity of variances.

An overall PERMANOVA was used to investigate whether land use type had a significant effect on community composition within each sample type, with group-by-group differences then assessed via pairwise tests where the overall test was significant. All data were fourth root transformed prior to analysis, as above, and tests were carried out using the *adonis* function within *vegan* based on 4999 permutations (Oksanen *et al.*, 2012). Where PERMANOVAs indicated significant differences, Similarity Percentage analysis (SIMPER; Clarke, 1993) was used to assess which taxa were principally responsible for pairwise group-to-group differences between land use categories.

2.2.8: Abundance, diversity and functional group representation

General Linear Models (GLMs) were used to assess variations in total macroinvertebrate abundance, diversity (assessed using Shannon Diversity Index scores) and FFG representation among land use categories. Where PCAs indicated significant variations among land use categories differed in water chemistry or physical variables (see Results), effects were controlled for where necessary. To establish whether any such physicochemical variations might confound potential effects of land use, dependent variables were first modeled against these abiotic covariates (mean pH, mean conductivity, PC1 scores from anion and cation data, elevation, mean depth, mean width, catchment area, distance from source), with stepwise deletion then used to remove all non-significant variables. Remaining significant terms for each dependent variable were included as covariates in each GLM carried out to test for differences between land use categories.

2.2.9: Stable isotope data analysis and mixing models

Initial intentions were to correct $\delta\,^{13}C$ values of invertebrate consumers and CPOM for lipid content using C:N ratios (Post *et al*. 2007): lipids are depleted in ^{13}C relative to proteins and carbohydrates (Tieszen *et al*., 1983), and $\delta\,^{13}C$ values derived from whole animals may be skewed by variable lipid content between individual organisms and study species when percentage lipid exceeds 5%. However, lipid correction led to unreliable mixing model dietary estimates (see below), as correction resulted in data points lying outside the convex hull implied by the sampled basal resources. This was likely due to epilithon values, which were uncorrected, as published correction factors for algal material composing epilithon were not available.Because of this, and as mean calculated $\delta\,^{13}C$ corrections would have been relatively small (+0.56 ± 0.83 and +1.77 ± 0.61 (mean ± 1 SD), for CPOM and macroinvertebrate consumers, respectively), uncorrected raw data were used in all mixing models.

Stable isotope data were treated initially using *R*'s SIAR *(Stable Isotope Analysis in R; version 4.1.3*) mixing model (Parnell *et al*., 2010). The *SIARsolomcmcv4* function was used to fit mixing models to estimate proportional contribution from terrestrial and in-stream production to consumer diets individually by site, functional feeding group and season. Mixing models were fitted for all sites where basal resources were isotopically distinct, but 10 sites were excluded where these overlapped or where consumers fell outside of the mixing polygons implied by basal resources and their associated error. All SIAR models were based on 500,000 iterations, with the first 50,000 discarded (Parnell *et al*., 2010). Trophic enrichment factors (TEFs) of 0.5 ± 0.5 ‰ for ^{13}C and 3.23 ± 1 ‰ for ^{15}N were assumed for primary consumers (Filterers, Grazers, Shredders) based on calculated mean difference between primary consumers and basal resources (see Section *4.2.8*). An additional trophic level of enrichment was added for Predators (i.e. TEFs of 1 ± 1 ‰ and 6.46 ± 2 ‰ were used for ^{13}C and ^{15}N, respectively). Ultimately, SIAR models were fitted for macroinvertebrate functional groups at 14 sites (GB, n = 3; CB, n = 4; DE, n = 3; MO, n = 4).

Variations in mean proportional contributions of terrestrial organic matter to consumer diets estimated by SIAR (hereafter, 'terrestrial resource use') were analysed using a General Linear Mixed Model (GLMM). Riparian land use, month of sampling and Functional Feeding Group, along with all possible interactions between these factors, were included as fixed effects. Site was included as a random term to account for potential non-independence due to repeated measures at each site through time. As all proportion data resulted in normally distributed, homoscedastic residuals, data were not transformed prior to analysis (Warton and Hui, 2011).

2.3: Results

2.3.1: Physicochemistry and land use

Principal component analysis (PCA) confirmed clear differences among site groups in land use (Fig. 2.1a) on both PC1 ($F_{3, 19} = 14.45$, $p < 0.001$) and PC2 ($F_{3, 19} = 10.75$, $p < 0.001$). PC1 scores (variance explained: 39.6 %) represented trends from moorland to broadleaves in the catchment or riparian zone, while PC2 scores (variance explained: 36.7 %) described trends from conifer to other land uses. On a pairwise basis, Deciduous vs. Buffer (Tukey's HSD: $p = 0.005$) and Moorland vs. Coniferous ($p = 0.001$) sites were separated on PC1, whilst Deciduous vs. Coniferous ($p < 0.001$) and Buffer vs. Coniferous ($p = 0.011$) were separated on PC2. Moorland vs. Deciduous sites were separated on both axes (PC1, $p = 0.017$; PC2, $p = 0.001$).

Other, potentially confounding, differences among site were less marked. Nevertheless, site types differed in both chemistry and physical character. Water quality PC1 (variance explained: 24.9 %; $F_{3, 19} = 4.834$, $p = 0.011$) represented increasing conductivity and major ions (Cl^-, $SO4^{2-}$, Na^+, K^+, Mg^{2+}, Ca^{2+}) and increased from Moorland to Deciduous sites ($p = 0.015$) and from Coniferous to Deciduous sites ($p = 0.018$) (Fig. 2.1c). Physical PC2 (Fig 2.1b; 29. 4 %; $F_{3, 19} = 10.55$, $p < 0.001$) reflected increasing altitude and stream depth at Moorland sites by comparison with both Buffer ($p = 0.001$) and Deciduous sites ($p < 0.001$).

2.3.2: Macroinvertebrate community composition

Macroinvertebrate community composition varied across land uses in riffle ($F_{3,22} = 1.7442$, p = 0.004), marginal ($F_{3,21} = 2.1634$, $p > 0.001$) and combined samples ($F_{3,21} = 2.116$, $p > 0.001$). Effects were strongest in riffle and combined samples, and between Moorland vs. Deciduous, Coniferous vs. Moorland and Coniferous vs. Deciduous sites (Table 2.2; Fig 2.2). Buffer sites were generally intermediate, although communities in marginal habitats differed between Deciduous and Buffer sites (Table 2.2). *Betadisper* tests indicated that differences between treatments across all sample types were not due to unequal dispersion between groups (Riffle: $F_{3,\ 19} = 0.1401$, p = 0.9347; Margin: $F_{3,\ 18} = 0.3255$, p = 0.8069; Combined: $F_{3,\ 18} = 0.0491$, p = 0.9851).

SIMPER analysis indicated that differences in community composition were due to community-wide changes in abundance, with no single taxon contributing > 7 % of the difference between any two land use categories (Table 2.3). The top five taxa responsible for differences in community composition among land use categories were relatively consistent across sample types, and represented a relatively small proportion of the total species pool. For example, differences between Deciduous sites and other land uses were principally driven by increased abundance of the shredding amphipod *Gammarus pulex*, decreases in the grazing ephemeropteran *Electrogena lateralis* and differences in the occurrence of *Leuctra* plecoptera (Table 2.3). Differences between conifer and other sites were mostly due to increased abundances of leuctrid and nemourid stoneflies, notably *Amphinemura sulcicollis* at the former.

Although riparian land use category did not significantly affect overall macroinvertebrate abundance or diversity, there were some significant variations in functional group representation (Table 2.4). In riffle samples, Shredders contributed more to communities at Deciduous sites than Buffer (Tukey's HSD: $p = 0.008$), Coniferous ($p = 0.006$) or Moorland ($p = 0.005$) sites (Table 2.5). In marginal habitats, communities at Deciduous sites contained a greater proportion of Shredders than all other land use categories (Buffer: $p = 0.030$; Coniferous: $p = 0.005$; Moorland: $p = 0.013$); Coniferous sites contained a higher proportion of Grazers ($p = 0.025$) and Predators ($p = 0.022$) than at Deciduous sites, and a lower proportion of Collector-Gatherers ($p = 0.024$) than at Moorland sites. Increased Shredder contributions at Deciduous sites by comparison with other land uses were still apparent when data from riffle and marginal samples were combined (Buffer: $p = 0.011$; Coniferous: $p = 0.004$; Moorland: $p = 0.008$).

2.3.3: Terrestrial resource use by macroinvertebrate functional groups

Contrary to prediction (ii), terrestrial resource use by macroinvertebrates did not vary significantly among riparian land use types overall ($F_{3, 95} = 0.416$, $p = 0.742$; Fig. 2.3), or when variations between months ($F_{3, 93} = 0.923$, $p = 0.433$) or FFGs ($F_{8, 87} = 0.620$, $p = 0.759$) were considered. Across all land use categories in both months, roughly 50 % (range: 33.1 - 75.8 %) of resources assimilated by all macroinvertebrate functional groups were of terrestrial origin (Fig. 2.3). When all land use categories were pooled, terrestrial resource use varied between functional feeding groups in ways that differed between months ($F_{3, 95} = 3.890$, $p = 0.012$). This effect reflected significantly increased terrestrial contributions to Grazer tissues in June ($p = 0.002$), but there were no other seasonal changes (Filterers: $p = 0.713$; Predators: $p = 0.998$; Shredders: $p = 0.892$: Fig. 2.4).

2.4: Discussion

Of the three predictions examined, only one was supported unequivocally: streams draining deciduous woodland had significantly more Shredders than other locations, and this contributed to significant variations in macroinvertebrate community composition among land uses. Contrary to expectations, there were no variations across land uses in functional group reliance on terrestrial resources. Nor were the effects of riparian buffers at these sites sufficient to mimic the effects on invertebrate communities of more extensive riparian woodlands. These outcomes provide only qualified support for the hypothesis that streams with contrasting riparian land use support functionally and compositionally different macroinvertebrates communities linked to different energetic pathways. Instead, 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)

Caution is required in the interpretation of non-experimental studies of this nature that are characterised by weak inference and risk of confounds. In this case, land use categories differed marginally on physicochemical criteria, and in particular treeless moorland streams were at higher elevations and were generally deeper than other land use types. However, the range over which these variables differed appeared insufficient to influence community composition: although moorland (MO) and buffer strip (GB) sites differed on physical criteria, they did not support different communities. Similarly, buffer strip (GB) sites and those draining larger areas of deciduous woodland (DE) differed with respect to water chemistry, but not in terms of overall macroinvertebrate community composition. Despite such potentially confounding influences, comparative studies such as this one provide a useful model for how streams respond to restoration of catchment tree cover, thereby increasing understanding of the resultant ecological changes (Naiman *et al*., 2012). This is particularly true where the decadal timescales involved in experiments manipulating riparian land use would be so long as to limit the use of experimentation, particularly where timely evidence is needed to inform management and climate change adaptation decisions.

There has been widespread advocacy in river research focused on water quality for sampling riffles to minimize the effects of any habitat variations among sites (Hilsenhoff, 1988; Chessman, 1995). However, where the focus is on biodiversity conservation or effects mediated through habitat structure, sampling a broader range of habitats can provide important information (Ormerod *et al*. 1993). Data from this study support the importance of investigating habitat-specific differences in community structure when assessing land use effects on stream ecosystems. Macroinvertebrate communities from marginal stream habitats were more strongly influenced by land use than those in riffles with respect to consumer functional group representation and overall community composition. The mechanism underlying these differences between marginal and riffle habitats are likely to lie in modification of the physical structure of marginal habitats by land use, with some streams having “softer” habitat features (i.e. vegetation at the water’s edge, debris dams) while others are dominated by tree roots, eroding banks or rock (Ormerod *et al*. 1993). Additionally, leaf litter and other terrestrial organic material often accumulate in marginal areas (Flores *et al*. 2013), with this likely to affect fauna from some functional groups. The shifts observed here from Grazers to Shredders in deciduous stream margins were consistent with this effect.

Despite changes in community composition across the study streams, resource use by macroinvertebrates in any functional group did not reflect riparian land use. This result is contrary to the expectation that resource availability should differ between deciduous woodland, grassland and conifer sites (Abehlo, 2001; Kiffney *et al.*, 2003; 2004). The stable isotopic results here are also contrary to the indication that there were more resources available for Shredders at deciduous sites. These findings suggest allochthonous sources may be underestimated in moorland catchments. This supports Leberfinger *et al.* (2011), who reported that stable isotope analysis indicated that shredding macroinvertebrates in open-canopy streams were heavily reliant on terrestrial organic matter, despite widespread availability of autotrophic resources. Moreover, the results of this study expand these findings to other functional groups, and suggest that a reciprocal pattern may exist, in that the importance of allochthonous organic matter may be similarly overestimated in streams within afforested catchments. Alternatively, any local riparian effects may be swamped by wider catchment effects or downstream export: there is evidence to indicate that even small reductions in catchment tree cover (~10 % deforestation in otherwise totally afforested catchments) weakens terrestrial-aquatic linkages (England and Rosemond, 2004). Resource use patterns may therefore reflect whole catchment land use, even where wider riparian land uses are extensive: in forested catchments very large areas of lateral tree cover may be needed continually offset resource subsidy losses to downstream reaches, particularly transport during high flow events (Wallace *et al.* 1995).

Conversely, observed resource use patterns may be mediated directly by invertebrate consumers, despite increasing availability of terrestrial organic matter with increasing catchment tree cover. Limited functional plasticity may have reduced the range of resource acquisition methods available to consumer taxa (i.e. morphological adaptations for rock scraping versus leaf fragmentation), for instance, leaving them unable to respond to differential resource availability across land use types. However, shredding taxa appeared to be deriving approximately half of their nutritional requirements from in-stream production, whilst grazing taxa often consumed large quantities of terrestrial organic matter, in contrast to resource use patterns typically assigned to these groups (Cummins and Klug, 1979). This may potentially be explained by differences in resource quality between terrestrial and in-stream production, with CPOM typically lower quality, being less macronutrient-dense than benthic epilithon in the study streams (see Section 4.4); macroinvertebrates often require elemental homeostasis with their total food sources (Hlaydz *et al.*, 2009), and CPOM alone may be insufficient to support growth and metabolism, particularly due to typically low Nitrogen content in this material. Shredding taxa may therefore have been ingesting and assimilating algal production often found attached to leaf litter (Hax and Golladay, 1993), whilst grazing taxa may have been supplementing their diets with fine terrestrial organic matter entrained within epilithic biofilms (Hamilton *et al.*, 2005). Diet switching observed in grazing taxa may have been due to increased availability of fine particulate organic matter (FPOM) facilitated by the breakdown of CPOM by shredding taxa during winter (Cummins *et al.*, 1989; Heard and Richardson, 1995). Evidence for increased dependence during summer (when in-stream production would typically be highest) may have been an artefact of isotopic tissue turnover in consumer tissues, with samples taken at any one time point likely representing a time-integrated measure of resource use over the preceding months (Hesslein *et al.*, 1993; Kaufman *et al.*, 2008).

The major management implication of these results arises from the apparent effects of deciduous woodland on community composition – but also from the importance of considering the extent of tree cover in riparian restoration or management. While narrow bands of riparian tree cover can moderate stream temperatures and attenuate diffuse pollution (Broadmeadow and Nisbet, 2004; Broadmeadow *et al*., 2011), more extensive tree cover has the potential to alter community composition and functional group representation. This is valuable evidence in illustrating how riparian restoration schemes might be tailored on a catchment-specific basis for desired restoration outcomes. Where the goal of management is to moderate thermal regimes while maintaining moorland land use, narrow buffer strips may be sufficient. In contrast, larger areas of catchment tree cover would be required to re-instate historical woodland stream communities and their strong links with terrestrial riparian habitats. At the same time, however, community-level effects of non-native conifers occurred apparently irrespective of the presence of deciduous buffer strips, suggesting that this management device might not deliver benefits in all circumstances (Ormerod *et al*. 1993; Broadmeadow and Nisbet, 2004).

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2.6: Tables and Figures

Table 2.1: Physical, Chemical and Land Use Characteristics of 24 sites used in investigations of land use effects on stream invertebrates.

Site	Latitude	Longitude	Mean pH	Mean Conductivity (µS)	Elevation (m)	Mean Width (m)	Mean Depth (cm)	Catchment Area (km^2)	Catchment Deciduous Tree Cover (%)	Upstream Buffer Length (m)	Mean Upstream Buffer Width (m)
CB1	51.802143	-3.437959	7.24	27	305	3.80	18.58	1.52	0.83	636	25.7
CB2	51.805484	-3.439536	6.87	25	293	2.95	20.0	1.52	1.07	289	9.5
CB3	51.795726	-3.446113	6.94	71	271	2.23	17.5	1.13	1.76	1138	21.9
CB4	51.811003	-3.378897	7.10	33	345	4.90	17.08	3.69	1.14	738	38.8
CB5	51.845202	-3.364456	7.06	30	389	6.70	24.76	6.62	0.71	1155	39.0
CB6	51.882940	-3.307550	6.82	79	161	4.30	18.56	6.67	3.71	3232	39.53
DE1	51.909325	-3.399013	7.14	101	253	4.38	19.08	4.42	16.83	1801	108.2
DE2	51.989194	-3.534207	6.65	81	251	1.70	13.42	1.06	18.88	926	88.5
DE3	51.849193	-3.161659	6.78	351	142	2.23	17.66	8.48	8.55	3715	74.65
DE4	51.746757	-3.178225	6.86	309	301	2.55	12.56	1.64	17.41	1160	102.5
DE5	51.843852	-3.047440	7.44	123	255	3.90	11.80	2.42	17.21	1107	220.5
DE6	51.846943	-3.031454	7.23	142	290	3.10	14.67	2.78	33.54	531	75.5
GB1	51.780906	-3.389626	7.08	74	289	4.45	14.17	4.90	1.22	869	25.8
GB2	51.827421	-3.446767	6.67	30	309	4.48	19.58	4.27	1.29	1323	14.9
GB3	51.873722	-3.56243	7.25	93	260	3.85	15.25	3.20	4.95	990	42.4
GB4	51.929562	-3.436339	6.99	58	164	4.70	16.54	7.22	4.65	4081	33.0
GB5	51.869681	-3.313687	7.08	45	203	4.68	12.41	2.99	3.00	1145	33.2
GB6	51.908379	-3.362074	6.94	64	214	4.15	22.25	8.50	6.56	2719	62.7

Table 2.1 Continued.

Site	Latitude	Longitude	Mean pH	Mean Conductivity (µS)	Elevation (m)	Mean Width (m)	Mean Depth (cm)	Catchment Area (km^2)	Catchment Deciduous Tree Cover (%)	Upstream Buffer Length (m)	Mean Upstream Buffer Width (m)
MO1	51.840551	-3.456573	7.10	29	340	4.23	23.30	3.23	0	0	0
MO2	51.868781	-3.467689	6.78	20	474	4.35	23.25	3.33	0	0	0
MO3	51.865707	-3.416319	7.79	44	465	3.38	19.50	3.66	0	0	0
MO4	51.876332	-3.489575	6.93	132	371	2.08	14.75	1.08	0	0	0
MO5	51.850042	-3.562145	7.18	91	396	3.48	19.58	3.60	0	0	0
MO6	51.872676	-3.667889	7.40	48	395	5.16	23.08	3.92	0	0	0

Table 2.2: 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 2.3 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 2.3: 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 2.2).

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 2.4: 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 2.5 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 2.5: Mean percentage contributions (± 1 S.E.) by different functional feeding guilds to total macroinvertebrate abundances in streams in South Wales draining different riparian land uses. Shared letters denote land use types where percentage representation did not differ significantly (Tukey's *post-hoc* comparisons following GLM: $p > 0.05$).

Functional Feeding Group	Land Use Type	Sample Type		
		Riffle	Margin	Combined
Collector Gatherer	Buffer	53.66 ± 9.74 a	37.89 ± 3.83 ab	49.50 ± 6.31 a
	Coniferous	42.45 ± 7.66 a	23.89 ± 7.14 a	34.88 ± 6.18 a
	Deciduous	31.25 ± 2.98 a	35.27 ± 8.02 bc	33.53 ± 5.49 a
	Moorland	47.30 ± 8.87 a	47.37 ± 7.14 ab	42.88 ± 6.60 a
Filterer	Buffer	4.66 ± 1.60 a	1.42 ± 0.71 a	3.68 ± 1.02 a
	Coniferous	8.95 ± 3.69 a	1.32 ± 0.67 a	5.69 ± 2.22 a
	Deciduous	8.52 ± 2.07 a	2.82 ± 1.13 a	6.11 ± 1.69 a
	Moorland	8.56 ± 6.95 a	1.25 ± 1.10 a	7.92 ± 6.67 a
Grazer	Buffer	33.67 ± 8.67 a	44.70 ± 6.44 ab	36.02 ± 5.19 a
	Coniferous	38.70 ± 8.27 a	59.21 ± 7.61 a	47.48 ± 6.52 a
	Deciduous	29.43 ± 8.09 a	27.19 ± 6.28 bc	27.81 ± 6.91 a
	Moorland	35.05 ± 7.59 a	41.32 ± 7.98 ab	39.54 ± 7.65 a
Predator	Buffer	4.72 ± 1.11 a	7.64 ± 1.02 ab	5.62 ± 1.01 a
	Coniferous	7.40 ± 1.51 a	13.21 ± 2.48 a	9.24 ± 1.51 a
	Deciduous	4.71 ± 1.57 a	4.14 ± 2.30 bc	4.52 ± 1.88 a
	Moorland	7.16 ± 2.27 a	5.64 ± 1.83 ab	6.46 ± 1.66 a
Shredder	Buffer	3.29 ± 1.40 a	8.34 ± 4.17 a	5.18 ± 1.62 a
	Coniferous	2.50 ± 2.23 a	2.37 ± 1.05 a	2.71 ± 1.77 a
	Deciduous	26.10 ± 9.33 b	30.58 ± 9.88 b	28.02 ± 9.49 b
	Moorland	1.94 ± 0.99 a	4.42 ± 1.77 a	3.21 ± 1.45 a

2.6.1: Figure Legends

Figure 2.1: Principal Component Analyses of variations in a.) land use, b.) physical character and c.) water quality among streams in South Wales draining different land uses: Buffer (solid convex hulls; ■), Coniferous (dashed convex hulls; ▲), Deciduous sites (dotted convex hulls ●) and Moorland (dot-dash convex hulls; ◆).

Figure 2.2: 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 convex hulls; ■), Coniferous (dashed convex hulls; ▲), Deciduous (dotted convex hulls ●) and Moorland (dot-dash convex hulls; ◆) sites.

Figure 2.3: 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 2.4: Estimated proportional terrestrial resource use in each of four macroinvertebrate functional groups collected for stable isotope analysis in streams in South Wales, averaged across all land use categories and two sampling occasions. Values presented are mean proportional terrestrial resource use ± 1 SE derived from SIAR. Asterisks (**) indicate seasonal differences significant at $p < 0.01$.

Figure 2.1:

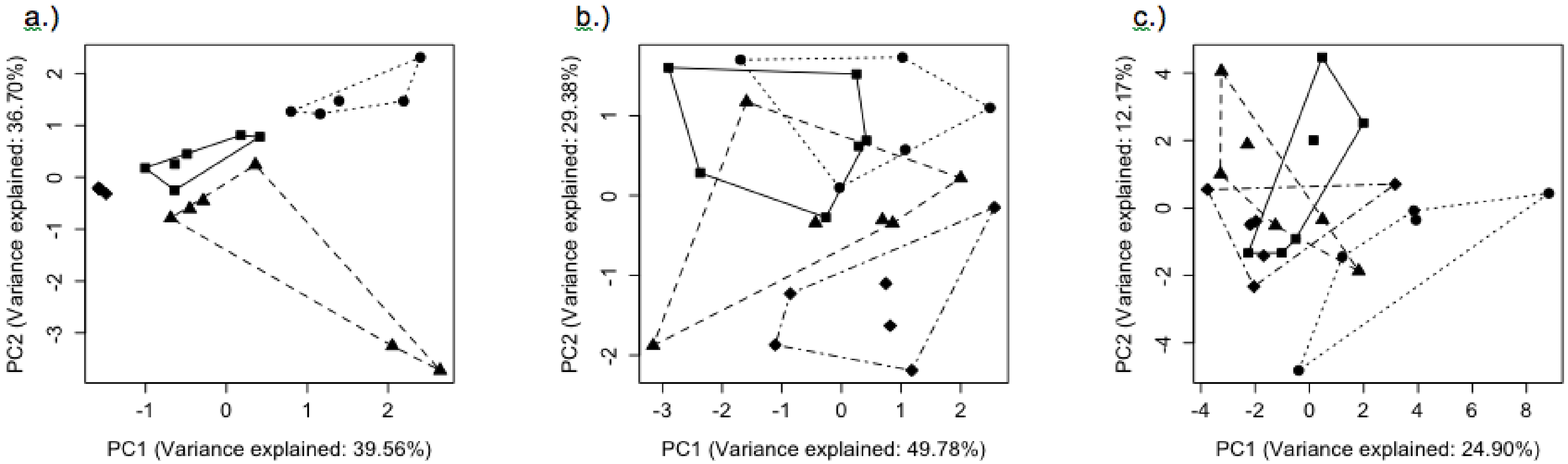

a.)
PC2 (Variance explained: 36.70%)
2
1
0
-1
-2
-3
-1
0
1
2
PC1 (Variance explained: 39.56%)
b.)
PC2 (Variance explained: 29.38%)
1
0
-1
-2
-3
-2
-1
0
1
2
PC1 (Variance explained: 49.78%)
c.)
PC2 (Variance explained: 12.17%)
4
2
0
-2
-4
-4
-2
0
2
4
6
8
PC1 (Variance explained: 24.90%)

Figure 2.2:.

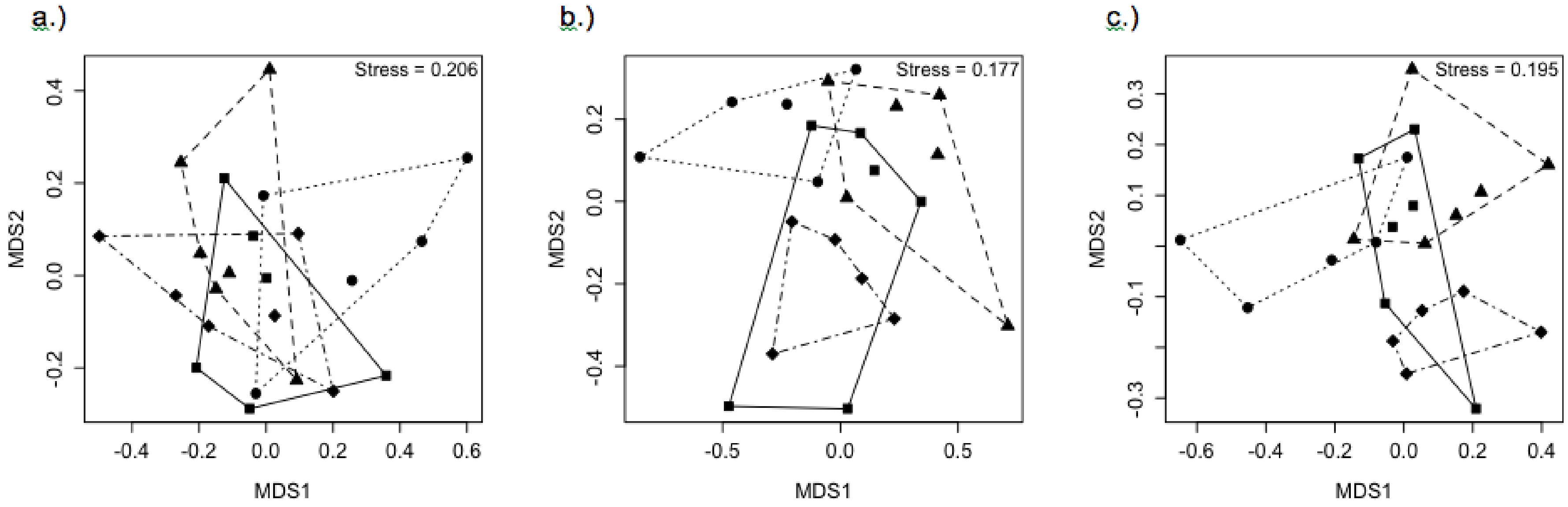
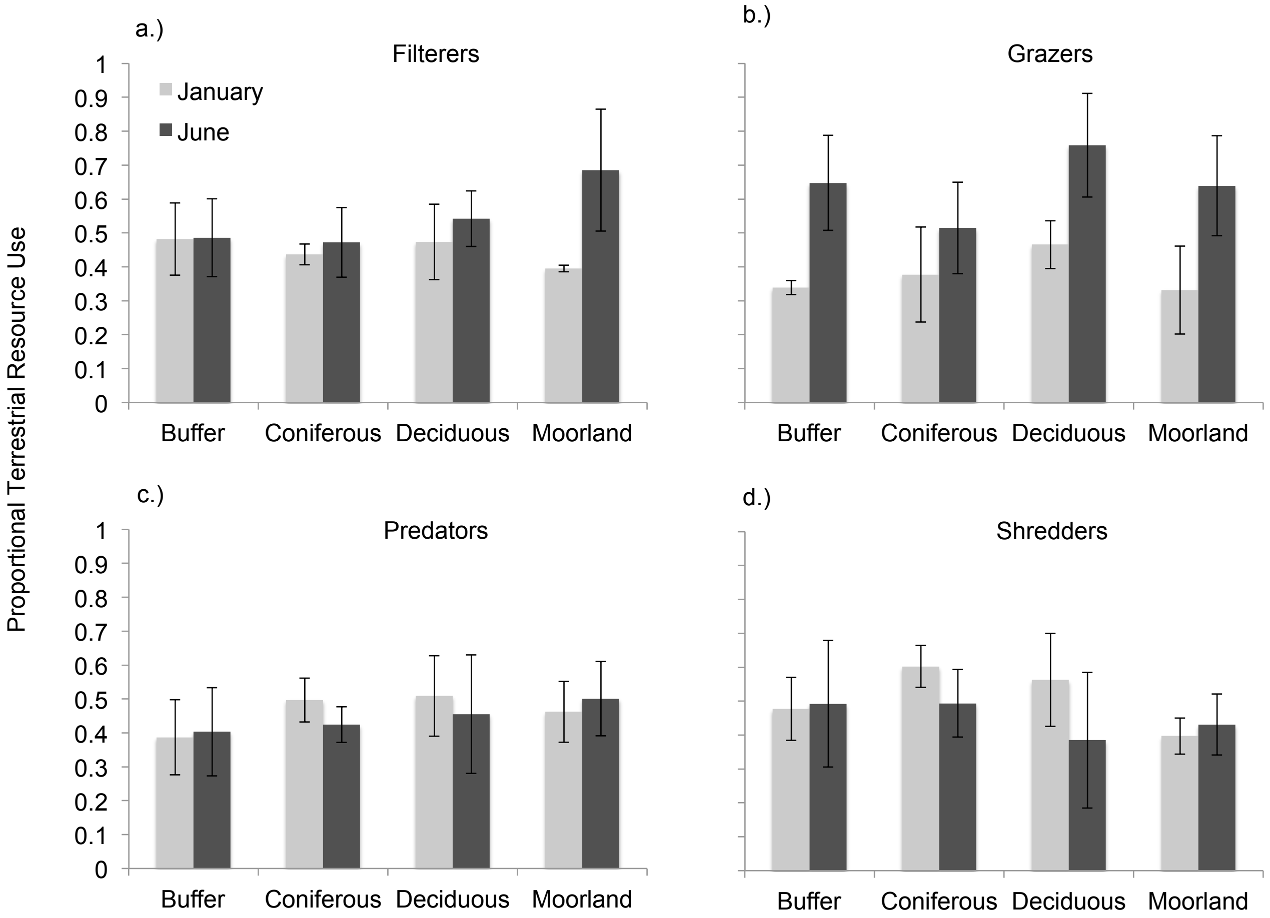
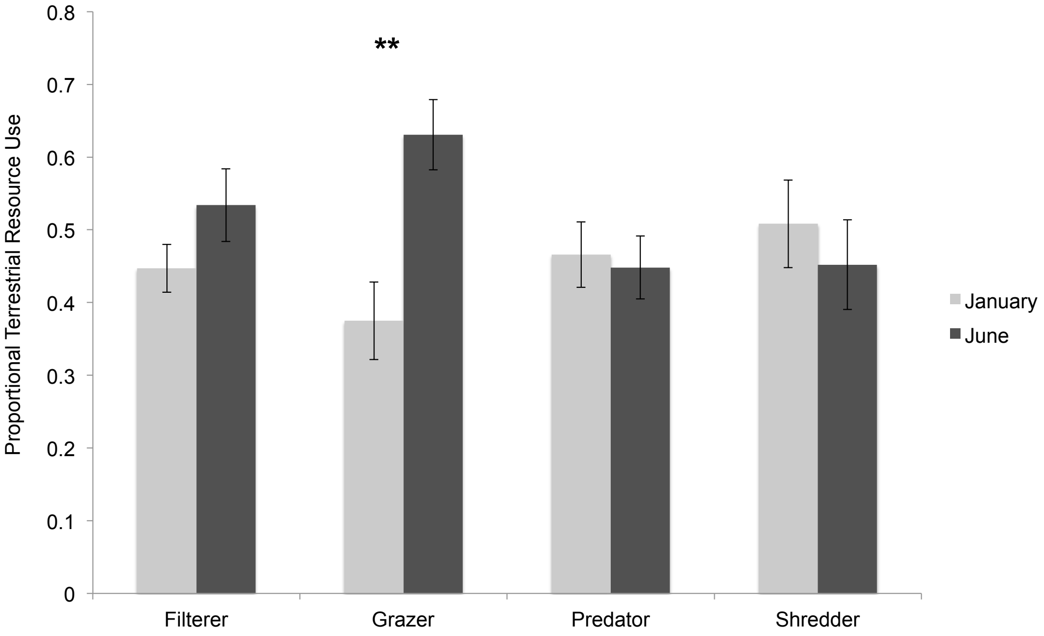

a.)
Stress = 0.206
MDS2
0.4
0.2
0.0
-0.2
-0.4
-0.2
0.0
0.2
0.4
0.6
MDS1
b.)
Stress = 0.177
MDS2
0.2
0.0
-0.2
-0.4
-0.5
0.0
0.5
MDS1
c.)
Stress = 0.195
MDS2
0.3
0.2
0.1
-0.1
-0.3
-0.6
-0.4
-0.2
0.0
0.2
0.4
MDS1

Figure 2.3:



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

Figure 2.4:



0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Proportional Terrestrial Resource Use
**
Filterer
Grazer
Predator
Shredder
January
June

Chapter 3: Effects of riparian tree cover on Coarse Particulate Organic Matter and macroinvertebrate biomass dynamics in temperate, upland streams

3.0: Summary

1. Although riparian zones are fundamental to stream ecosystem function, there are relatively few quantitative studies of the effects of contrasting riparian types on headwater biomass. This is despite the importance of riparian management in mitigating catchment-scale effects on streams, for example from agriculture or climate change.

2. The research presented in this chapter assesses variations over two years in the biomass, density and functional composition of macroinvertebrates in four pairs of upland headwater stream respectively draining (i) open moorland; (ii) moorland with deciduous riparian zones; (iii) deciduous woodland; and (iv) conifer forest with deciduous riparian zones. Stocks of coarse particulate organic matter (CPOM) were also measured.

3. Streams draining extensive deciduous woodland had invertebrate biomass (~ 500 mg m^{-2} dry mass) 2 times greater than streams in moorland and 1.5 times those with broadleaf buffer strips, though the latter pair did not differ. Invertebrate biomass was lowest in streams draining conifer.

4. Elevated macroinvertebrate biomass in deciduous streams was linked directly to variations among specific Functional Feeding Groups, with Shredders (> 2000 %) and

Filterers (> 400 %) at substantially greater biomass than in treeless streams. Other functional groups were unaffected.

5. Riparian effects were mediated by organic litter supplies: sample macroinvertebrate density and biomass increased with CPOM stocks irrespective of land use, but CPOM stocks were significantly greater at deciduous woodland sites than all others.

6. These data illustrate how riparian deciduous trees enhance basal resources and increase biomass from secondary production in temperate, upland streams, but only where woodland cover is extensive. This implies that the maintenance of terrestrial-aquatic linkages might require the conservation or restoration of riparian broadleaves at scales sufficient to offset downstream export – which in low retention headwaters can be substantial.

3.1: Introduction

The notion that riparian zones affect stream ecosystem function is one of the most widely accepted in freshwater ecology. The ecotone between land and water occupies a key position in theory ranging from the River Continuum Concept (Vannote *et al*., 1980) and stream-valley linkage (Hynes, 1975), to the influence of riparian controls on community composition (Naiman and Décamps, 1997) and functional feeding classification (Cummins and Klug, 1979; Cummins *et al*., 1989). While some riparian effects on streams reflect physical and chemical processes, others are ecological and energetic, and many stream organisms from invertebrates to vertebrates depend on subsidies supplied by adjacent terrestrial habitats (Wallace *et al*., 1997; Nakano *et al*., 1999; Baxter *et al*., 2005).

The principles underlying terrestrial-aquatic linkages are widely used as a basis for river conservation and management. In temperate regions, where landscapes have been extensively modified, lateral “buffer strips” of native broadleaves are advocated as a means of reducing the effects of catchment-wide agriculture, forestry or urbanization on stream ecosystems (Osbourne and Kovacic, 1993; Broadmeadow and Nisbet, 2004). As such, effects of riparian tree cover on sediments, nutrients, acidification and habitat structure have all been widely investigated (Ormerod *et al*., 1993; Gurnell *et al*., 2002; Broadmeadow and Nisbet, 2004; Sweeney *et al*., 2004). More recently, attention has turned to the value of riparian broadleaves in protecting headwater ecosystems from temperature increases associated with global climate change (Battin *et al*., 2007; Ormerod, 2009; Palmer *et al*., 2009; Seavy *et al*., 2009), thereby maintaining stream temperatures at levels optimum for cool-water fish such as salmonids (Zoellick, 2004; Broadmeadow *et al*., 2011).

Despite this advocacy, quantitative, replicated comparisons of the ecological character of streams draining different riparian zones are surprisingly scarce – particularly in upland, temperate regions (Allan and Johnson, 1997; Allan, 2004). Moreover, although the abiotic effects of buffer strips are recognized, their effects on stream food webs, production and biomass are less widely quantified. Past studies have shown how shade cast by riparian vegetation can reduce both in-stream primary production and macroinvertebrate biomass (Behmer and Hawkins, 1986; Hill *et al.*, 1995; Quinn *et al.*, 1997; Kiffney *et al.*, 2003, 2004; Riley *et al.*, 2009). In contrast, allochthonous subsidies of Coarse Particulate Organic Matter (CPOM) from riparian zones can make a major contribution to in-stream production and biomass (Cummins *et al.*, 1989; Wallace *et al.*, 1997). Supply and retention of these allochthonous resources is likely to differ between riparian land use types (Abehlo, 2001), with greater catchment tree cover expected to contribute larger resource subsidies.

Changes in the available resource base in streams are likely to affect macroinvertebrate communities particularly strongly. This faunal group contains taxa that range from those adapted to process detrital material (Shredders, Filterers) to those primarily reliant upon in-stream primary production by epilithic biofilms (Grazers) (Cummins and Klug, 1979; Cummins *et al.*, 1989). Changes in community composition with riparian character are, therefore, likely (Chapter 2). A further possibility is that changes in energy flux from riparian zones will affect the biomass of stream macroinvertebrates as major secondary consumers. Given that invertebrates are pivotal in the conversion and transfer of energy from basal resources to top-predators (Malmqvist, 2002), the effects of riparian land use on this group has important bearing upon consequences for resident populations of game fish (Battin *et al.*, 2007; Riley *et al.*, 2009; Naiman *et al.*, 2012; Chapter 5).

This study assesses quantitative differences in benthic macroinvertebrate biomass, density and functional composition across streams that differ in riparian tree cover, and examines whether any differences reflect allochthonous resource availability. Testing the overall hypothesis that streams in contrasting land use support functionally and compositionally different macroinvertebrates communities linked to different energetic pathways, three specific predictions were evaluated: (i) total macroinvertebrate biomass and density should be increased in streams draining wider deciduous woodland, largely determined by increased contributions by functional groups linked to detrital processing (Filterers and Shredders); (ii) enhanced macroinvertebrate biomass should be driven by terrestrially-derived resources in the form of benthic CPOM; (iii) streams with riparian buffer zones of deciduous broadleaf trees would have macroinvertebrate biomass, density and CPOM intermediate between streams in wider deciduous woodland and open moorland.

3.2: Methods

3.2.1: Study sites

The general study area has been described elsewhere (Chapters 2; Larsen *et al*., 2009). In outline, it involved an upland (altitude 150 – 900 m) region of South Wales with a temperate maritime climate (precipitation 1200 – 2500 mm: Met Office, 1971 - 2000 averages) and rural land uses underlain by Old Red Sandstone that gives rise to circumneutral and mostly unpolluted runoff.

From a wider pool of 24 upland headwater streams sampled as part of an earlier survey (Chapter 2), eight were selected for this quantitative study to represent four distinct riparian land uses (Table 3.1): open moorland catchments were dominated by rough grassland and low-density sheep grazing (Moorland; MO; n = 2); moorland with deciduous buffer (Buffer; GB; n = 2), where moorland catchments had narrow (~30 – 40 m) riparian strips of native deciduous woodlands mostly of alder *Alnus glutinosa*, birch *Betula pendula*, ash *Fraxinus excelsior* and oak *Quercus* spp.; catchments which still had relatively extensive areas of remnant deciduous woodland (Deciduous; DE; n = 2) in the riparian zone (~ 100 – 200 m), though with moorland beyond this; and coniferous buffer (Coniferous; CB; n = 2), where catchments were dominated by exotic conifer plantations of mostly sitka spruce *Picea sitchensis*, with deciduous trees in the riparian zone (~ 10 – 40 m). Previous analysis illustrated that these sites contrasted clearly on catchment land use with only minor confounding differences (Chapter 2).

3.2.2: Physical, chemical and land use characteristics

Catchment land use data were obtained using ArcGIS (version 9.2; ESRI, 2009). The Arc HydroTools package (version 9; Center for Research in Water Resources, University of Texas, TX, USA) was used to determine catchment area, which was then combined with the Countryside Council for Wales' habitat land-cover map (Countryside Council for Wales, 2004) to apportion land use by percentage cover. Riparian buffer lengths and widths were estimated at 100 m intervals along each stream using Google Earth (version 5.2; Google, Inc., 2012), which was also used to determine site elevations and distance from source data. Stream widths and depths were measured on-site at four 10 m intervals along the sampling reach. Conductivity and pH were spot-checked during a high flow period in October 2011, using a Hanna HI 98129 low-range pH/Conductivity/TDS Tester (Hanna Instruments, Ltd.) (Table 3.1; Chapter 2).

3.2.3: Density and biomass sampling

Macroinvertebrates and CPOM standing stocks were collected at each site using 5 x 0.07 m^2 Hess samples (Hess, 1941; upstream net: 1mm mesh; downstream net: 500µm mesh; EFE-UK and GB Nets Ltd., UK) from fast-flowing riffles in February, June and October of 2011 and 2012 (i.e. 6 occasions). All samples were immediately preserved in 70 % Industrial Methylated Spirits (IMS: Fisher Scientific UK) on site, and stored in 1 litre plastic pots.

Preserved samples were processed by rinsing in a 500 µm sieve, with samples then transferred to a sorting tray, and all macroinvertebrates (> 500 µm: Hauer and Lamberti, 2006) removed using forceps. They were identified to genus, except Diptera (Athericidae, Ceratopogonidae, Chironomidae, Pedicidae, Simuliidae, Tabanidae, Tipulidae) and selected Coleoptera (Dytiscidae, Gyrinidae, Scirtidae), which were identified to family, and Annelida, which were identified to subclass. Following identification, all individuals within a sample belonging to each individual taxon were transferred to glass vials for drying at 60 ˚C for 48 h and subsequently weighed to the nearest 0.1 mg. Biomass data were expressed per m^2 of streambed. CPOM, defined as all non-woody vascular plant material > 1 mm^2 (Cummins, 1974), was rinsed from each sample into a 1 mm sieve. CPOM from each Hess sample and also dried, weighed and converted to per m^2 estimates, as above.

3.2.4: Functional feeding groups

Taxa were assigned to one of five functional feeding groups (FFGs), according to the classification of Cummins and Klug (1979): “Shredders” are adapted to process CPOM; “Grazers” are primarily dependent on in-stream primary production, predominantly epilithic algae; “Collector-Gatherers”, referred to as detritivores under some classifications (Moog, 1995), utilise benthic fine particulate organic matter (FPOM); “Filterers” obtain suspended materials from the water column, via a variety of mechanisms; “Predators” capture and consume other animal taxa. Moog (1995) provides a database recording the predominant feeding strategy in most European stream invertebrates, and this was used here supplemented by information from Meritt and Cummins (1996) and Hauer and Lamberti (2006).

3.2.5: Statistical analysis

All statistical analyses were conducted in R Version 2.15.2 (R Development Core Team, 2012), with mixed effects models fitted using the *lme* function within the *nlme* package (Pinheiro *et al*., 2013). General linear mixed effects models (GLMMs) were used to assess differences in macroinvertebrate production between land use types site-pairs and sampling periods, with site fitted as a random term, in order to account for non-independence of samples taken from the same location. Separate models were fitted to assess effects upon total macroinvertebrate biomass, total macroinvertebrate density, FFG-by-FFG biomass and proportional representation, and CPOM standing stocks, with models including Land Use Type, Month and Year as explanatory variables, along with all relevant two-way (including Month:Year, to investigate Sampling-Period-specific differences), and three-way interactions. Where overall terms were significant, factor levels were compared using Tukey’s Honestly Significant Difference (HSD) *post-hoc* comparisons.

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

3.3: Results

3.3.1: CPOM biomass

Quantities of benthic CPOM varied significantly among riparian land uses ($F_{3, 213} = 43.41$, $p < 0.001$), being greatest at Deciduous sites than any other site type (Tukey's HSD: $p < 0.001$ in all cases), and lowest in Moorland (Fig. 3.1). Standing stocks at Coniferous and Buffer sites were intermediate, and did not differ significantly from each other ($p = 0.557$). These differences were consistent through the study period, and did not depend on month ($F_{6, 213} = 1.15$, $p > 0.337$) or year ($F_{3, 213} = 1.04$, $p > 0.377$) of sampling. Seasonal variations in CPOM reflected greater October biomass than in February ($p = 0.001$) but not June ($p = 0.099$; Fig. 3.2). This effect was, however, dependent on the year of sampling ($F_{2, 213} = 7.39$, $p < 0.001$), with standing stocks in February significantly lower than those in June during 2011 ($p = 0.002$), whilst not differing during 2012 ($p > 0.569$).

3.3.2: Total macroinvertebrate biomass

Both total macroinvertebrate biomass ($F_{3, 213} = 14.57$, $p < 0.001$) and density ($F_{3,213} = 15.84$, $p < 0.001$) varied among land uses over the course of the whole study and was greater at Deciduous sites and lower at Coniferous sites (Tukey's HSD: $p < 0.01$ in all cases) than in the other three land use types ($p < 0.05$ in all cases) when averaged across all sampling periods (Table 3.2). Moorland and Buffer sites supported intermediate macroinvertebrate biomass, and did not differ significantly from one another ($p = 0.971$). There were some seasonal differences in macroinvertebrate biomass variations among land use types although they were not consistent between years ($F_{6, 213} = 2.67$, $p = 0.016$). There were, however, no concurrent effects on macroinvertebrate density ($F_{6, 213} = 2.00$, $p = 0.067$). Macroinvertebrate biomass averaged across all land use types varied with season ($F_{2, 213} = 6.92$, $p = 0.001$) and year (2011 > 2012; $F_{1, 213} = 12.75$, $p < 0.001$), with October having significantly lower biomass than either February ($p = 0.01$) or June ($p = 0.001$). Total macroinvertebrate density varied between years (2011 > 2012: $p = 0.009$) but not between seasons ($p > 0.05$ in all cases).

Total macroinvertebrate biomass ($F_{1, 189} = 94.96$, $p < 0.001$) and density ($F_{1, 189} = 138.63$, $p < 0.001$) both increased significantly in samples with greater standing stocks of CPOM (Fig. 3.3). These relationships were independent of land use type (Biomass: $F_{3, 189} = 2.49$, $p = 0.062$; Density: $F_{3, 189} = 0.53$, $p = 0.661$), month (Biomass: $F_{2, 189} = 0.41$, $p = 0.665$; Density: $F_{2, 189} = 2.12$, $p = 0.122$) or year (Biomass: $F_{1, 189} = 0.74$, $p = 0.393$; Density: $F_{1, 189} = 0.02$, $p = 0.888$).

3.3.3: Functional feeding groups

Biomass of each functional feeding group differed significantly between at least two land use types when averaged across all sampling periods (Table 3.2). Collector-Gatherer and Filterer biomass were lowest in Coniferous streams compared to all other land use types (Tukey's HSD: $p < 0.05$ in all cases). Grazer biomass was significantly higher in Deciduous compared to Coniferous streams ($p = 0.03$), though Grazer biomass at Coniferous streams did not differ from that in either Buffer ($p = 0.997$) or Moorland ($p = 0.777$) sites, and differences between the latter pair were also non-significant ($p = 0.880$). Predator biomass was higher in Moorland than Coniferous sites ($p = 0.002$), but did not differ between all other land use types ($p > 0.05$ in all cases). Shredder biomass was higher in Deciduous streams than in all other land uses ($p < 0.05$ in all cases), which did not differ significantly from one another ($p > 0.05$ in all cases).

These land use effects on functional group biomass were consistent among months, years and individual sampling periods for Collector-Gatherers (Month: $F_{6, 213} = 0.90$, $p = 0.498$; Year: $F_{3, 213} = 1.04$, $p = 0.377$; Sampling Period: $F_{6, 213} = 1.26$, $p = 0.277$), Predators (Month: $F_{6, 213} = 0.50$, $p = 0.810$; Year: $F_{3, 213} = 2.54$, $p = 0.058$; Sampling Period: $F_{6, 213} = 2.24$, $p = 0.051$) and Shredders (Month: $F_{6, 213} = 1.10$, $p = 0.365$; Year: $F_{3, 213} = 1.42$, $p = 0.238$; Sampling Period: $F_{6, 213} = 1.26$, $p = 0.276$). Variations in Filterer biomass were somewhat more transient, and differed between months ($F_{6, 213} = 2.18$, $p = 0.047$) but not years ($F_{3, 213} = 0.18$, $p = 0.913$). Variations among land uses in Grazer biomass were dependent on individual sampling period ($F_{6, 213} = 4.31$, $p < 0.001$). The biomass of several functional feeding groups also showed significant seasonal variation, when averaged across all land use types; differences between months varied between years of sampling for Collector-Gatherers ($F_{2, 213}$

= 4.65, $p = 0.011$), Filterers ($F_{2, 213} = 5.68$, $p = 0.004$), Grazers ($F_{2, 213} = 7.50$, $p < 0.001$) and Predators ($F_{2, 213} = 5.17$, $p = 0.007$), whilst biomass did not vary temporally for Shredders (Month: $F_{2, 213} = 0.39$, $p = 0.676$; Year: $F_{1, 213} = 2.12$, $p = 0.147$; Sampling Period: $F_{6, 213} = 0.46$, $p = 0.631$).

Functional Feeding Group representation also varied proportionally among land uses when averaged across all sampling periods (Table 3.3). Coniferous sites supported a lower proportion of Collector-Gatherer taxa and greater proportion of Grazer taxa than all other land use types (Tukey's HSD: $p < 0.05$ in all cases). Deciduous sites had a greater proportion of Shredder taxa than all other land use types ($p < 0.001$ in all cases). Moorland site supported a greater proportion of Predators, when compared to Coniferous and Deciduous sites ($p < 0.05$ in all cases). Filter representation was lower at Coniferous and Moorland sites than at Buffer or Deciduous sites ($p < 0.05$ in all cases).

These effects did not vary through time for Filterers (Month: $F_{6, 213} = 1.68$, $p = 0.127$; Year: $F_{3, 213} = 1.51$, $p = 0.213$; Sampling Period: $F_{6, 213} = 0.83$, $p = 0.552$), Predators (Month: $F_{6, 213} = 0.74$, $p = 0.620$; Year: $F_{3, 213} = 1.42$, $p = 0.240$; Sampling Period: $F_{6, 213} = 1.53$, $p = 0.170$) or Shredders (Month: $F_{6, 213} = 1.10$, $p = 0.367$; Year: $F_{3, 213} = 0.96$, $p = 0.413$; Sampling Period: $F_{6, 213} = 1.88$, $p = 0.090$). Patterns did, however, vary among sampling periods for Grazers ($F_{6, 213} = 2.48$, $p = 0.025$) and Collector-Gatherers ($F_{6, 213} = 2.99$, $p = 0.008$). Temporal variation was also apparent in FFG proportional representation, when averaged across all land use types (Table 3.4).

3.3.4: Relationships between functional feeding groups and CPOM biomass

As for overall macroinvertebrate biomass, Shredder biomass increased with CPOM biomass across samples (F1, 189 = 7.63, p = 0.006), though the relationship varied seasonally ($F_{2,\ 189}$ = 5.85, p = 0.003; Fig. 3.4). Similarly, the proportion of total macroinvertebrate biomass composed of Shredders was significantly positively related to CPOM biomass ($F_{1,\ 189}$ = 17.22, P < 0.001), but the relationship varied between months ($F_{1,\ 189}$ = 4.52, p = 0.012) and years of sampling ($F_{1,\ 189}$ = 9.93, p = 0.002). The biomass or proportional representation of all other functional feeding groups was not significantly related to CPOM biomass (Table 3.5).

3.4: Discussion

Of the three specific predictions evaluated in this chapter, there was clear evidence to support the first and second: total macroinvertebrate biomass and density was enhanced in streams draining deciduous woodland largely because of positive effects on Filterers and Shredders. Moreover, this effect was linked clearly to standing stocks of organic litter: macroinvertebrate density and biomass increased in samples with large CPOM stocks irrespective of land use, but CPOM stocks were significantly greater at Deciduous sites than all others. The third prediction was not supported, given that macroinvertebrate biomass and density in streams with riparian buffer strips were indistinguishable from those in moorland streams. In combination, these results illustrate how riparian broadleaves can enhance supplies of CPOM to headwaters, but effects on community composition and biomass only arise where broadleaf cover is extensive. This result has clear relevance to the restoration and management of riparian zones.

Though these results suggest that catchment tree cover may exert a strong influence on macroinvertebrate consumers in headwater streams, it should be noted that the non-experimental nature of studies like this can lead to potential confounds. However, prior analyses of these sites indicated minimal differences across land use categories on a wide range of physicochemical variables (Chapter 2). Moreover, though this study was relatively limited in terms of replication, effect sizes were generally large and most were consistent across the whole study period. Despite being limited to weak inference, such observational studies can provide a model for stream ecosystem responses to changes in catchment land uses, and supply data needed to inform management and habitat restoration measures (Goodwin *et al*., 1997; Naiman *et al*., 2012). This study would therefore likely have benefitted from an increased understanding of processes affecting terrestrial subsidy supply to in-stream consumers: differential litter input, downstream export and retention might have ultimately mediated the land use effects observed (Wallace *et al*., 1995; Eggert *et al*., 2012). For instance, Buffer sites may have had reduced litter input and lower capacity for retention than Deciduous streams. Moreover, differential rainfall patterns between years may have emphasised such effects, with downstream export likely more marked during a notably wetter 2012 (annual rainfall: 1496.4 mm), compared to 2011 (929.5 mm) (Met Office data for Cardiff Bute Park weather station: 51°48’49”N, 3°10’81”W), with summer stream-flow increased by as much as 250% in 2012 compared to 2011 (National River Flow Archive Data for Afon Mellte: 51°76’10”N, 3°57’49”W). Such processes might therefore explain site-to-site, seasonal and inter-annual variability evident in CPOM and macroinvertebrate biomass.

Notwithstanding these caveats, these results confirm how riparian broadleaves can enhance invertebrate biomass in upland streams – except where broadleaf buffer strips have limited cover. Whilst catchments with riparian buffer strips had similar macroinvertebrate biomass and density to open moorland sites, streams with larger areas of riparian woodland supported double the invertebrate biomass per unit area of streambed. These results contrast with some previous studies investigating effects of riparian forest on in-stream communities, however, which often report reductions in macroinvertebrate biomass compared to open reaches, linked to decreased primary productivity (Behmer and Hawkins, 1986; Kiffney *et al*., 2003, 2004; Riley *et al*., 2009). Such investigations have generally examined buffer strips narrower (10 – 20 m) than those considered here (30 – 40 m). Results of this study may therefore help elucidate reasons for such findings: the very narrow buffer strips investigated by others may reduce in-stream primary production via shading, without compensating for this with adequate inputs of terrestrial organic matter. As terrestrial resource subsidy inputs are, however, likely to co-vary positively with catchment tree cover (Wallace *et al*., 1997; Kawaguchi and Nakano, 2001; Baxter *et al*., 2005; Earl and Semlitsch, 2013), the wider buffer strips or retained areas of deciduous forest examined here may be able to mitigate or even reverse this outcome. Although standing stocks of benthic CPOM in Deciduous streams in this study (~10 – 80 g m^{-2}) were in the lower range of those reported for forested streams worldwide (1 > 1000 g m^{-2}: Abehlo, 2001; Pozo and Elosegi, 2005), they appeared sufficient to offset likely decreases in primary productivity and support increased macroinvertebrate biomass. This supports suggestions by previous authors that inputs and retention of CPOM may prove key in connecting stream food webs with their terrestrial riparian zones (Muotka and Laasonen, 2002; Lepori *et al*., 2005).

Data from this study provided further support for the suggestion that riparian broadleaf buffer strips in conifer plantations may be insufficient to offset wider catchment influence on stream communities (Ormerod *et al*. 1993; Broadmeadow and Nisbet, 2004; Chapter 2). Here, lower macroinvertebrate biomass was apparent at Coniferous sites, compared to all other riparian land uses, despite the presence of riparian broadleaf cover. This effect did not appear due to CPOM availability, however, as standing stocks were similar to Buffer sites, which had macroinvertebrate biomass equivalent to that at unshaded Moorland sites. Reduced macroinvertebrate biomass may have therefore been attributable to consistent year-round shading provided by evergreen conifers in the wider riparian zone, differential litter quality or water chemistry changes often associated with conifer plantations. As CPOM stocks at Buffer and Coniferous sites were equivalent, litter quality may have explained differential invertebrate biomass. Conifer needles, which likely entered the streams via lateral input, are often of poorer quality (higher C:N, lower P concentrations: Valachovic *et al*., 2004), have increased toughness (Soma and Saitô, 1983) and are often high in antimicrobial compounds (Bärlocher and Oertli, 1978) compared to broadleaf litter, limiting their palatability to detritivore taxa. Moreover, water chemistry did not appear to be a limiting factor, and did not differ considerably between Coniferous sites and the other streams in this study during spot checks (Table 3.1; Chapter 2), though effects are often episodic (Kowalik *et al*., 2007).

Land use effects observed in this study were mediated by differential responses of individual functional groups, with biomass of Shredding and Filtering taxa increasing with the presence of tree cover: sites with larger areas of deciduous woodland supported 20 times the biomass of Shredders, and four times the biomass of Filterers, compared to open moorland streams. This was likely driven by greater resource availability for both groups, which are often largely dependent on terrestrial organic matter, in coarse or fine forms, respectively (Cummins and Klug, 1979). The concurrent increase of these two functional groups provides support for suggestions that filtering taxa may be facilitated by comminution of terrestrial detritus by upstream Shredder populations (Heard and Richardson, 1995). These functional groups did not show increases at sites with narrow buffer strips of riparian tree cover, however, suggesting that quantities of benthic CPOM in these streams were not great enough to support increased numbers of these taxa – this may suggest a minimum amount of catchment tree cover may be required to supply sufficient subsidies to support these groups. Seasonal variation in relationships between Shredder and CPOM biomass demonstrated that the importance of allochthonous resource subsidies might vary temporally, and predominant resource bases for consumers are likely to shift with availability throughout the year. The magnitude of seasonal, and particularly inter-annual differences observed in this study, also highlighted the necessity of longer-term monitoring in assessing riparian land use effects on stream ecosystems.

The presence of riparian tree cover did not affect other functional groups examined, despite the potential for diminished in-stream resources. Grazing taxa are generally considered to be highly dependent on in-stream biofilms as the main component of their diet (Cummins and Klug, 1979; Moog 1995), for instance, and biofilm production is generally negatively correlated with shading associated with riparian vegetation (Hill *et al.*, 1995; Kiffney *et al.*, 2003; 2004). As such, Grazers could be predicted *a priori* to be the group most negatively affected by tree cover. Surprisingly, Grazer biomass was not significantly reduced in the shaded Buffer or Deciduous sites, when compared to the Moorland sites. This could be explained by functional or dietary plasticity in the feeding of grazing taxa (Dangles, 2002), with individuals at these sites incorporating increased allochthonous resources into their diets, to compensate for reduced biofilm availability (Chapter 2).

The major finding of this study – that catchment land use influences stream macroinvertebrate biomass – has implications for management practices. These results suggest that reinstatement of riparian buffer strips (30 - 40 m) in moorland catchments could protect upland streams from various anthropogenic impacts, such as climate change (Broadmeadow *et al*., 2011) or catchment-wide agriculture (Osbourne and Kovacic, 1993; Broadmeadow and Nisbet, 2004), without reducing macroinvertebrate production. Restoring or maintaining larger areas of riparian forest (> 100 m) in headwater streams may, however, confer additional benefits; by potentially providing a larger pool of basal resources, forested streams may increase consistent, year-round resource availability to consumers. Further investigation is required, however, in order to establish why effects of buffer strips on macroinvertebrate production vary between studies. This may simply reflect the extent of catchment forest cover, or might be driven by other stream-specific, geographic (e.g. upland vs. lowland) or historical (e.g. Harding, 1998) factors. The streams examined in this study were largely oligotrophic, for example, as evidenced by the low macroinvertebrate biomass (~ 500 mg m^{-2}), relative to literature-wide values (~ 0.5 – 100 g m^{-2}: Rinne, 1990; Wallace *et al*., 1997; Fuchs *et al*., 2003; Helms *et al*., 2009; Riley *et al*., 2009). Land use effects may therefore differ for more productive lowland streams, providing an alternate explanation for the outcome of studies where riparian tree cover appears to reduce macroinvertebrate production (Riley *et al*., 2009). If potential benefits of larger areas of riparian forest are generalizable across upland streams, however, management schemes aiming to protect or restore tree cover need to explicitly consider the spatial extent of riparian forest when establishing desired conservation outcomes.

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3.6: Tables and Figures

Table 3.1: Site physical and chemical characteristics for the eight sites used in this investigation. Site codes: CB = Coniferous Buffer; DE = Deciduous; GB = Grassland Buffer; MO = Moorland.

Site	Latitude	Longitude	Mean pH	Mean Conductivity (µS)	Elevation (m)	Mean Width (m)	Mean Depth (cm)	Catchment Area (km^2)	Catchment Deciduous Tree Cover (%)	Upstream Buffer Length (m)	Mean Upstream Buffer Width (m)
CB2	51.805484	-3.439536	6.87	25	293	2.95	20.0	1.52	1.07	289	9.5
CB4	51.811003	-3.378897	7.10	33	345	4.90	17.1	3.69	1.14	738	38.8
DE1	51.909325	-3.399013	7.14	101	253	4.38	19.1	4.42	16.83	1801	108.2
DE5	51.843852	-3.04744	7.44	123	255	3.90	11.8	2.72	17.21	1107	220.5
GB3	51.873722	-3.56243	7.25	93	260	3.85	15.3	3.20	4.95	990	42.4
GB5	51.869681	-3.313687	7.08	47	203	4.68	12.4	2.99	3.00	1145	33.2
MO3	51.865707	-3.416319	7.79	44	465	3.38	19.5	2.18	0	0	0
MO6	51.872676	-3.667889	7.40	48	395	5.16	23.1	2.91	0	0	0

Table 3.2: Biomass (mg m^{-2}: mean ± 1 s.e.) of each Functional Feeding Group (FFG), along with totals, across all sampling periods. 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 3.3: Proportion of total biomass (mean ± 1 s.e.) belonging to each Functional Feeding Group (FFG), across all sampling periods. 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 †	0.358 ± 0.037 a	0.346 ± 0.035 a	0.217 ± 0.025 b	0.369 ± 0.030 a
Filterer †	0.073 ± 0.016 a	0.010 ± 0.004 b	0.080 ± 0.014 a	0.0297 ± 0.010 b
Grazer †	0.282 ± 0.034 a	0.400 ± 0.035 b	0.236 ± 0.029 a	0.280 ± 0.030 a
Predator	0.216 ± 0.033 ab	0.171 ± 0.028 a	0.164 ± 0.028 a	0.288 ± 0.035 b
Shredder	0.070 ± 0.016 a	0.081 ± 0.020 a	0.304 ± 0.037 b	0.034 ± 0.010 a

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

Table 3.4: Proportion of total macroinvertebrate biomass (mean ± 1 s.e.) belonging to each Functional Feeding Group (FFG), across all land use types. Shared letters for 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	February	June	October
Collector-Gatherer	0.315 ± 0.029 a	0.426 ± 0.029 b	0.226 ± 0.023 c
Filterer †	0.065 ± 0.013 a	0.029 ± 0.007 b	0.049 ± 0.010 ab
Grazer	0.305 ± 0.026 a	0.269 ± 0.026 a	0.327 ± 0.033 a
Predator	0.192 ± 0.025 a	0.173 ± 0.021 a	0.264 ± 0.034 a
Shredder	0.123 ± 0.023 a	0.103 ± 0.022 a	0.140 ± 0.024 a

† Interaction terms indicated that differences between months were dependent upon year of sampling.

Table 3.5: Relationships between Coarse Particulate Organic Matter (CPOM) biomass, and biomass and proportional representation of each Functional Feeding Group (FFG). 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**

3.6.1: Figure Legends

Figure 3.1: CPOM biomass (mg m^{-2}: mean ± 1S.E.) dynamics across land use types and sampling periods. Land use categories: CB = Coniferous, DE = Deciduous, GB = Buffer, MO = Moorland. Y-axis scales differ between graphs.

Figure 3.2: Macroinvertebrate biomass (mg m^{-2}: mean ± 1S.E.) 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 3.3: 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 3.4: Seasonal relationships between log (+1) transformed CPOM biomass and Shredder biomass. Solid lines of best fit as predicted by Linear Mixed Effects models, dashed lines represent predicted standard errors around the mean.

Fig 3.1:

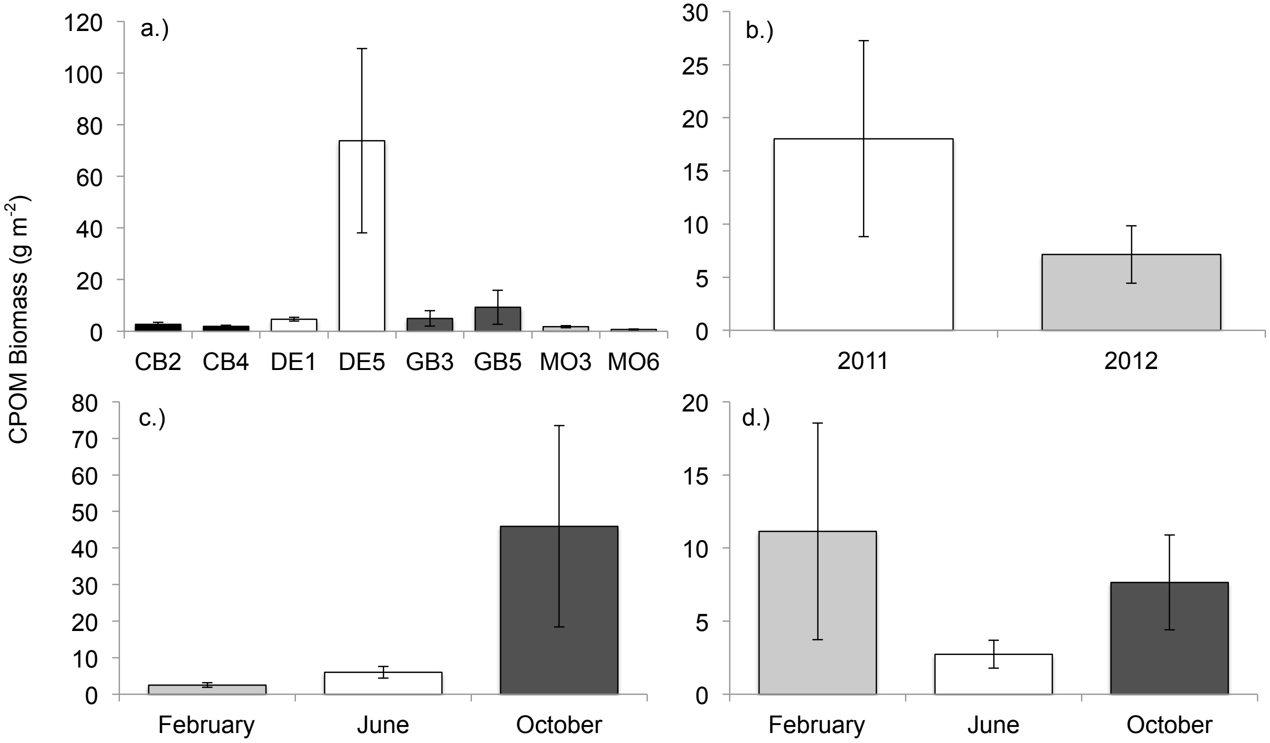

CPOM Biomass (g m^{-2})
a.)
120
100
80
60
40
20
0
CB2
CB4
DE1
DE5
GB3
GB5
MO3
MO6
b.)
30
25
20
15
10
5
0
2011
2012
c.)
80
70
60
50
40
30
20
10
0
February
June
October
d.)
20
15
10
5
0
February
June
October

Figure 3.2:

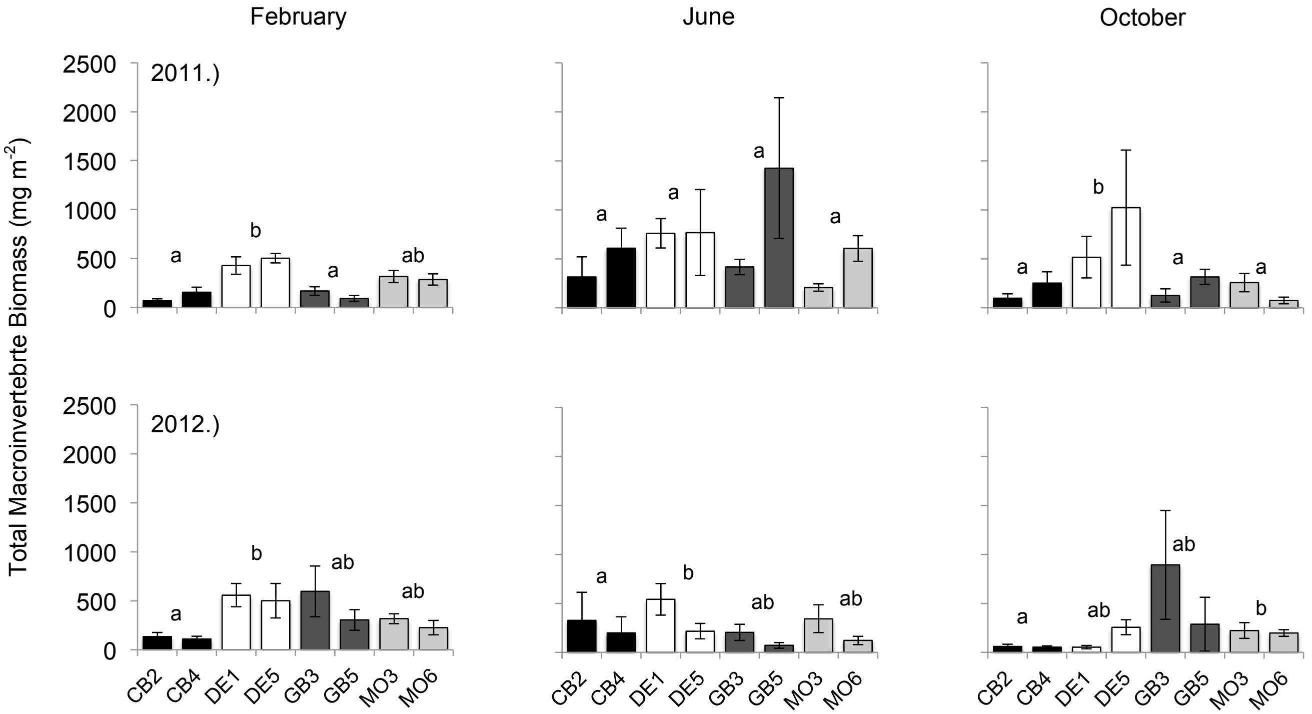

February
June
October
Total Macroinvertebrte Biomass (mg m-2)
2500
2000
1500
1000
500
0
2011.)
2012.)
a
b
a
ab
a
a
a
a
b
a
a
a
a
b
ab
ab
a
b
ab
ab
ab
a
ab
b
CB2
CB4
DE1
DE5
GB3
GB5
MO3
MO6

Figure 3.3:

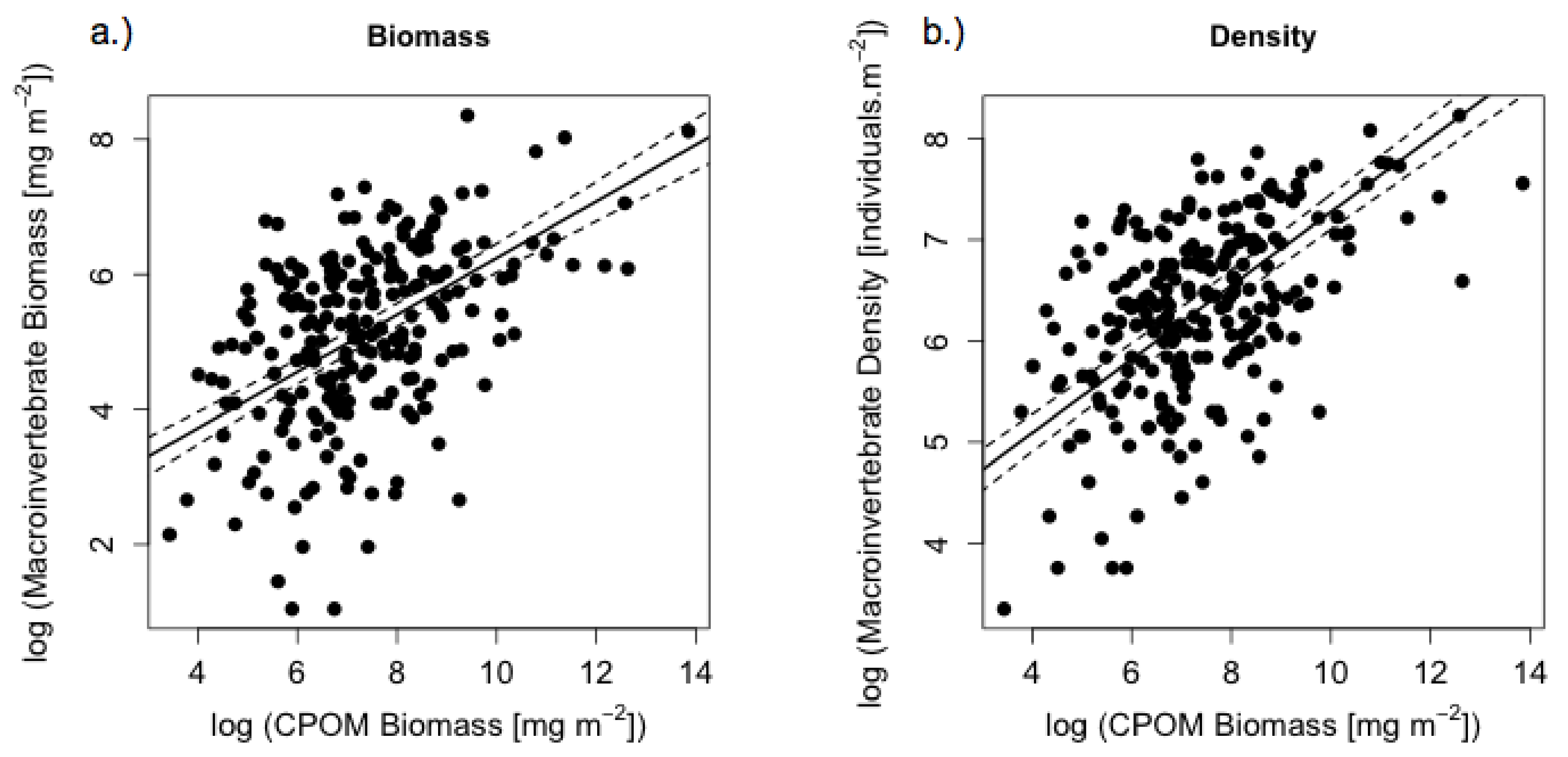
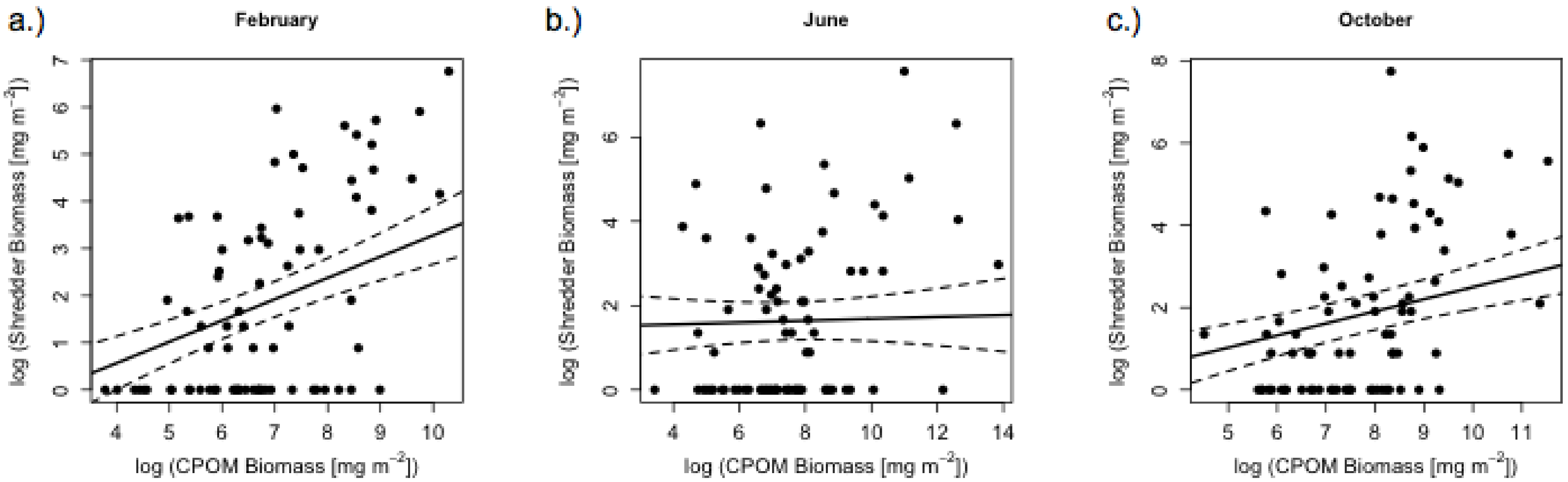

a.)
Biomass
log (Macroinvertebrate Biomass [mg m^{-2}])
2
4
6
8
4
6
8
10
12
14
log (CPOM Biomass [mg m^{-2}])
b.)
Density
log (Macroinvertebrate Density [individuals.m^{-2}])
4
5
6
7
8
4
6
8
10
12
14
log (CPOM Biomass [mg m^{-2}])

Figure 3.4:


a.)
February
log (Shredder Biomass [mg m^{-2}])
0
1
2
3
4
5
6
7
4
5
6
7
8
9
10
log (CPOM Biomass [mg m^{-2}])
b.)
June
log (Shredder Biomass [mg m^{-2}])
0
2
4
6
4
6
8
10
12
14
log (CPOM Biomass [mg m^{-2}])
c.)
October
log (Shredder Biomass [mg m^{-2}])
0
2
4
6
8
5
6
7
8
9
10
11
log (CPOM Biomass [mg m^{-2}])

Chapter 4: Effects of experimental litter subsidies on macroinvertebrate community structure and function in temperate moorland streams

4.0: Summary

1. Many headwater stream ecosystems in deforested landscapes are now disconnected from the energetic subsidies they once received naturally as inputs of deciduous leaf litter from adjacent terrestrial habitats. Although the repair of stream food-webs in such locations is often a priority, there are few experimental data from which to judge likely outcomes.

2. This chapter reports the results of a replicated field experiment in which stream reaches in treeless headwater catchments were subsidised in winter with leaf litter at volumes typical of woodland streams (0.75 kg dry mass m^{-2}). Effects on macroinvertebrate biomass, density, functional group composition and incorporation of terrestrial material into invertebrate diet were investigated.

3. Litter addition increased mean standing stocks of benthic Coarse Particulate Organic Matter (CPOM) in the experimental reaches by approximately 300 times, from an average of ~140 mg m^{-2} to ~40 g m^{-2}, but effects were transient. Moreover, no aspect of macroinvertebrate composition, biomass, density or resource use was affected by comparison with reference streams.

4. These results contrast with effects expected from existing deciduous woodland catchments where litter inputs are a major energetic resource for invertebrate

consumers. Possible explanations are that limitations in experimental scale and duration, low retention of added material or prior adjustment of the invertebrate community to autotrophic production all affected outcomes. Riparian woodland restoration intended to increase headwater production should have sufficient extent to overcome such effects.

4.1: Introduction

Cross-boundary transfers of matter and energy between adjacent habitats can have major effects on food webs, with subsidies often shaping interspecific interactions and mediating ecosystem processes within recipient communities (Marczak *et al*., 2007). The interface between stream ecosystems and terrestrial riparian systems is one such example of an ecotone, and energetic linkages between these two habitats are often pronounced (Baxter *et al*., 2005). Reciprocal fluxes of matter and energy between these systems can affect communities in both habitats by determining local abundance of stream fishes (Kawaguchi *et al*., 2003) or mediating secondary production of macroinvertebrates (Wallace *et al*., 1997; Paetzold *et al*., 2006). Headwater stream organisms are particularly dependent on inputs of terrestrially fixed carbon provided by riparian primary producers (Vannote *et al*. 1980; Cummins *et al*., 1989), with subsidy supply having profound, community-wide, consequences for aquatic consumer abundance and biomass (Wallace *et al*., 1997; Wallace *et al*., 1999).

It follows that land use change in riparian habitats has the ability to disrupt terrestrial-freshwater linkages by altering the extent of resource subsidy inputs (Vannote *et al*., 1980; Baxter *et al*., 2005; Marcarelli *et al*., 2011; Earl and Semlitsch, 2013). For example, reductions in riparian tree cover are likely to influence both the amount of terrestrially produced organic matter supplied to a stream (Abelho, 2001) and the quantity of solar radiation available to in-stream autotrophs, with consequences for macroinvertebrate food-webs (Hill *et al*., 1995; Kiffney *et al*., 2003, 2004). This is important given that large areas of temperate, upland regions have been cleared of native woodland to be replaced by agriculture, urban land or commercial forestry (Harding *et al*., 1998; Kaplan *et al*., 2009). So far, however, research in this area has focused largely on the potential consequences of weakening terrestrial-aquatic linkages via reductions in supply of leaf litter and terrestrial invertebrates to stream food webs (Wallace *et al*., 1997; Wallace *et al*., 1999; Nakano *et al*., 2001). The consequences of attempting to restore terrestrial subsidies to stream consumers are less well understood (Richardson, 1991; Melody and Richardson, 2004; Pretty and Dobson, 2004), particularly where streams currently have an absence of tree cover and are thus predominantly dependent upon in-stream autotrophic production (Dobson *et al*., 1995). This is despite growing interest in the restoration of native riparian tree cover in deforested catchments, particularly headwaters (Battin *et al*., 2007; Ormerod, 2009; Palmer *et al*., 2009; Seavy *et al*., 2009). Macroinvertebrate communities provide a key linkage between basal resources and higher predators in such streams (Malmqvist, 2002). Understanding how increasing litter subsidies might be mediated via macroinvertebrate consumers may therefore be crucial in anticipating food-web consequences of riparian restoration (Naiman *et al*., 2012).

Using a replicated reach-scale experiment with a before-after-control-impact (B-A-C-I) design, the research reported in this chapter tests the hypotheses that increasing terrestrial resource subsidies to autotrophic streams, in the form of leaf litter, will (i) increase biomass and density of macroinvertebrate consumers; (ii) alter community functional composition, favouring taxa adapted to process and assimilate detrital leaf material; and (iii) increase incorporation of terrestrially derived organic matter into tissues of taxa representing various functional groups.

4.2: Materials and Methods

4.2.1: Experimental design and study sites

The general study area has been described elsewhere (Chapter 2; Larsen *et al*., 2009). In outline, it involved an upland (altitude 150 – 900 m) region of South Wales with a temperate maritime climate (precipitation 1200 – 2500 mm: Met Office, 1971-2000 averages) and rural land uses underlain by Old Red Sandstone that gives rise to circumneutral and mostly unpolluted runoff.

From a wider pool of 24 streams surveyed previously to assess invertebrate communities and appraise their stable isotopic character (Chapter 2), four were selected to optimize general physicochemical similarity (Table 4.1), community composition, ease of discriminating isotopically between terrestrial and in-stream production, and feasibility of adding large quantities of leaf litter (experimental sites only). All were in moorland (MO), and had no riparian or catchment tree cover. Reaches of 20 m length along two of the streams were designated as controls (n = 2; MO3 and MO6; see Chapter 2 for site codes) and two as treatment sites (n = 2; MO2 and MO5) to which leaf litter would be added.

4.2.2: Study site physicochemistry

Physicochemistry of the study sites is provided in detail elsewhere (Table 2.1). Briefly, stream depths and widths were measured on site at three 10 m intervals centered on the sampling reach. Site elevations were measured using Google Earth (Version 5.2; Google, Inc., 2012). Catchment area was estimated using the *Arc Hydrotools* package (Version 9;

Center for Research in Water Resources, University of Texas, TX, USA) within ArcGIS (Version 9.2; ESRI, 2009). Three replicate water samples were taken to assess pH and conductivity following a high flow event in October 2011 using a Hanna HI 98129 low-range pH/Conductivity/TDS Tester (Hanna Instruments, Ltd.) (Table 4.1).

4.2.3: Leaf litter addition

Broadleaf litter for addition to the experimental reaches, predominantly that of *Quercus*, *Acer,* and *Castanea* spp. was collected from Cyfarthfa Park, Merthyr Tydfil, UK (51°75’80”N, 3°39’00”W) shortly after abscission during late October 2011 and stored outdoors in unsealed refuse sacks until required. Litter mixtures contained a small quantity of woody debris in the form of twigs < 1 cm in diameter which were not removed before use.

Litter was first added to the experimental sites during early November 2011, and thereafter at fortnightly intervals (n = 6 occasions with equal litter mass) until mid January 2012 at quantities equivalent to inputs into other Welsh streams draining broadleaves (Pye *et al*., unpublished data). In total, approximately 3 kg dry mass of litter was added per metre length of stream bank, giving a total of 60 kg dry mass per experimental stream reach, equivalent to 0.75 kg per m^2 of streambed. This is within the range reported for most types of deciduous forest worldwide (Abelho, 2001; Pozo and Elosegi, 2005). Litter dry weight was estimated from wet samples taken from the storage sacks following collection after air-drying at 60 ˚C for 48 h. Dry mass accounted for approximately 30 % of the total wet weight.

4.2.4: Macroinvertebrate density and biomass

Macroinvertebrate density, biomass and standing CPOM stocks at each study reach were assessed using a 0.07 m^2 Hess-type sampler (Hess, 1941; upstream net: 1mm mesh; downstream net), with five replicates taken haphazardly from fast-flowing riffle sections in February, June and October 2011 during the pre-treatment year, and at 4, 12, 20 and 40 weeks after the last litter addition (February, April, June and October 2012). All macroinvertebrates were immediately preserved in 70 % industrial methylated spirits (IMS: Fisher Scientific, UK).

In the laboratory, preserved samples were rinsed in water into a 500 µm sieve, transferred to a sorting tray and all macroinvertebrates (> 500 µm: Hauer and Lamberti, 2006) removed using forceps. Remaining Coarse Particulate Organic Matter (CPOM), defined as all non-woody vascular plant material > 1 mm^2 (Cummins, 1974), was then rinsed in a 1 mm sieve and retained. Collected macroinvertebrates were identified to genus, except Diptera (Athericidae, Ceratopogonidae, Chironomidae, Pedicidae, Simuliidae, Tabanidae, Tipulidae) and selected Coleoptera (larval Dytiscidae, Gyrinidae, Scirtidae), which were identified to family, and Annelida, which were identified to subclass. All individuals from each sample were separated by taxon (genus/family/subclass) and transferred to a glass specimen tube for drying. Total CPOM within each sample was treated similarly. All macroinvertebrates and CPOM samples were then dried at 60 ˚C for 48 h and weighed to the nearest 0.1 mg to give individual taxon or CPOM biomass per Hess sample. Data were then converted to give dry biomass per m^2 of streambed.

4.2.5: Functional feeding groups

Taxa collected were assigned to one of five Functional Feeding Groups (FFG), after Cummins and Klug (1979): Shredders are adapted to process CPOM; Grazers are primarily dependent on in-stream primary production, predominantly epilithic algae; Collector-Gatherers, referred to as detritivores under some classifications (Moog, 1995), utilise benthic fine particulate organic matter (FPOM); Filterers obtain suspended materials from the water column, including other animals, via a variety of mechanisms; Predators capture and consume other animal taxa. Macroinvertebrates were assigned these five groups using Moog (1995), based on predominant feeding strategy, using supplementary information from Merritt and Cummins (1996), and Hauer and Lamberti (2006). Absolute and proportional total biomass, densities were calculated for each FFG and Hess sample.

4.2.6: Macroinvertebrate stable isotope analysis

Potential assimilation of added leaf litter into macroinvertebrate consumers was assessed using stable isotopic analysis (SIA) on four taxa, taken to represent four functional feeding groups and two trophic levels: *Baetis* spp. (Ephemeroptera: Baetidae) representing Collector-Gatherers; *Leuctra* spp. (Plecoptera: Leuctridae) representing Shredder-Detritivores; *Hydropsyche* spp. (Trichoptera: Hydropsychidae) representing filter feeders; and *Dinocras cephalotes* (Plecoptera: Perlidae), representing Predators (Moog, 1995; Merritt and Cummins, 1996). Each of these was persistent, common and widespread within the study area, present in each site during each sampling period. Three of these taxa (except *D. cephalotes*) were processed at the genus level due to the difficulties of species-level identification on the live, unpreserved individuals preferable for consumer isotopic composition (Xu *et al.*, 2011). This method assumes that all species within the relevant genera are functionally equivalent, as supported by available evidence (Moog, 1995).

4.2.7: Stable isotope sampling and processing

Preliminary work showed that study organisms had stream-specific isotopic compositions prior to litter addition. Control reaches situated 50 m upstream from the experimental reaches could thus be used concurrently with reference streams to appraise isotopic variations when assessing dietary changes following the experimental addition of leaf litter.

Samples for stable isotope analysis were collected in April and October during the pre-treatment year and then concurrently with density samples during the post-treatment year, at 4, 12 and 20 weeks following litter addition. The target invertebrate taxa were collected via kick sampling, with relevant taxa removed with forceps, and transferred to plastic vials. CPOM samples for isotopic analysis were also obtained kick samples, whilst epilithic biofilm (hereafter, epilithon), representing in-stream autochthonous production, was scraped from three cobbles within the sampling reach using a penknife. Samples of seston (FPOM suspended within the water column), a third potential food source for consumers, were isolated from flowing stream water using a 53 μm^2 phytoplankton net (EFE-UK and GB Nets Ltd., UK), modified with 1 mm^2 screen to limit entrance by CPOM and drifting invertebrates.

All samples for isotopic analysis were frozen at -18 ºC within 8 hours of collection. Following subsequent thawing, CPOM samples were rinsed with deionised water to remove macroinvertebrates. Small invertebrates present within epilithon and seston samples were removed using forceps. To minimise the effect of intraspecific variation, and make up the biomass required for SIA, collected macroinvertebrates were combined into integrated samples of varying numbers of individuals (*Baetis*: 10-15; *D. cephalotes*: 3-5; *Hydropsyche*: 2-5; *Leuctra*: 10-15), dependent on individual size and relative abundance.

Samples were transferred to glass vials and freeze-dried at -60 ºC for 48 h. Dried samples were ground until homogenized, and weights required for analysis (1 ± 0.2 mg for invertebrate tissue, 3 ± 0.2 mg for autotrophic material) were packaged within tin capsules (Elemental Microanalysis Ltd., UK) and transferred to a sterile 96 well plate. All samples were then submitted to the University of California, Davis, Stable Isotope Facility for dual $\delta\ ^{13}C$ and $\delta\ ^{15}N$ analysis using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, U.K.). These apparatus have a reported long-term standard deviation of 0.2 ‰ for ^{13}C and 0.3 ‰ for ^{15}N. Where reported, stable isotope values are given in delta (δ) notation, where quantities of each isotope are expressed as parts per thousand (‰) deviation from international standards (Vienna Pee Dee Belemnite for carbon and atmospheric air for nitrogen).

4.2.8: Statistical analyses

Statistical analyses were conducted in R Version 2.15.2 (R Development Core Team, 2012). General Linear Mixed Models (GLMM) constructed using the *lme* function within the *nlme* package (Pinheiro *et al*., 2013) were used to assess differences in total macroinvertebrate biomass, density, CPOM biomass, FFG-by-FFG biomass and proportional FFG representation between control and experimental reaches before and after litter addition. All models included site type (experimental vs. control), sampling period and the interaction between these two factors as fixed effects, while individual site identity was included as a random term, to account for non-independence of samples collected from individual sites. Tukey's Honest Significant Difference (HSD) *post-hoc* comparisons were used to examine differences between factor levels. Where necessary, data were log or Box-Cox transformed to meet linear model assumptions of normally distributed, homoscedastic residuals and a lack of spatiotemporal autocorrelation. Due to their proportional nature, FFG representation data were transformed using arcsine square root (Sokal and Rohlf, 1995) or modified empirical logistic transformations (Warton and Hui, 2011), dependent upon which met linear model assumptions.

The incorporation of terrestrial litter into invertebrate diets was appraised using the SIAR *(Stable Isotope Analysis in R)* package, *version 4.1.3* (Parnell *et al*., 2010). SIAR is a mixing model based on Bayesian inference, which estimates the relative proportion of a range of sources to the diet of consumers as probability distributions, and allows for incorporation of the inherent uncertainties (i.e. standard deviations) in the isotopic signals of sources, consumers and trophic enrichment factors (TEFs) (Parnell *et al*., 2010). Trophic enrichment factors measure the extent to which the relative proportions of stable isotopes change predictably as they move between trophic levels, and can have extremely significant consequences for the output of Bayesian mixing models (Bond and Diamond, 2011). As a result, TEFs in this study were determined from real data. An estimate of ^{15}N enrichment between each trophic level was obtained by subtracting the mean $\delta^{15}N$ of sampled basal resources (CPOM and epilithon) across all study sites and sampling periods from the mean $\delta^{15}N$ of the two primary consumers collected (*Baetis* and *Leuctra*). This gave a TEF of 3.23 ‰, which was similar to the mean enrichment value (3.4 ‰) used most commonly (Post 2002). A standard deviation of ± 1 was assumed, in order to account for variation in this TEF between taxa and/or sampling periods. These values were used in all fitted mixing models except those for *D. cephalotes*: SIAR is typically used for consumers one trophic level above their putative food sources, and as this study aimed to assess how potential changes were conserved through the food web, models for the secondary consumer *D. cephalotes* had one further level of trophic enrichment added (i.e. TEFs of 1 ± 1 ‰ and 6.46 ± 2 ‰ were used for ^{13}C and ^{15}N, respectively). This allowed an assessment of ultimate basal resource incorporation in *D. cephalotes*, rather than determined reliance on proximate primary consumer prey. As isotopic values of seston were invariably intermediate between terrestrial and in-stream production at the sites, seston was not included as a putative food resource in mixing models fitted for consumers. Instead, a mixing model was used to assess the proportional contribution of these two resources to seston biomass (Table 4.2), with a minor TEF for ^{15}N of 1 ± 1 assumed to account for potential microbial colonisation of this resource.

A general linear model (GLM) was used to assess whether CPOM and epilithon were significantly distinct with respect to $\delta\ ^{13}C$ values prior to fitting mixing models, as SIAR is unable to estimate proportional dietary contributions reliably when sources do not differ (Parnell *et al.*, 2010). Basal resource data were pooled to create long-term averages across all sampling occasions, to minimise the effect of spatiotemporal variation. Where basal resources were distinct, SIAR models, based on 500,000 iterations, with the first 50,000 discarded (Parnell *et al.*, 2010), were then fitted on a consumer-by-consumer, site-by-site basis, to assess initial diets of study taxa, and responses following litter addition.

4.3: Results

4.3.1: CPOM biomass

Although site type (experimental vs. reference) did not affect CPOM standing stocks across the entire study ($F_{1,125} = 0.680$, $p = 0.411$), litter addition increased benthic CPOM biomass at experimental sites: values were significantly affected by sampling period ($F_{6,125} = 5.111$, $p = 0.001$; Fig. 4.1a) and varied between site types during one or more sampling periods (treatment*time interaction: $F_{6,125} = 7.985$, $p < 0.001$). *Post-hoc* comparisons indicated increased standing stocks of CPOM within the experimental reaches during February 2012 (Fig. 4.1a), compared to both concurrent stocks in reference reaches (Tukey's HSD: $p < 0.001$), and experimental reaches during the pre-treatment year (February; June; October 2011: $p < 0.001$ in all cases). CPOM stocks then fell to pre-treatment levels by April 2012, 12 weeks after the conclusion of litter addition pulses. CPOM in experimental sites during this period did not differ significantly from either pre-treatment levels (February; June; October 2011: $p > 0.05$ in all cases) or reference reaches ($p = 0.988$), and remained low until sampling ended in October 2012.

4.3.2: Macroinvertebrate biomass and density

Despite significant increases in CPOM availability following experimental addition, total macroinvertebrate biomass was unaffected by manipulation. Biomass varied significantly with sampling period ($F_{6,125} = 3.908$, $p < 0.001$) and between experimental and refence sites ($F_{1,125} = 24.149$, $p < 0.001$), but this reflected background differences even prior to manipulation, and there was no significant time-treatment interaction ($F_{6,125} = 0.922$, p =

0.482; Fig 4.1b). Similarly, macroinvertebrate density differed significantly between sampling periods ($F_{6,125}$ = 2.964, p = 0.010) and between experimental and control sites ($F_{1,125}$ = 20.709, p < 0.001), but not due to litter addition (treatment*time interaction: $F_{6, 125}$ = 0.818, p = 0.558; Fig. 4.1c).

4.3.3: Functional feeding groups

Responses of individual Functional Feeding Groups to litter addition were generally minimal. Neither the biomass nor density of Collector-Gatherers (Biomass: $F_{6, 125}$ = 1.041, p = 0.402; Density: $F_{6, 125}$ = 2.028, p = 0.067), Grazers (Biomass: $F_{6, 125}$ = 0.366, p = 0.899; Density: $F_{6, 125}$ = 0.765, p = 0.600), Predators (Biomass: $F_{6,125}$ = 1.173, p = 0.325; Density: $F_{6,125}$ = 1.672, p = 0.133) and Shredders (Biomass:$F_{6, 125}$ = 0.624, p = 0.711; Density: $F_{6,125}$ = 1.068, p = 0.385) differed significantly between the experimental and control streams as a result of litter addition, as revealed by non-significant interaction terms. Filterer biomass differed significantly between sampling periods ($F_{6, 125}$ = 2.490, p = 0.026), due to significantly increased biomass at the control sites during April 2012 (Tukey’s HSD: p = 0.016), though there was no concurrent density response ($F_{6, 125}$ = 2.110, p = 0.057). No proportional contribution of individual FFG biomass or density to total values were affected by litter addition with the exception of Filterers, which differed between study periods (Proportion Biomass: $F_{6,125}$ = 2.711, p = 0.017; Proportion Density: $F_{6,123}$ = 2.306, p = 0.038) due to increases at reference sites during April 2012.

4.3.4: SIAR mixing models

When averaged across all sampling periods, δ ^{13}C values for CPOM and epilithon were significantly different at all sites (Tukey's HSD: $p < 0.001$ in all cases). Individual epilithic samples at MO5 and MO6 were, however, extremely variable and, at different times, could be either more or less enriched in ^{13}C (MO5 range: -13.43 ‰ to -33.76 ‰; MO6 range -25.46 ‰ to -41.37 ‰) relative to terrestrial production (MO5 long-term mean = -29.48 ‰; MO6 long-term mean= -28.64 ‰). Mixing models were therefore only fitted for MO2 (Experimental and Control reaches) and MO3. Dietary responses to litter addition in the experimental reach at MO2 were minimal for all focal taxa, and there were no effects following litter addition compared to either the upstream control reach or the reference site (Fig. 4.2; Table 4.2). All models indicated more or less equal reliance on terrestrial and in-stream production by all consumers sampled, though with some seasonal variation (Table 4.2).

4.4: Discussion

Overall, these data illustrate how litter addition elevated benthic CPOM at the experimental sites, but the effect was short-lived. Moreover, there were no effects on macroinvertebrate biomass, density, functional feeding group composition, or dietary incorporation of terrestrial subsidies into focal invertebrate taxa. These outcomes provide no support for any of the hypotheses tested, and this contrasts with the expectations that headwater streams should be heterotrophically-dependent (Richardson, 1991; Melody and Richardson, 2004; Pretty and Dobson, 2004). Increased CPOM availability in such streams typically results in community-wide changes in macroinvertebrate assemblage structure, including increases in biomass and changes in functional composition, but these were not evident in this study. Possible explanations for the weak effects observed here include limitations in experimental scale and duration, low retention of added material or prior adjustment of the invertebrate community to autotrophic production all affected outcomes. These possibilities are evaluated below.

Supplied litter subsidies and subsequent increases in benthic CPOM (ca. 30,000 % compared to pretreatment levels) may have been insufficient to support increased macroinvertebrate biomass. Standing stocks of CPOM at both MO2 (60.83 ± 44.39 g m^{-2}: Mean ± 1 SE) and MO5 (22.02 ± 13.05 g m^{-2}) during February 2012 were, however, comparable to those at two contemporaneously monitored sites with extensive riparian deciduous tree cover (4.65 ± 1.91 g m^{-2}; 76.34 ± 54.17 g m^{-2}: see Chapter 3), and were within the lower range typically reported for forested streams worldwide (1 > 1000 g m^{-2}: Abelho, 2001; Pozo and Elosegi, 2005). Alternatively, increases in standing stocks of CPOM may have been too short-lived to become a viable food resource for in-stream consumers; aquatic detritivores require microbial colonization of recalcitrant litter material before it becomes palatable (Golladay *et al.*, 1983; Graca, 2001), and litter supplied may not have been retained long enough for this to occur. That standing stocks were still significantly elevated four weeks following cessation of litter addition does, however, suggest that CPOM availability was at least elevated all winter (early November to mid-February). Litter should, therefore, have been *in situ* sufficiently long for microbial colonization and breakdown to commence, making subsidies available to consumers (Golladay *et al.*, 1983). Moreover, though CPOM levels were not significantly higher in April 2012, mean standing stocks were still on average 1500 % greater than pre-treatment levels (~2 g m^{-2} vs. ~140 mg m^{-2}). Nevertheless, subsidies may still have been too small-scale, transient or insufficiently incorporated into food webs to influence macroinvertebrate communities and detritivorous taxa; woodland streams typically have continual supplies of litter from lateral areas, and as such have elevated CPOM availability year-round (Abehlo, 2001; Elosegi and Pozo, 2005; Chapter 3). Additionally, energy-flow and community composition in streams can often reflect catchment-wide, rather than reach-scale, land use (Allan *et al*., 1997; Kauffman *et al*. 1997; Harding *et al*., 1998; England and Rosemond, 2004; Chapter 2). Effects in the 20 m experimental reaches may have therefore been swamped by larger catchment land use influences.

If subsidy supplies were, in principle, sufficient to influence in-stream consumers, however, resident macroinvertebrate communities may have mediated the lack of effects observed. For instance, Shredder biomass in these moorland streams prior to litter addition was generally low (Chapter 3), and initial Shredder populations may have proven inadequate to respond to this subsidy pulse in such a way as to elevate total macroinvertebrate biomass and density significantly. This suggests that larger-scale, multi-year subsidies may be required to allow Shredder populations to become more fully established, and for shifts in community functional composition to become apparent. Alternatively, non-response may have been due to consumer resource preference; epilithon is generally a higher quality resource than CPOM (Marcarelli *et al*., 2011), and C:N ratios of 10.83 ± 3.35 (mean ± 1 SD) and 43.99 ± 20.96 were observed in this study, for epilithon and CPOM, respectively. Macroinvertebrate taxa may, therefore, have preferentially selected higher-quality epilithon, at the expense of subsidized terrestrial resources; responses to subsidies in many freshwater ecosystems are often dependent upon interactive effects between the quantity and quality of subsidized resources, relative to available autochthonous production (Marcarelli *et al*., 2011). Streams in heavily shaded, heterotrophic catchments could, therefore, benefit from increased inputs of terrestrial organic matter to a greater degree than unshaded streams, where high quality autotrophic primary production may be more widely available (Hill *et al*., 1995; Kiffney *et* *al*., 2003, 2004). This mirrors recent findings in lentic ecosystems, where responses to litter subsidies co-varied with canopy cover in woodland ponds (Earl and Semlitsch, 2013). This suggests that changes in food web structure likely to result from restoration of riparian tree cover may not begin to take effect until canopy closure occurs and light becomes limiting to in-stream autotrophs. If so, stream macroinvertebrate communities would then be forced, via resource availability, to become more fully dependent upon allochthonous subsidy inputs.

Though largely inconclusive, these data emphasise the importance of considering magnitude and duration of subsidy pulses when attempting to restore energetic linkages across ecotones. In upland headwater streams, input and retention of leaf litter in restored streams should be sufficient to offset downstream export of CPOM, which is often substantial (Wallace *et al*., 1995; Eggert *et al*., 2012). As such, this outcome provides further support for suggestions that riparian woodland restoration intended to increase headwater production should have sufficient extent to overcome such effects (Chapter 2; Chapter 3).

4.5: References

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4.6: Tables and Figures

Table 4.1: Physical and chemical characteristics of upland Welsh sites used in an experiment evaluating the effects of terrestrial leaf litter subsidies.

Site I.D.	Site Type	Latitude	Longitude	Mean pH	Mean Conductivity (µS)	Elevation (m)	Mean Depth (cm)	Mean Width (m)	Catchment Area (km^2)	Distance from Source (km)
MO2	Experimental	51.868728	-3.468676	6.78	20.33	474	23.25	4.35	3.33	2.17
MO3	Reference	51.867111	-3.419194	7.80	43.67	465	19.50	3.38	3.66	2.18
MO5	Experimental	51.849353	-3.561866	7.18	90.67	396	19.58	3.48	3.60	1.97
MO6	Reference	51.873047	-3.668318	7.40	48	395	23.08	4.98	3.92	2.91

Table 4.2: Proportional contribution of Coarse Particulate Organic Matter (CPOM) to consumer diets and seston composition in upland streams used to evaluate effects of terrestrial leaf litter subsidies. Values reported are mean estimated proportions, along with lower (L.C.I.) and upper (U.C.I.) 95% credibility intervals, as determined from fitted SIAR mixing models.

Site	Sampling Period	Consumer taxa														
		Baetis			*Dinocras*			*Hydropsyche*			*Leuctra*			Seston		
		Mean	L.C.I.	U.C.I.	Mean	L.C.I.	U.C.I.	Mean	L.C.I.	U.C.I.	Mean	L.C.I.	U.C.I.	Mean	L.C.I.	U.C.I.
MO2 Control	April 2011	0.33	0.02	0.62	0.54	0.28	0.81	0.43	0.10	0.69	0.38	0.10	0.62	0.63	0.25	0.98
	October 2011	0.43	0.17	0.67	0.63	0.40	0.88	0.49	0.21	0.76	0.54	0.18	0.85	0.68	0.26	1.00
	February 2012	0.46	0.21	0.69	0.54	0.30	0.78		N/A†		0.65	0.24	0.99	0.69	0.21	1.00
	April 2012	0.54	0.30	0.79	0.54	0.31	0.78		N/A†		0.54	0.22	0.83	0.66	0.36	0.96
	June 2012	0.54	0.30	0.78	0.52	0.27	0.77		N/A†		0.52	0.19	0.82	0.61	0.23	0.95
MO2 Experimental	April 2011	0.31	0.00	0.62	0.48	0.16	0.75	0.44	0.12	0.70	0.39	0.07	0.64	0.68	0.37	0.93
	October 2011	0.47	0.18	0.71	0.58	0.29	0.84		N/A†		0.58	0.29	0.84	0.76	0.41	1.00
	February 2012	0.42	0.10	0.69	0.56	0.28	0.82		N/A†		0.64	0.35	0.91	0.77	0.45	1.00
	April 2012	0.49	0.20	0.75	0.56	0.30	0.81	0.63	0.31	0.92	0.59	0.29	0.86	0.61	0.26	0.96
	June 2012	0.52	0.24	0.77	0.48	0.18	0.75		N/A†		0.52	0.22	0.77	0.67	0.37	0.92
MO3	April 2011	0.66	0.32	1.00	0.64	0.40	0.89	0.64	0.28	0.99	0.58	0.11	0.74	0.39	0.08	0.64
	October 2011	0.51	0.18	0.81	0.56	0.32	0.81	0.47	0.18	0.73	0.48	0.18	0.75	0.50	0.16	0.80
	February 2012	0.53	0.24	0.89	0.55	0.32	0.79	0.44	0.12	0.71	0.48	0.16	0.77	0.47	0.10	0.77
	April 2012	0.73	0.39	1.00	0.56	0.32	0.79	0.51	0.16	0.82	0.48	0.15	0.78	0.30	0.20	0.56
	June 2012	0.75	0.46	1.00	0.57	0.34	0.82	0.48	0.16	0.77	0.42	0.11	0.70	0.46	0.15	0.73

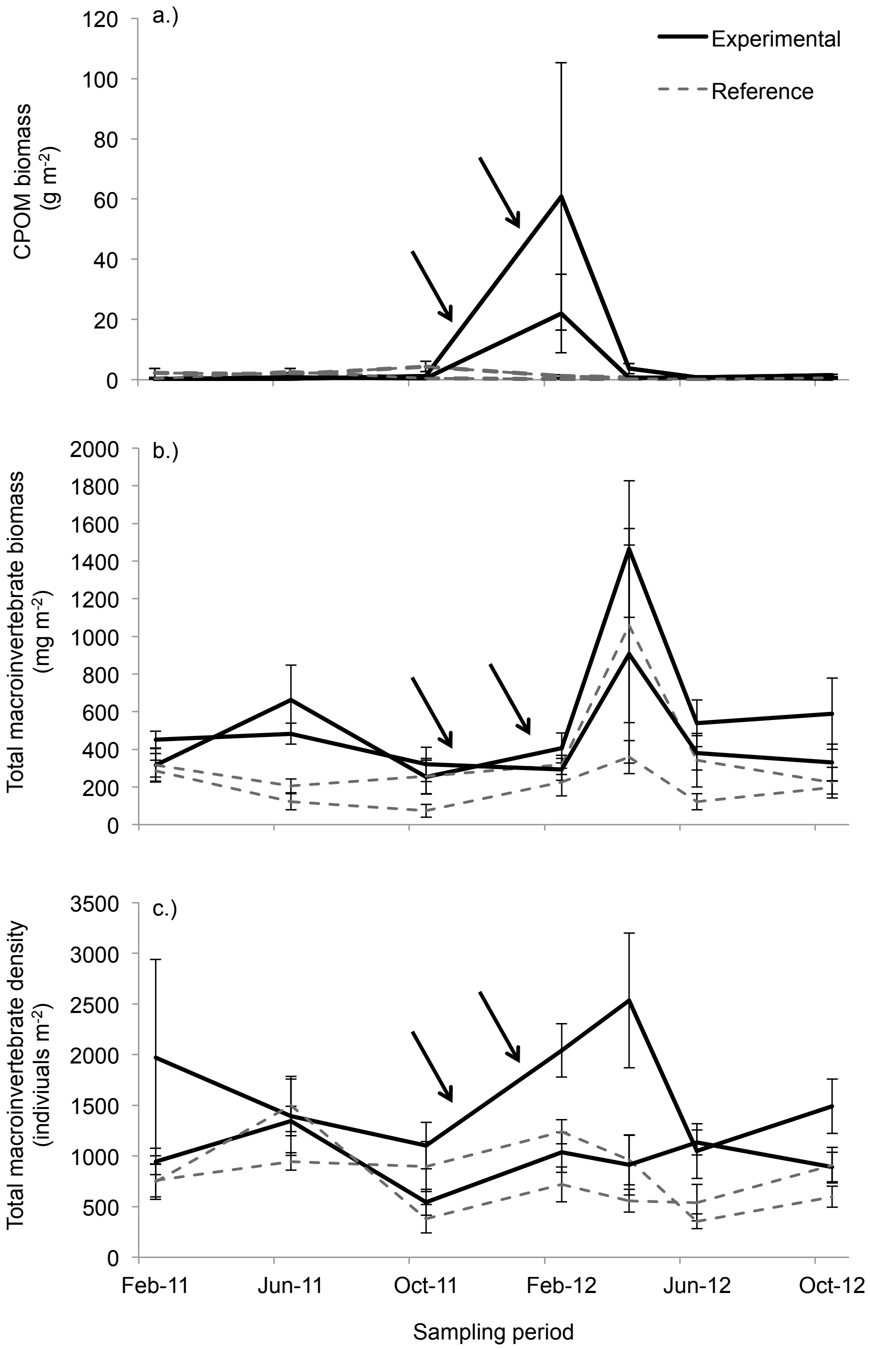
† Time periods where consumer was not present at sampling sites.

4.6.1: Figure Legends

Figure 4.1: Standing stocks of benthic CPOM a.), macroinvertebrate biomass b.) and macroinvertebrate density c.), in stream reaches subject to experimental leaf-litter addition (n = 2; solid lines) and adjacent reference sites (n = 2; dashed lines). Approximate start and end of litter addition are indicated by arrows (litter was added at fortnightly intervals from early Nov. 2011 – mid Jan. 2012). Values shown are mean ± 1 SE.

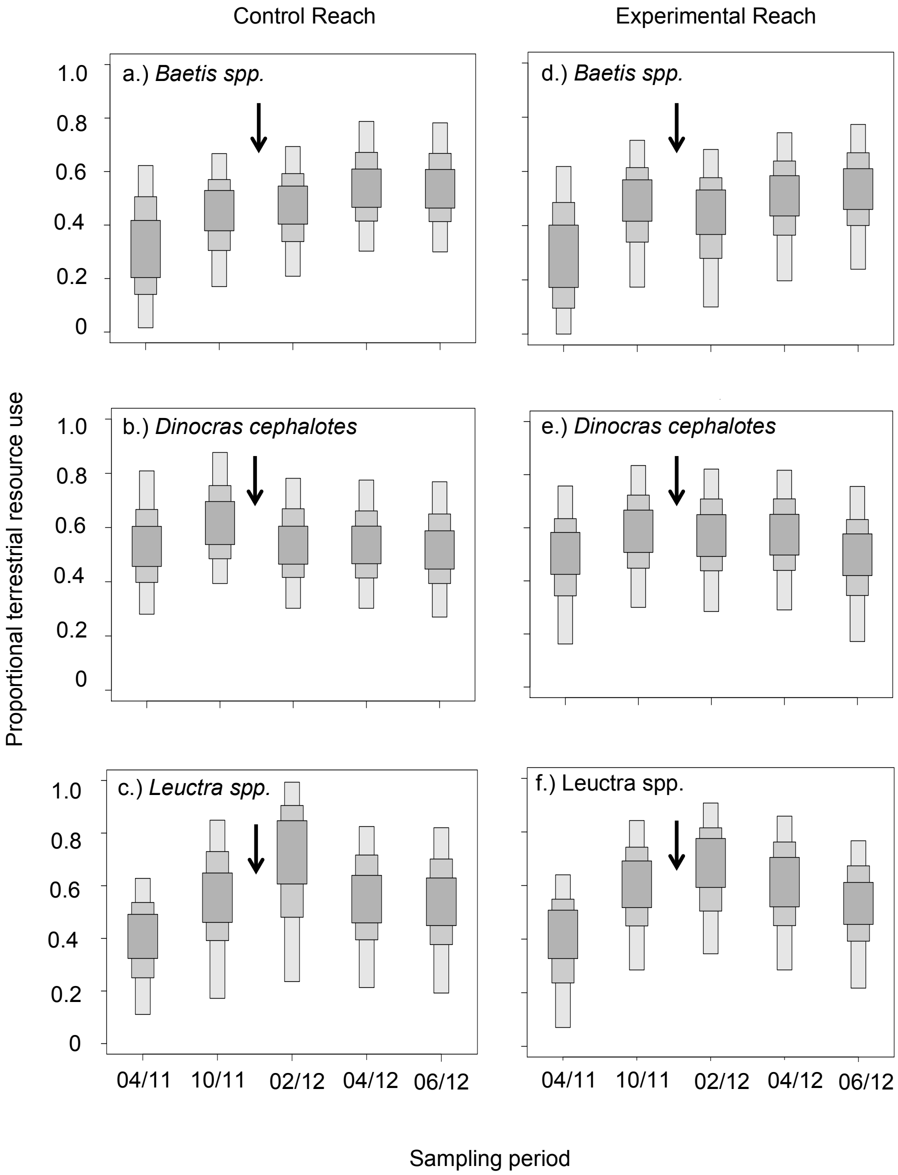
Figure 4.2: Proportional contribution of CPOM to the diets of focal consumer taxa (*Baetis spp*., *Dinocras cephalotes* and *Leuctra spp*.) across sampling periods, as estimated by SIAR Bayesian mixing models. Litter addition occurred between the second and third sampling periods, as indicated by arrows (mid Nov. 2011 – mid Jan. 2012). Bars represent 25, 50 and 95% credibility intervals for these estimates.

Figure 4.1:



a.)
Experimental
Reference
CPOM biomass (g m^{-2})
0
20
40
60
80
100
120
b.)
Total macroinvertebrate biomass (mg m^{-2})
0
200
400
600
800
1000
1200
1400
1600
1800
2000
c.)
Total macroinvertebrate density (indiviuals m^{-2})
0
500
1000
1500
2000
2500
3000
3500
Feb-11
Jun-11
Oct-11
Feb-12
Jun-12
Oct-12
Sampling period

Figure 4.2:


Control Reach
Experimental Reach
a.) *Baetis spp.*
b.) *Dinocras cephalotes*
c.) *Leuctra spp.*
d.) *Baetis spp.*
e.) *Dinocras cephalotes*
f.) Leuctra spp.
1.0
0.8
0.6
0.4
0.2
0
Proportional terrestrial resource use
04/11
10/11
02/12
04/12
06/12
Sampling period

Chapter 5: Effects of riparian land use on salmonid fish populations in temperate, upland streams

5.0: Summary

1. Stream-dwelling salmonids (Family: Salmonidae) are at risk from climate change because of their physiological and life-history requirement for cooler waters. Due to the economic and ecological importance of salmonids, there is interest in adaptive management strategies to limit impacts, for example the restoration of riparian tree cover that might reduce and stabilize headwater temperatures. Riparian trees might also affect allochthonous food subsidies to salmonids, but such effects are still poorly quantified.

2. Using upland temperate streams with differing catchment tree cover as surrogates for contrasting adaptation options, this study appraised whether (i) density, biomass and individual size; (ii) dietary reliance on terrestrial production in brown trout (*Salmo trutta)* varied with land use; and (iii) whether trout use of terrestrial production across sites tracked that in aquatic macroinvertebrates.

3. Contrary to expectation, riparian land use had no systematic effect on trout density, individual size or dependence on terrestrial production. There was, however, a trend toward reduced salmonid and total fish biomass at streams draining conifer forest, in contrast to all other riparian land use types. Rather than reflecting land use, trout dependence on terrestrial resources was highly variable among streams, mirroring

patterns in macroinvertebrates. On average, trout used more in-stream (62 ± 3 %: mean ± 1 SE) than terrestrial (38 ± 3 %) production.

4. These results imply that restoration of riparian broadleaf cover in deforested upland catchments is unlikely to change either brown trout production, or the relative importance of basal resources supporting communities in such streams. These data provide potential support for suggestions that, beyond a minimum threshold, salmonid production is constrained by density-dependent effects on territory size rather than food supply. Restoration of semi-natural riparian broadleaf cover should therefore be able to confer thermal benefits to salmonid populations without adversely affecting food web dynamics or jeopardizing fish production.

5.1: Introduction

Many salmonid populations worldwide are in decline due to factors at least partially attributable to changes in global climate (Parrish, 1998; Bradford and Irvine, 2000). Evidence is also increasing that salmonids will be susceptible to predicted future warming, based on their physiology, complex life histories and use of climate-sensitive marine and freshwater environments (Ficke *et al*., 2007; Jonsson and Jonsson, 2009; Clews *et al*. 2010; Elliot and Elliot, 2010). The mechanisms are numerous, but include requirements of all life stages for cool-water environments, sensitivity to varying flow conditions and indirect effects through stressors or resources, such as prey abundance, with which climate interacts (Ficke *et al*., 2007; Jonsson and Jonsson, 2009; Clews *et al*. 2010; Elliot and Elliot, 2010).

Concern about the economic and ecological effects of climate change on salmonids is prompting widespread interest in adaptive management strategies that may be able to limit adverse effects on these species. Salmonids might also be affected where riparian management is used to protect other organisms or restore functions in the ecosystems they occupy. For example, the restoration or enhancement of broadleaf tree cover in riparian zones is advocated as a potential means of protecting temperate, headwater stream ecosystems used often by migratory salmonids during spawning (Battin *et al*., 2007; Ormerod, 2009; Palmer *et al*., 2009; Seavy *et al*., 2009; Clews *et al*. 2010). Empirical and modeling evidence demonstrates the capacity of this technique to offset significant climate impacts for many salmonid populations (Zoellick, 2004; Battin *et al*., 2007; Broadmeadow *et al*, 2011).

Changes in riparian land use have the potential not only to affect stream thermal regimes and discharge (Bosch and Hewlett, 1982; Bradshaw *et al*. 2007; Broadmeadow *et al*, 2011), but also influence fish populations and communities through wider resource availability (Schlosser, 1991). Indeed, there is some evidence that past attempts to restore riparian zones have under-emphasised consequences for ecosystem processes and nutrient cycling (Goodwin *et al*., 1997; Naiman *et al*., 2012). Stream food webs are intimately linked with their surrounding terrestrial riparian zone by a complex flux of matter and energy in the form of organisms and their products, for example the input to streams from leaf fall or export from the emergence of aquatic insects (Wallace *et al*., 1997; Nakano and Murakami, 2001; Baxter *et al*., 2005). Changes in riparian canopy cover can shift the autotrophic-heterotrophic balance of stream food webs both through such reciprocal subsidies and through changes in autochthonous algal production relative to stocks of allochthonous detritus (Wallace *et al*., 1997; Kawaguchi and Nakano, 2001). These modifications to energy flows are liable to affect food supply to salmonids, either directly via supply of terrestrial invertebrates (Wipfli, 1997; Kawaguchi and Nakano, 2001; Allan *et al*., 2003), or indirectly via effects on aquatic macroinvertebrate secondary production (Wipfli and Musselwhite, 2004; Riley *et al*. 2009; Chapter 3), with shifts towards terrestrial dependence as forest cover increases. Moreover, because food supply is a key driver of fish production, effects on prey abundance mediated through riparian vegetation are likely to influence salmonid production (Wipfli and Baxter, 2010).

So far, the array of studies appraising the potential trophic effects of riparian broadleaves for salmonids as part of climate change adaptation along temperate headwaters is limited (Riley *et al*., 2009; Broadmeadow *et al*., 2011). This reflects the very recent implementation of this restoration approach and the long timescales required for full riparian restoration. Cross-sectional analysis of sites with existing riparian broadleaves of varying extent and cover provide a valuable approach on which to base predictions. Additionally, modern ecological methods – specifically the analysis of stable isotopes of carbon and nitrogen – increasingly offer a valuable means for assessing energetic linkages between terrestrial and aquatic ecosystems alongside the conventional measurement of fish density and biomass under different canopy types (Rybczynski *et al.* 2008; Ishikawa *et al.*, 2012). This is because allochthonous and autochthonous production are often isotopically distinct, and therefore their origins in freshwater organisms can be estimated (Doucett *et al.*, 1996; Ishikawa *et al.*, 2012).

The work described in this chapter used a suite of upland Welsh streams with contrasting riparian land use to assess variations in salmonid biomass, density and apparent energetic sources supporting production as revealed by stable isotopes. The study tested the hypothesis that increasing broadleaf cover in the riparian zone affects salmonid production, with effects mediated by food availability, in the form of stream macroinvertebrates (Chapter 3). Specific predictions were that (i) salmonid biomass, density and individual size would reflect available stream macroinvertebrate biomass, being greatest in deciduous woodland, lowest in conifer, and intermediate in moorland and buffer strip streams (Chapter 3); (ii) the use of terrestrially-fixed organic matter by *Salmo trutta* populations would be increased at streams with deciduous cover, compared to those draining moorland; and (iii) the use of terrestrial production by *S. trutta* populations would track that of local macroinvertebrate communities - to which trout should be trophically connected. Opportunistically, other fish species at the sites were also sampled and their biomass determined.

5.2: Materials and Methods

5.2.1: Study sites

The general study area has been described elsewhere (Chapter 2; Larsen *et al*., 2009) and in outline comprised an upland (altitude 150-900 m) region of South Wales with a temperate maritime climate (precipitation 1200-2500 mm: Met Office, 1971-2000 averages) and rural land uses underlain by Old Red Sandstone that gives rise to circumneutral, oligotrophic and mostly unpolluted runoff.

Fish populations were surveyed across a total of 18 second to third order streams that overlapped substantially with an earlier macroinvertebrate survey (Chapter 2). Sites were chosen to optimise accessibility, permissions and/or feasibility of electrofishing. The streams were also selected to represent four distinct riparian land use types, that were, respectively, open grassland/moorland streams, (Moorland; MO; n = 6); grassland buffer sites (Buffer; GB; n =5): grassland catchments with 10 - 40 m bands of native broadleaves in the riparian zone, mostly of alder *Alnus glutinosa*, birch *Betula pendula*, ash *Fraxinus excelsior* and oak *Quercus* spp; Deciduous sites (Deciduous; DE; n = 3): where catchments still had relatively extensive areas of remnant deciduous woodland in the riparian zone (width ~ 75 – 220 m), though with grassland/moorland beyond this; Coniferous sites (Coniferous; CB; n = 4): where catchments were dominated by exotic conifer plantations of mostly sitka spruce *Picea sitchensis*, with deciduous trees in the riparian zone (~ 15 – 65 m). This range of riparian and wider catchment land uses was considered to provide a range surrogate locations that might represent future outcomes of riparian zone restoration.

5.2.2: Physicochemical character

Catchment land use data were obtained using ArcGIS (Version 9.2; ESRI, 2009). The *Arc Hydrotools* package (Version 9; Center for Research in Water Resources, University of Texas, TX, USA) was used to determine catchment area, which was then combined with the Countryside Council for Wales' habitat land-cover map (Countryside Council for Wales, 2004) to apportion land use by percentage cover (Table 5.1). Riparian buffer lengths and widths were estimated at 100m intervals along each stream using Google Earth (Version 5.2; Google, Inc., 2012), which was also used to determine site elevations and distance from source data. Width and depth were measured at 10m intervals in each reach. Potential differences in ionic composition among land uses was assessed from water samples collected during base-flow in June. Conductivity, total dissolved solids and pH were assessed at each site immediately following a storm event in October 2011, as values are likely to be at their most extreme during high flow, and any associated acid episodes can influence acid sensitive taxa (Soulsby, 1995; Kowalik, 2007). Physicochemistry of each sampling site is described in greater detail in Chapter 2.

5.2.3: Electrofishing survey

Fish populations at the study sites were surveyed at base-flow during August 2012 via quantitative electrofishing in representative 30 m reaches that were enclosed with stop nets (mesh size: 10 mm^2). Reaches sampled in each stream had been used previously in macroinvertebrate assessments (Chapter 2; Chapter 3), but at two sites (MO2 and MO5) new reaches (500 m upstream of the previously used reaches) were chosen to avoid interference from an experimental manipulation of litter supply conducted the previous winter (Chapter

4). Resident fish were captured in a standard three-pass depletion procedure, using a battery-powered Pulsed DC Electracatch bankside set-up (Smith-Root Europe, Ltd.) at a frequency of 50 Hz – considered to optimize Salmonid catches (Beaumont, 2011) – and applied voltage was determined based upon site-specific conductivity. This three-pass method generally captures a large pool of all individuals present, and produces data representative of total abundance in upland streams (Kruse *et al.*, 1998). Fish caught during each pass were transferred immediately to a holding container containing stream water. After each pass, individuals were identified to species (using Maitland, 1972), weighed to the nearest gram, and had fork length (FL) measured to the nearest millimeter. Biomass and abundance data from fish collected during all three passes at each site were totalled and converted to m^{-2} estimates for analysis.

5.2.4: Length-mass regression and mass estimation of larger fish

Due to a fault with a high-range balance during remote fieldwork, the mass of brown trout > 135 mm (around 20 % of fish in the total sample) could not be accurately measured in the field. Instead, the mass of these larger individuals was determined using a length-mass regression, based on the observation that these two values are extremely closely correlated (Elliott, 1984). Though there are published estimates of this relationship (Elliott, 1984), local factors can affect it (Ormerod *et al.*, 2004). A specific length-mass regression was therefore fitted to all trout < 135 mm collected during this survey as:

$$WM = -0.007232*FL + 0.00001152*FL^3 + 0.3559$$

Where WM is the Wet Mass (g) of each individual, and FL is its measured Fork Length (mm). This model, with its cubic term to capture non-linear gain in mass per unit length, described the original data very closely (adjusted $R^2 = 0.975$, $F_{2, 450} = 8625$, $p < 0.001$), and was therefore used to model the wet weight of all individuals larger > 135 mm, with these values then used in all subsequent analyses of salmonid and total fish biomass.

5.2.5: Stable isotope collection, processing and analysis

The stable isotopic composition of a consumer's tissues, particularly ratios of $^{12}C/^{13}C$ and $^{14}N/^{15}N$, can be used to estimate both its dependence on isotopically distinct food resources, and its trophic position (Post, 2002; Layman *et al*., 2012). When applied to species within a food web, isotopic methods can be used to infer trophic pathways (Layman *et al*., 2012). Stable isotope analysis is particularly conducive to tracing energy flow through terrestrially subsided stream ecosystems because allochthonous and autochthonous production are often isotopically distinct (Ishikawa *et al*., 2012). Isotopic methods are being used increasingly to quantify trophic groupings, positions in food-webs, food web structure, energy flow and reliance on terrestrial production (Rybczynski *et al*. 2008; Layman *et al*, 2012).

To assess potential systematic variation in terrestrial reliance between streams in different riparian land use, this study used dual $\delta\,^{13}C$ and $\delta\,^{15}N$ analysis, with coarse particulate organic matter (CPOM) used as a proxy for total terrestrial production, and attached epilithon used as a proxy for total autotrophic production (Ishikawa *et al*., 2012). This method allows for estimates of the relative importance of terrestrial versus in-stream organic matter to the diets of brown trout populations providing that the two resources are isotopically distinct. This condition was satisfied at 13 of the sites (see *SIAR Mixing Models* below).

To estimate isotopic composition in trout at each site, a sub-sample of five 1+ individuals collected via electrofishing (FL = 94.64 ± 19.00 mm; mass = 10.94 ± 8.43 g; mean ± 1 SD) were sacrificed humanely, and retained. Sacrificed individuals were stored in screw-top vials, and frozen at -18 °C within 8 hours of capture. Epilithon from three rocks located throughout the sampling reach was collected contemporaneously to provide a concurrent estimate of the isotopic composition of in-stream production. Epilithon and CPOM (collected via kick sampling: see Chapter 2) were sampled similarly during June 2010 and January 2011 at all sites, as part of an earlier survey (Chapter 2). Additional samples were also collected at irregular intervals from a subset of sites (MO2, MO3, MO5, MO6, DE1 and DE5) at which both resources were sampled in-depth at irregular intervals between April 2011 and June 2012 (Chapter 4). Macroinvertebrate samples for isotopic analysis were collected from all streams during June 2010 and January 2011 via kick sampling, assigned to one of four major functional feeding groups (FFGs) following Moog (1995), and data analysed previously (Chapter 2).

Trout and epilithon samples were later thawed for preparation, and lateral muscle tissue was removed from each fish posterior to the dorsal fin using a scalpel and transferred to a glass vial for freeze-drying at -60 °C for 48 hours. White muscle tissue was chosen for analysis due to its small isotopic variability, and ability to reflect accurately the isotopic composition of salmonid diets (Pinnegar and Polunin, 1999). Following freeze-drying, tissue samples from each individual were removed with forceps from the larger area of excised tissue, homogenized, and 1 ± 0.2 mg was weighed into a tin capsule. Collected integrated CPOM and epilithon samples were also freeze-dried and homogenized, with 3 ± 0.2 mg then similarly encapsulated for analysis. Macroinvertebrate samples were processed previously using the same general procedure (Chapter 2)

All isotopic samples were analysed at the University of California, Davis, Stable Isotope Facility for dual $\delta\ {}^{13}C$ and $\delta\ {}^{15}N$ analysis, using a PDZ Europa ANCA-GSL elemental analyser, interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, U.K.). The reported long-term standard deviation of these apparatus is 0.2 ‰ for ${}^{13}C$ and 0.3 ‰ for ${}^{15}N$ (as determined from laboratory standards). Where reported, stable isotope values are expressed in delta (δ) notation, where quantities of each isotope are expressed as parts-per-thousand (‰) deviation from international standards (Vienna Pee Dee Belemnite for carbon and atmospheric air for nitrogen)

5.2.6: Statistical analyses

All statistical analyses were conducted in the statistical computing package R (version 2.15.2; R Core Development Team, 2012), with stable isotope mixing models completed within the SIAR package (*Stable Isotope Analysis in R; version 4.1.3*; Parnell *et al*., 2010), and mixed effects models carried out using the *lme* function in the *nlme* package (version 3.1.108; Pinheiro *et al*., 2013).

5.2.7: General linear models

Following an earlier analysis of macroinvertebrate data from the same sites (Chapter 2), possible variation across streams in factors that might confound the assessment of riparian land use effects trout biomass, density and individual mass were first modeled against abiotic covariates (mean pH, mean conductivity, PC1 scores from anion and cation data, elevation, mean depth, mean width, catchment area, distance from source, presence of a downstream reservoir), and stepwise deletion used to remove all that were not related significantly to fish variables. Any remaining significant variables were included as covariates in General Linear Models (GLM) carried out to examine variations in total salmonid density (individuals m^{-2}), salmonid biomass (g m^{-2}), mean salmonid individual mass (g), mean salmonid length (mm), total fish density (individuals m^{-2}), total fish biomass (g m^{-2}) and proportional contribution of terrestrial organic matter to the diet of sub-sampled brown trout as estimated using SIAR (see below). Site MO4 was fishless (probably due to downstream barriers to migration), and thus excluded from all subsequent analyses.

5.2.8: SIAR mixing models

Estimations of the ultimate incorporation of terrestrial versus in-stream resources to trout diet at each site were obtained using $\delta\,^{13}C$ and $\delta\,^{15}N$ values in fish tissue and basal resources using the SIAR mixing model. SIAR uses Bayesian inference to estimate the relative proportion from possible sources to the diet of consumers as probability distributions, and allows for incorporation of the inherent uncertainties (i.e. standard deviations) present in the isotopic signals of sources, consumers and trophic enrichment factors (TEFs) (Parnell *et al.*, 2010). TEFs are the extent to which heavier isotopes are preferentially taken up or excreted at each trophic level (Martínez del Rio *et al.*, 2009; Parnell *et al.*, 2010). This study used TEFs of 1 ± 1‰ for ^{13}C, and 6.46 ± 2‰ for ^{15}N (based on mean difference between primary consumers and basal resources in an earlier study: see Chapter 4) in all models. These TEFs assumed that trout were approximately two trophic levels removed from primary production, whilst incorporating potential for variability.

The isotopic composition of consumer tissues typically reflects resource use over timescales ranging from months to years (Hesslein *et al.*, 1993). Moreover, spatiotemporal variability in isotopic signals of epilithic biofilms is often pronounced (Ishikawa *et al.*, 2012; Chapter 4). As such, to estimate isotopic signatures in basal resources at each site, whilst limiting the effect of seasonal and inter-annual variation in isotopic signals, mean $\delta\ ^{13}C$ and $\delta\ ^{15}N$ values were calculated using both data collected concurrently with fish samples in August 2012, and from samples collected as part of prior survey work conducted at the same sites during June 2010 and January 2011 (Chapter 2). Additonal supplementary data, collected at irregular intervals between April 2011 and June 2012, were also included from a subset of sites (Chapter 4: see section 5.2.5).

SIAR models were then fitted for trout at sites where basal resources were isotopically distinct: data from GB1 were excluded from the analysis, due to considerable overlap between isotopic composition of terrestrial and instream resources. Isotopic data from MO2 and MO5, where sampling locations were moved upstream for logistical reasons (see *Study Sites*), revealed large-scale spatial variation in epilithic $\delta\ ^{13}C$ values within these two sites; epilithic data were therefore deemed not equivalent to those collected during previous sampling occasions at the downstream sampling location, with mixing models not fitted due to lack of replication for basal resource data. Similarly, instream epilithic $\delta\ ^{13}C$ signatures at both MO5 and MO6 were found to be extremely temporally varible, and were alternatively more and less depeleted in ^{13}C than terrestrial production at various sampling occasions (see Chapter 4). Data from these four sites therefore violated mixing model assumptions, and were resultantly exlcuded from subsequent analyses. Ultimately, SIAR models were fitted for *S. trutta* populations at 13 of the 18 surveyed sites (Buffer, n = 4; Coniferous, n = 4; Deciduous, n = 3; Moorland, n = 2). All final fitted models were carried out using the *siarmcmcdirichletv4* function within SIAR, and were based on 500,000 iterations, with the first 50,000 discarded (Parnell *et al.*, 2010).

Data from all sites where mixing models could be applied were used in proportional contribution models. A mixed effects model was used to test whether the mean proportional contribution to trout diets of resources originating in epilithon versus CPOM was significantly different when pooled across all sites. Site identity was included as a random term in this mixed effects model to account for the non-independence of proportion data from each location. As all proportion data resulted in normally distributed, homoscedastic residuals in all models, data were not transformed prior to analysis (Warton and Hui, 2011).

Relationships between estimates of terrestrial organic matter incorporation into trout and macroinvertebrate FFGs were assessed using linear regression, at sites where both were available (n = 10). Separate regression models were fitted for each of four functional feeding groups (Filterers, Grazers, Predators and Shredders) sampled during two seasons (June 2010 and January 2011), and mean invertebrate resource use (i.e. averaged across all functional groups) in each season. To test which macroinvertebrate FFG was most likely to contribute most to trout diets in each season, deviation from a 1:1 relationship between terrestrial resource use by each macroinvertebrate group versus that by trout was assessed. This assumed that the invertebrate groups with terrestrial resource use more similar to fish were likely to be relatively more important as dietary components. Slopes for these relationships were compared using an ANCOVA model, with interaction terms used to test for whether the difference between the two slopes was significantly greater than zero (McDonald, 2009).

5.3: Results

5.3.1: Total species captured

A total of 738 fish from seven species were captured across 17 sites: Brown Trout, Atlantic Salmon (*Salmo salar*), European Bullhead (*Cottus gobio*), European Minnow (*Phoxinus phoxinus*), Northern Pike (*Esox lucius*), European Eel (*Anguilla anguilla*) and Stoneloach (*Barbatula barbatula*). Trout was the numerically dominant fish species across all streams, comprising approximately 75 % of all individuals captured. Trout was also the dominant salmonid species, with *S. salar* occurring at only two locations (GB3 and GB6).

5.3.2: Fish biomass and density

Contrary to expectations, there were no significant variations between land uses in salmonid density ($F_{3, 12} = 0.015$, $p = 0.997$), mean individual wet weight ($F_{3, 12} = 0.938$, $p = 0.453$) or length ($F_{3, 11} = 0.741$, $p = 0.549$: Table 5.1). Nor were there variations in total fish density ($F_{3, 12} = 0.658$, $p = 0.593$). There did appear to be a non-significant trend toward differential biomass, for both total fish ($F_{3, 13} = 2.695$, $p = 0.089$) and salmonids ($F_{3, 10} = 3.173$, $p = 0.072$), with potenital reductions appearent at Coniferous sites, relative to all other land use types (Fig. 5.1).

5.3.3: Incorporation of terrestrial organic matter by brown trout

Proportional contribution of terrestrial organic matter to trout tissues was highly variable among sites and not systematically affected by riparian land use category ($F_{3,9} = 3.405$, $p =$

0.067). Marginal significance does, however, suggest that greater replication at the site level may have revealed somewhat greater dependence on terrestrial production in afforested Deciduous and Coniferous catchments, when compared to moorland catchments with or without riparian broadleaf buffer strips (Fig. 5.1c). Averaged across all sites, trout were significantly ($F_{1, 24} = 26.52$, $p < 0.001$) more reliant on production originating in epilithic biomass (0.620 ± 0.033: mean ± 1 SE) than terrestrial organic matter (0.380 ± 0.033). Reliance on terrestrial production by trout and invertebrates among streams was additionally positively related among streams when using macroinvertebrate data from June 2010 (adjusted $R^2 = 0.378$, $F_{1, 8} = 6.468$, $p = 0.035$) and January 2011 (adjusted $R^2 = 0.422$, $F_{1, 8} = 7.576$, $p = 0.025$) (Fig. 5.2). Terrestrial reliance in trout was also related to that in grazing (adjusted $R^2 = 0.370$, $F_{1, 8} = 6.289$, $p = 0.037$), shredding (adjusted $R^2 = 0.602$, $F_{1, 8} = 14.62$, $p = 0.005$) and predatory (adjusted $R^2 = 0.646$, $F_{1, 8} = 17.45$, $p = 0.003$) taxa collected during January 2011 (Fig. 5.3), but not those sampled during June 2010 (Grazers: $F_{1,8} = 1.448$, $p = 0.2632$; Predators: $F_{1,8} = 2.698$, $p = 0.139$; Shredders: $F_{1, 8} = 2.087$, $p = 0.187$). No similar relationships were apparent in filtering taxa in either season (June 2010: $F_{1,6} = 3.833$, $p = 0.098$; January 2011: $F_{1,8} = 1.778$, $p = 0.219$).

When compared to seasonal averages for all functional groups, trout were similarly reliant on terrestrial production to invertebrates ($F_{1, 16} = 4.262$, $p = 0.056$), but in June 2010 they were less so ($F_{1, 16} = 4.680$, $p = 0.046$) (Fig. 5.3). Trout were also less reliant on terrestrial production than Grazers ($F_{1, 16} = 5.363$, $p = 0.034$), Predators ($F_{1, 16} = 6.773$, $p = 0.019$), and Shredders ($F_{1, 16} = 8.117$, $p = 0.012$) sampled in January 2011 (Fig. 5.2).

5.4: Discussion

The three major features to arise from these upland data are (i) the presence or absence of broadleaf cover in catchments had no effect on the density or size of either salmonids or all stream fishes. However, catchment conifer forest cover may potentially reduce biomass, relative to other land use types. (ii) For the most widespread salmonid species, brown trout, land use had, at most, minor effects on the relative use of terrestrial and in-stream production, though on average they were more connected to the latter and (iii), patterns of terrestrial vs. in-stream, resource use by brown trout generally tracked those in aquatic invertebrates on a stream-specific basis. In combination, the data unequivocally support only the third hypothesis.

Although these results suggest that catchment land use has generally minimal effects on stream fish populations, mensurative studies of this nature are at from risk from potentially confounding influences. Such comparative methods can provide a useful model for stream restoration and catchment land use change (Goodwin *et al.*, 1997; Naiman *et al.*, 2012), particularly as the decadal timescales required to reinstate mature riparian vegetation typically negate experimentation. Moreover, comparisons across land use types were generally free from major physicochemical confounds (Chapter 2). Other methodological aspects of this study may, however, also merit caution, including interpretation of stable isotope data, particularly in light of somewhat anomalous results: trout populations were nearly always more reliant on in-stream production than all macroinvertebrate functional groups across all study streams. This could suggest an in-stream food source important to trout that was not sampled, or could be due to greater-than-average isotopic fractionation occurring through several trophic levels, skewing fish isotopic composition toward that of in-stream production; indeed, the processes governing isotopic fractionation in food-webs are currently poorly understood, and system-specific rates can be variable (Martínez del Rio *et al.*, 2009). Variability is generally small, however, and was incorporated into the Bayesian mixing models employed here, and hence results are generally robust to such factors (Parnell *et al.*, 2010). Alternatively, disagreement between fish and invertebrate data could reflect the timescales over which stable isotope samples were collected, with macroinvertebrates sampled up to two years prior to fish. Isotopic turnover times in fish tissues can be very slow in wild fish populations, however, often taking up to several years for complete replacement to occur (Hesslien *et al.*, 1993). These 1+ fish would have been resident in the study streams for streams for approximately a year and a half prior to sampling, suggesting their tissues would likely reflect a time-integrated measure over an approximately equivalent period. Moreover, the strong positive relationships between stream-to-stream reliance on terrestrial resources in fish collected during 2012 and macroinvertebrates sampled during 2011 suggests that resource use patterns at the study sites were generally inter-annually stable.

Notwithstanding these issues, these data demonstrate that riparian broadleaf cover of varying extents did not appear to influence stream salmonid populations negatively, relative to those inhabiting treeless moorland catchments. The data provide limited support for potentially reduced total fish and salmonid biomass in streams draining wider conifer forest, in spite of the presence of riparian broadleaf buffer strips. This effect did not appear to be linked to water chemistry (Chapter 2), which is often a confounding factor when investigating effects of non-native conifer forests on stream communities (Ormerod *et al.*, 1993; Kowalik *et al.*, 2007). More likely, reduced fish biomass was due to decreased prey availability, as originally hypothesised: macroinvertebrate biomass was found to be markedly reduced in streams draining conifer, relative to other riparian land use types, during an earlier survey (Chapter

3). Increased prey availability at streams draining deciduous woodland, relative to those with buffer strips and those in moorland catchments, did not, however, appear to support resultantly increased fish biomass. As such, these findings provide only equivocal support for the original food-availability hypothesis. A possible explanation for such effects is that, beyond a certain minimum threshold, density-dependent factors such as territory size might become limiting to production rather than food supply (Chapman, 1966; Grant and Kramer, 1990). Indeed, mean salmonid density was remarkably consistent across all riparian land use types in this study, potentially providing support for this mechanism. However, salmonid biomass (mean ± 1 SD for all sites: 5.4 ± 3.4 g m^{-2}; range: ~1.5 - 14.4 g m^{-2}) was intermediate in the study streams compared to literature-wide estimates (~ 0.1 – 25.0 g m^{-2}: Chapman and Knudsen, 1980; Glova and Sagar, 1994; Kawaguchi and Nakano, 2001; Zoellick, 2004). This suggests that if density effects were responsible, such factors could be habitat- or ecoregion-dependent (McCormick and Harrison, 2011), or mediated by the specific salmonid species investigated (Chapman and Knudsen, 1980; Zoellick, 2004).

Stable isotope data indicate that terrestrial resource reliance in brown trout was variable on a site-to-site basis, but did not differ significantly between riparian land use types. This validates prior suggestions that variability in consumer resource use between sites may be driven by catchment-specific factors other than land use; variables such as resource quality, retention or relative availability, have previously been highlighted as potentially important in determining the magnitude of subsidy responses (Muotka and Laasonen, 2002; Marcarelli *et al.*, 2011). There was, however, a trend toward reduced reliance on terrestrial production in moorland streams with or without broadleaf buffer strips,though effects sizes were small, with differences between land uses, if apparent, reflecting only relatively minor (10 – 15 %) differences in relative resource use. Moreover, average resource reliance across all sites highlighted that both terrestrial and aquatic resources are important in supporting salmonid food webs in these upland streams, regardless of surrounding land use. This suggests that factors affecting the productivity of either resource may influence fish production in such streams. Mixing model data also emphasized the importance of in-stream autotrophic production to fish, even in the most heavily forested catchments sampled, with this energy pathway typically comprising the main component of trout diets (50-70 % of total). This, coupled with the lack of reduction in fish production in these streams, may suggest a lack of light limitation for benthic algal species, or a shift in algal community composition, favouring more shade-tolerant assemblages or those able establish on the surface of decaying terrestrial matter (Hax and Golladay, 1993). Resource-use patterns in trout were most similar to mean invertebrate terrestrial resource reliance across all streams, suggesting that trout were not preferentially ingesting any singe functional group. This is in agreement with typical findings of gut content analyses, which demonstrate that salmonids often ingest a wide range of invertebrate prey, comprising large components of the total community present in the downstream drift (Elliot, 1973; Wipfli, 1997).

Overall, these data suggest that restoration of riparian broadleaf cover in such upland streams should not significantly affect salmonid production, biomass per unit area or mean individual size. Additionally, unless land use changes act to affect the resource base ultimately available to invertebrate consumers on a site-to-site basis, large-scale shifts in trophic dynamics and terrestrial subsidy dependence are probably unlikely to occur. Riparian restoration schemes in upland streams should therefore be able to confer thermal benefits of riparian tree cover to fish populations (Battin *et a*l., 2007; Broadmeadow *et al.*, 2011), without sacrificing either food supply or constraining growth and production in these communities. However, afforestation of upland catchments with non-native conifer forest may negatively impact both fish and the wider food-webs on which they are reliant (Chapter 2; Chapter 3), with near-stream broadleaf buffer strips unable to offset such effects.

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5.6: Tables and Figures

Table 5.1: Fish production metrics across stream categories of contrasting riparian land use in upland South Wales. All values reported are means ± 1 SE. After accounting for potentially confounding influences, land use category did not significantly ($\alpha = 0.05$) affect any of the investigated variables.

	Land Use Category			
	Buffer (n = 5)	Coniferous (n = 4)	Deciduous (n = 3)	Moorland (n = 6)
Total Fish Density (individuals m^{-2})	0.34 ± 0.09	0.39 ± 0.17	0.34 ± 0.19	0.53 ± 0.12
Total Salmonid Density (individuals m^{-2})	0.32 ± 0.08	0.34 ± 0.14	0.32 ± 0.17	0.32 ± 0.06
Mean Salmonid Mass (g)	19.86 ± 4.49	13.79 ± 7.29	21.60 ± 4.28	23.60 ± 2.35
Mean Salmonid Length (mm)	106.54 ± 8.81	85.80 ± 13.04	111.47 ± 10.86	117.32 ± 3.18

Table 5.2: Proportional reliance of *Salmo trutta* populations on terrestrial production (as represented by CPOM) in, streams of contrasting riparian land use in upland South Wales, estimated by SIAR Bayesian mixing models. Values reported are means estimates along with upper and lower 95% credibility intervals. Proportional contributions not attributable to CPOM in these two-source models are comprised of epilithic biomass.

Site	Mean Proportional Terrestrial Reliance	Lower 95% C. I.	Upper 95% C. I.
CB1	0.33	0.12	0.53
CB2	0.49	0.29	0.69
CB3	0.51	0.25	0.75
CB4	0.48	0.13	0.87
DE1	0.47	0.20	0.72
DE3	0.35	0.07	0.59
DE5	0.54	0.24	0.84
GB2	0.13	0.00	0.38
GB3	0.24	0.00	0.52
GB5	0.39	0.08	0.67
GB6	0.32	0.06	0.56
MO1	0.30	0.08	0.51
MO3	0.38	0.09	0.64

5.6.1: Figure Legends

Figure 5.1: Land use effects on a.) total fish biomass b.) salmonid biomass c.) proportional use of terrestrial organic matter by *Salmo trutta* populations. Values reported are mean ± 1SE.

Figure 5.2: The relationships between reliance on terrestrial production (as represented by CPOM) by *Salmo trutta* and macroinvertebrate a.) Grazer, b.) Predator, and c.) Shredder functional groups in January 2011. Solid lines represent linear model fits.

Figure 5.3: Relationships between *Salmo trutta* reliance on terrestrial production (as represented by CPOM), and mean seasonal macroinvertebrate reliance in a.) January and b.) June. Solid lines represent linear model fits.

Figure 5.1:

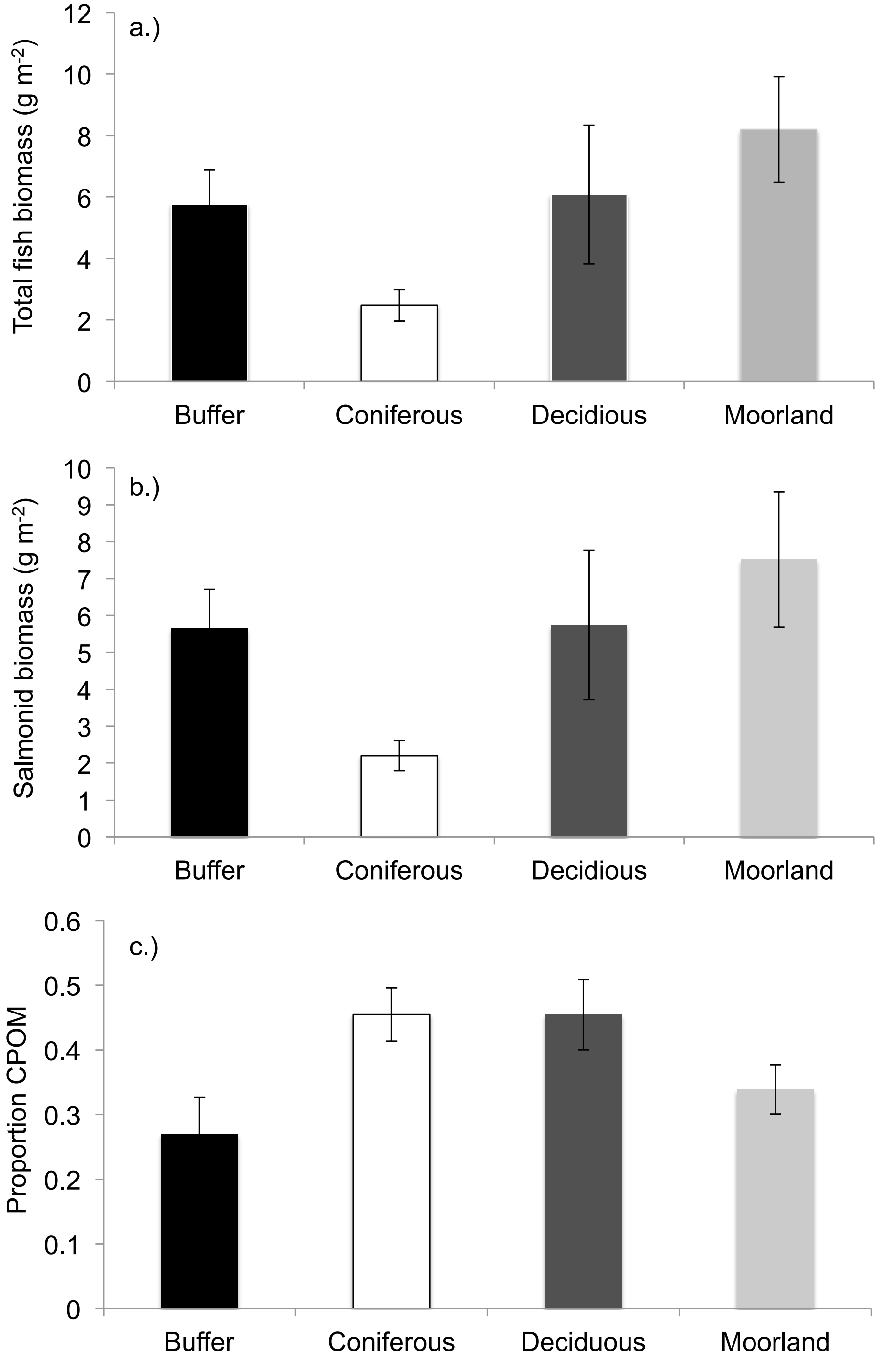

a.)
Total fish biomass (g m-2)
0
2
4
6
8
10
12
Buffer
Coniferous
Decidious
Moorland
b.)
Salmonid biomass (g m-2)
0
1
2
3
4
5
6
7
8
9
10
Buffer
Coniferous
Decidious
Moorland
c.)
Proportion CPOM
0
0.1
0.2
0.3
0.4
0.5
0.6
Buffer
Coniferous
Deciduous
Moorland

Figure 5.2:

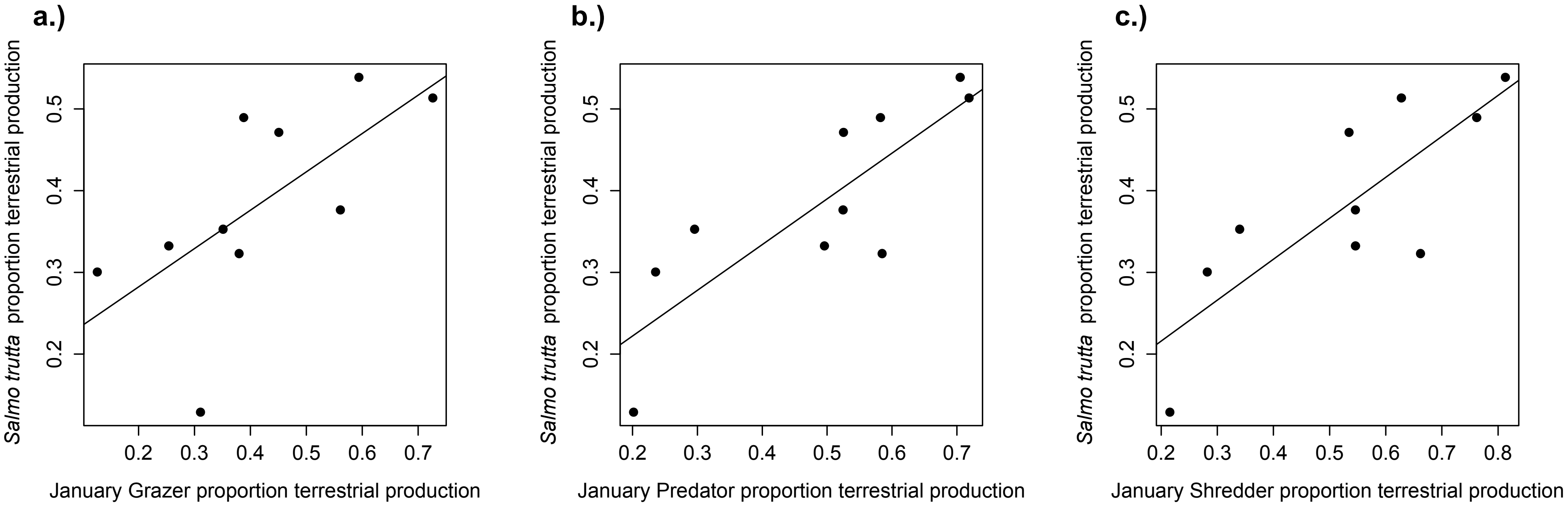
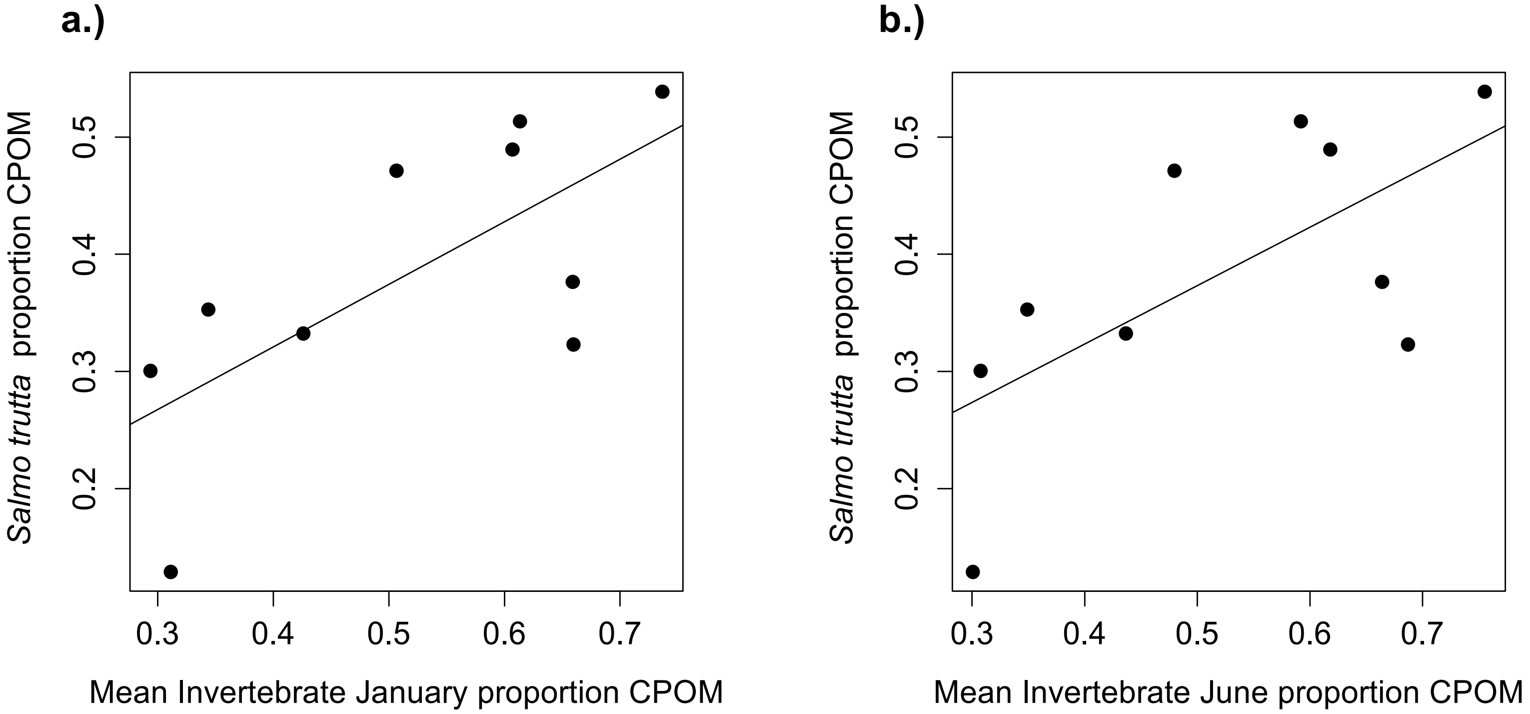

a.)
b.)
c.)
Salmo trutta proportion terrestrial production
0.2
0.3
0.4
0.5
0.2
0.3
0.4
0.5
0.6
0.7
0.8
January Grazer proportion terrestrial production
January Predator proportion terrestrial production
January Shredder proportion terrestrial production

Figure 3:


a.)
b.)
Salmo trutta proportion CPOM
0.2
0.3
0.4
0.5
0.3
0.4
0.5
0.6
0.7
Mean Invertebrate January proportion CPOM
Mean Invertebrate June proportion CPOM

Chapter 6: General discussion

6.1: Discussion

6.1.1:Background

The overarching aim of this study was to assess potential compositional, functional and trophic changes in stream communities likely to accompany variations in riparian tree cover in upland catchments, with an emphasis on consequences for salmonid fish. Understanding the outcomes of such change is key for anticipating the efficacy of conservation and management efforts (Goodwin *et al*., 1997; Naiman *et al*., 2012): restoration of riparian broadleaf buffer strips is widely advocated for minimising the impacts of catchment-wide human land use activities on stream ecosystems, including agriculture, forestry and urbanisation (Goodwin *et al*., 1997; Broadmeadow and Nisbet, 2004). Furthermore, attention has recently been drawn to the potential utility of restoration or maintenance of riparian tree cover to offset many of the negative aspects of climate change on river ecosystems, particularly in upland headwaters (Ormerod, 2009; Seavy *et al*., 2009; Palmer *et al*. 2008, 2009; Wilby and Dessai, 2010). To reiterate points made earlier, whilst effects of riparian tree cover on abiotic processes, including water temperature, habitat structure and sediment and nutrient delivery, are generally well understood (Gurnell *et al*., 2002; Sweeney *et al*., 2004; Broadmeadow and Nisbet, 2004; Broadmeadow *et al*., 2011), little is known of potential biotic consequences. For example, such land use change would likely shift the balance of allochthonous inputs and autotrophic production (Hill *et al*., 1995; Abelho, 2001; Kiffney *et al*., 2003, 2004), with consequences for resource availability, stream food-webs and fish production. Using a combination of surveys and experiments, this project assessed the impacts of differential catchment and riparian tree cover on stream communities and trophic pathways leading to fish, using upland streams representing surrogates for a range potential restoration outcomes. The findings provided partial support for the original hypothesis that animal communities in streams with increasing catchment tree cover are relatively more dependent on terrestrial resources than those in treeless catchments, due to increased allochthonous inputs. The magnitude of this effect depended, apparently, on the extent of riparian broadleaf cover.

6.1.2: Synthesis

Chapter 2 showed that catchment tree cover influenced the composition and structure of stream macroinvertebrate communities, by increasing numbers of detritivorous taxa, but only where riparian forest cover was extensive. Moreover, contrasting effects were apparent, dependent on whether wider catchment tree cover was composed of deciduous broadleaf versus coniferous species. Chapter 3 explored these findings further, investigating the consequences of land use for allochthonous resource availability and macroinvertebrate biomass. That broadleaves substantially increased the biomass of benthic Coarse Particulate Organic Matter (CPOM) and macroinvertebrates, relative to streams in moorland or with narrow riparian buffer strips was confirmed. Macroinvertebrate biomass was also markedly reduced in coniferous forest streams relative to other land use types. This effect was again largely mediated by detritivore taxa adapted to process terrestrial leaf litter subsidies.

Chapter 4 investigated whether experimentally increasing leaf litter supply to moorland streams would elevate local macroinvertebrate biomass, to levels comparable with those found in broadleaf woodland catchments. However, though litter input was able to increase standing stocks of benthic CPOM to levels equivalent to those found in forest streams, consequences for resident macroinvertebrate communities were not apparent. Possible reasons were the relatively short duration of the intervention, an insufficient initial base of invertebrate taxa adapted to process detrital material, or the influence of larger catchment land-use influences.

Chapter 5 integrated findings from prior studies in this research, assessing the consequences for resident fish populations, specifically salmonids. Land use effects on fish populations were generally minimal, though there was a trend towards reduced salmonid biomass at streams draining coniferous forest, relative to other land use types. Salmonid populations did not, however, appear to respond to increased benthic food availability in streams draining broadleaf woodland. It was therefore speculated that beyond a threshold, density-dependent factors, rather than food availability, might mediate the carrying capacity of these species in such streams.

In combination, these results demonstrated how catchment land use plays a key role in structuring stream invertebrate communities and ecosystem processes, but effects appear relatively less important for fish populations, for which other influences may become overriding. The major finding was that wider catchment land use could be relatively more important than near-stream cover in mediating stream food-web dynamics and community composition. Whilst riparian zone management may therefore be crucial for offsetting abiotic impacts on streams (Broadmeadow and Nisbet, 2004; Broadmeadow *et al*., 2011), wider land use may ultimately influence biotic communities, primarily via changes in relative resource availability. These results therefore provide empirical support for prior suggestions that the influence of catchment-wide land use could play a crucial role in maintaining the integrity of riverine ecosystems (Allan *et al*., 1997; Kauffman *et al.* 1997), while expanding this to a community and food-web context in upland streams.

6.1.3: Strengths of the approach used and potential caveats

Studies conducted as part of this project were largely observational, and thus potentially liable to confounds. However, care was taken to select a study area that contained contrasting catchment land uses, but was largely free from other potentially confounding influences; streams in all land uses were generally similar in size and spanned a relatively narrow altitudinal range. Additionally, the largely homogeneous geology results in relatively consistent water chemistry across all streams, limiting the potential for differential acidification or nutrient availability, which can often confound land use effects on streams (Weatherly and Ormerod, 1987; Johnes *et al*., 1996; Kowalik *et al*., 2007).

Though reliant on weak inference, the approach used allowed for investigation of hypotheses on a ‘real-world’ scale, using streams representative of those likely to benefit from riparian restoration projects. Studies using such quasi-experimental design with relatively high, catchment-scale replication are, though often widely advocated, relatively rare (Allan and Johnson, 1997; Allan, 2004). Moreover, the scope for using experimental studies to assess the efficacy of riparian restoration projects is limited by the decadal timescales involved in reestablishing forest cover. Investigations such as those carried out as part of this project can therefore provide data needed to inform management practices in the short-to-medium term.

The range of methodologies used in these studies allowed for quantifications of changes in gross energy flow via multiple lines of enquiry: the complementary approaches of community structure and stable isotope analysis allowed for comparative assessment of how basal resources supporting stream food-webs can vary across land use types, though the results implied that such methods are not always in agreement. Furthermore, the often considerable inter-annual variation in many variables measured in these studies emphasized the importance of multi-year and multi-season sampling in such field investigations.

6.1.4: Future directions

The findings of this project highlighted several research gaps that warrant further investigation. For example, CPOM availability appeared key in influencing macroinvertebrate community structure and composition, particularly by supporting increased numbers of shredding and filtering taxa. A greater understanding of mechanistic processes governing CPOM dynamics may therefore prove critical for predicting stream community responses to land use change. A range of past studies has investigated catchment land use influence on input, retention and breakdown of CPOM (Wallace *et al.*, 1995; Abelho, 2001; Pozo and Elosegi, 2005). Despite this, less information exists on interactive effects between CPOM availability and factors such as flow rate, extreme climactic events (e.g. storms) and in-stream habitat structure, and how these facilitate retention, breakdown and export. Recent attention has, however, been drawn to the importance of such issues

(Eggert *et al*., 2012; Scalley *et al*., 2012; Kominoski and Rosemond, 2011; Flores *et al*., 2013). An increased understanding of such processes, and how they are influenced by riparian land use, could therefore allow for accurate estimation of annual CPOM budgets. Such information may be crucial for establishing critical thresholds of catchment tree cover needed to supply sufficient quantities of CPOM to support "woodland" communities on a catchment-specific basis.

Reasons for the lack of response of moorland stream communities to elevated litter subsidies also merit further investigation. Understanding the size and duration of increased subsidy pulses required to shift moorland stream communities to those more representative of woodland will likely prove key for predicting restoration outcomes. Future experiments that are larger in scale or conducted over longer periods may therefore be able to elucidate reasons for such findings. Additionally, understanding interactions between resource quantity and quality in riverine litter subsidy investigations may further explain the differential responses evident across various studies (Marcarelli *et al*., 2011; Earl and Semlitsch, 2013)

Management schemes with an emphasis on increasing fish production could benefit from further investigation into whether territory size is limiting to salmonid populations in low-order upland headwaters. If so, understanding how land management practices impact such abiotic factors, and whether these can be improved concurrently during restoration schemes, could prove crucial. For instance, pool availability is often limiting to fish (Chapman, 1966; Grant and Kramer, 1990). Addition of large woody debris to streams can, however, increase pool formation and resultantly boost fish production (Cederholm *et al*., 1997). Inclusion of such factors in riparian restoration schemes may therefore be able to protect streams from adverse impacts of climate change and catchment land use, whilst simultaneously improving upland streams as fish habitat.

The results of the project also highlighted methodological issues that warrant future research. For instance, observed resource use patterns in macroinvertebrates in the study streams, as revealed by stable isotope analysis, did not accord with those traditionally ascribed for such taxa (Cummins and Klug, 1979; Moog, 1995). Instead, these data suggested that although resource acquisition and methods of ingestion might differ between macroinvertebrate functional groups, ultimate energetic pathways do not, with relatively equal reliance on in-stream and terrestrial production apparent across all groups. Future studies should therefore aim to confirm that such patterns are not an artefact of SIA, arising as a result of unreliable estimates of the isotopic composition of autotrophic production (France, 1995; 1996). However, the isotopic composition of terrestrial versus in-stream production was distinct and relatively temporally stable at most of the study sites, suggesting results are likely to be reasonably reliable (Doucett *et al*., 1996; Ishikawa *et al*., 2012). If so, these findings support recent suggestions that the importance allochthonous production to streams draining treeless ecosystems may be underestimated (Leiberfinger *et al*., 2011). Furthermore, data from this set of studies additionally implies that use of terrestrial resources in forest stream food-webs may be overemphasised.

Once such remaining uncertainties associated with differential tree cover have been resolved, sufficient data should be available to allow for robust predictions on how stream communities might respond to future restoration efforts. However, future studies could assess the general applicability of these findings to other stream types. For instance, lowland streams, which are often productive and support communities linked to production by in-stream macrophytes, may show contrasting responses, with this potentially explaining the findings of others (e.g. Riley *et al*., 2009).

6.1.5: Management implications and conclusions

Several key implications for the conservation and management of upland streams arise from the findings of this project. The data gathered highlighted the need to explicitly consider the spatial extent of tree cover maintained or restored as part of riparian management activities: where fish production is the sole aim of riparian restoration or conservation efforts, these results, coupled with the findings of past investigations, suggest that relatively narrow buffer strips of near-stream tree cover would likely be sufficient to offset climate change and other anthropogenic impacts in upland streams, without affecting fish populations directly. If, however, the ultimate management goal is the protection or reinstatement of historical woodland communities and associated ecological processes, larger areas of riparian broadleaf cover would be needed to reconnect stream communities with adjacent forest habitats. Such general guidelines therefore provide a distinct set of restoration options for upland streams, dependent upon desired conservation outcomes.

The mutually-corroborative evidence provided by the studies presented in this thesis demonstrate that riparian restoration actions in upland areas are likely to prove generally neutral or beneficial, with negative influences on the restored stream ecosystems appearing to be minimal. This evidence is valuable, given that such restoration action is becoming increasingly urgent due to the accelerated rate of warming predicted to occur over the next several decades. The findings of this set of studies should therefore allow land managers to anticipate how alternative catchment land use scenarios are likely to influence the ecology of upland river networks, prior to instigating such restoration work. Within this framework, river managers can commence experimental restoration projects on upland streams in deforested catchments, whilst having appropriate baselines for predicted restoration outcomes. Moreover, by monitoring the resultant ecological change effected by restoration of catchment tree cover in real-time, future studies will be able to confirm whether the ‘restoration surrogate’ approach used in this series of studies translates to ‘real-world’ settings. Such confirmation would strengthen the use of such cross-sectional surveys, whilst providing evidence of the ability of this methodology to predict the outcomes and efficacy of future restoration work.

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