

2023

The macroinvertebrate fauna of augmented river gravels: community composition and function

Green, Benjamin James

<https://pearl.plymouth.ac.uk/handle/10026.1/21024>

<http://dx.doi.org/10.24382/5062>

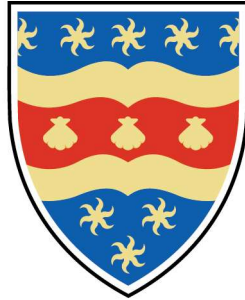
University of Plymouth

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

<Pearl placeholder>

Copyright Statement

This copy of the thesis has been supplied on condition that anyone who consults it is understood to recognise that its copyright rests with its author and that no quotation from the thesis and no information derived from it may be published without the author's prior consent.



UNIVERSITY OF PLYMOUTH

University of Plymouth

The macroinvertebrate fauna of augmented river gravels: community composition and function

By

Benjamin James Green

A thesis submitted to the University of Plymouth in partial fulfilment for the degree of

RESEARCH MASTERS

School of Biological and Marine Sciences

April 2023

Acknowledgments

If I were to thank everybody that has supported me throughout the duration of my ResM I would in no doubt extend over the word limit for a ResM thesis. However, I would like to thank several key people without whom this work would not have been possible.

I would like to thank my DoS David Bilton and my second supervisor Andy Foggo, for their ongoing guidance and recommendations throughout, both professionally and personally. I would also like to thank Shane Griffin, Jane Akerman, Druean Perry, Archibald James Prescott, Giulia La Bianca, Alan Laing, Pete Cotton, Sarah Lane, John Gardiner, Dixii, Lollylhulhu and Liz Emery for assistance in the field, in the office and online. Finally, I would like to thank my late friends Lucy Dunn, Nick Frewin and Will Davies along with my long-suffering parents and family, for their enduring support.

Author's declaration

At no time during the registration for the degree of Research Masters has the author been registered for any other University award without prior agreement of the Doctoral College Quality Sub-Committee.

Work submitted for this research degree at the University of Plymouth has not formed part of any other degree either at the University of Plymouth or at another establishment.

A programme of advanced study was undertaken, which included the modules:

- Postgraduate Research Skills and Methodology (BIO 5131)
- Health and Production in Aquaculture (BIO 504)

Word count of main body of thesis: 14758

Signed:



Date: 1st April 2023

Benjamin James Green

The macroinvertebrate fauna of augmented gravels: community composition and function.

Abstract

Restoration of riverine ecosystems is a key aspect of river management, driven by concerns over water sustainability and declining biodiversity caused by anthropogenic and environmental perturbations. Anthropogenic perturbations include agricultural sedimentation and nutrient input, deforestation, and river regulation including damming, which disturbs longitudinal, lateral and vertical connectivity. Restoring perturbed riverine systems is costly, and many such restorations are ineffective, with restored systems continuing to degrade. Gravel augmentation, the adding of in-stream gravels, focusses mainly on improving habitat for salmonids, and is one method frequently used to mitigate the impacts of damming. The impact of these augmentations on riverine macroinvertebrates and ecosystem functioning in catchments with altered riparian inputs of leaf litter is, however, still unclear, given the lack of work to date investigating leaf litter combined with macroinvertebrate assemblage structure.

This thesis investigates, for the first time, macroinvertebrate assemblage composition, functional diversity and leaf litter breakdown at macro and meso-scales across two low-order, sediment-starved streams on Dartmoor, UK, subject to gravel augmentation. Investigations used macroinvertebrate survey techniques, leaf litter breakdown experiments and univariate and multivariate analyses to explore potential shifts in ecosystem functioning and impacts to the food web related to augmentation. In total, 5641 individuals from 44 taxa were recorded across both catchments. Evidence was found that augmentation led to small and large-scale differences in assemblage structure and functioning, which has the potential to influence both higher and lower trophic levels. Leaf litter breakdown was found to be higher in augmented reaches, although whether associated differences in macroinvertebrate assemblage, diversity, functionality and leaf pack mass loss were due solely to augmentation or a combination of augmentation and other biological and environmental factors remains unclear and merits further study.

Table of Contents

Copyright statement	i
The macroinvertebrate fauna of augmented river gravels: community composition and function	ii
Acknowledgements	iii
Authors declaration	iv
Abstract	1
List of figures	4
List of tables	6
Chapter One: General introduction	8
Aims	14
Chapter Two: Macroinvertebrate communities of two gravel-augmented Dartmoor rivers	
Introduction	15
Materials and methods	
Study catchments	18
Sampling methods	19
Data analyses	21
Results	
Univariate analyses	22
Multivariate analyses	24
Functional feeding group analysis	28
Discussion	29

Chapter Three: The effects of gravel augmentation on leaf litter breakdown and the composition of leaf pack invertebrate assemblages

Introduction	35
Materials and methods	
Study catchments	38
Leaf pack experiments	40
Data analyses	41
Results	
Univariate analyses	42
Functional feeding group analysis	46
Multivariate analyses	48
Discussion	50
Chapter Four: Conclusion	55
References	59

List of figures

Figure 1. The location of Dartmoor National Park unaugmented/augmented gravel study reaches. The inset shows catchments within the British Isles: a) River Avon catchment, b) South Teign catchment. Individual sample reaches are marked on the map and coloured white/grey to distinguish augmentation state.

Figure 2. Non-metric multidimensional scaling (nMDS) ordination of macroinvertebrate abundance across unaugmented and augmented reaches of the two study catchments. Convex hulls (shaded polygons) are overlain to clarify groupings according to catchment and augmentation state, where A = River Avon, ST = South Teign, U = unaugmented and AUG = augmented, respectively. Sample codes indicated in small black letters; species indicated in red, (A) = indicates adult forms for taxa which occurred as both adult and larvae; for full taxonomic classification see Table 2. Blue arrows represent vectors of environmental variables related to nMDS axes.

Figure 3. Non-metric multidimensional scaling (nMDS) ordination of macroinvertebrate abundance across unaugmented and augmented reaches of the two study catchments, together with control reaches sampled (labelled and coloured convex hulls), Where A = River Avon, ST = South Teign, U = unaugmented and AUG = augmented, respectively. Sample codes indicated in small black letters.

Figure 4. Individual functional feeding group abundances across catchments and augmentation states; (a) River Avon catchment and (b) South Teign catchment. Graph codes: G/C = gatherer/collector, S/D = shredder/detritivore, F/C = filterer/ collector, P/P/E = piercer/predator/engulfer, S = scraper.

Figure 5. Location of Dartmoor National Park leaf pack study reaches. The inset shows catchments within the British Isles: a) River Avon catchment, b) South Teign catchment. Individual leaf pack installation reaches are marked on the map and coloured white/grey to distinguish augmentation state.

Figure 6. Mean total mass loss across micro and 5mm mesh leaf packs at catchments: River Avon unaugmented (AU), River Avon augmented (AA), South Teign unaugmented (STU) and South Teign augmented (STA). Error bars represent standard error (SE) of the mean.

Figure 7. Mean number of (a) individual abundance, (b) species richness, (c) Hill-Shannon numbers and (d) Hill-Simpson numbers found in 5mm mesh leaf packs at catchments: River Avon unaugmented (AU), River Avon augmented (AA), South Teign unaugmented (STU) and South Teign augmented (STA). Error bars represent standard error (SE) of the mean.

Figure 8. Individual functional feeding group abundances across catchments and augmentation states: (a) River Avon catchment and (b) South Teign catchment. Graph codes: G/C = gatherer/collector, S/D = shredder/detritivore, F/C = filterer/ collector, P/P/E = piercer/predator/engulfer, S = scraper.

Figure 9. Non-metric multidimensional scaling (nMDS) ordination of macroinvertebrate abundance across unaugmented and augmented reaches of the two study catchments. Convex hulls (shaded polygons) are overlain and coloured to clarify groupings according to catchment and augmentation state, where AA = River Avon augmented, AU = River Avon unaugmented, STA = South Teign augmented, STU = South Teign unaugmented and states AUG and UNAUG respectively. Sample codes indicated in small black letters; species indicated in red, (A) = adult forms for taxa which occurred as both larvae and adults; for full taxonomic classifications see Table 6.

List of tables

Table 1. Surber sample and reference catchment information.

Table 2. Species list with assigned functional feeding group (FFG) and individual abundances across all reaches/catchments (AU – River Avon unaugmented, AA – River Avon augmented, STU – South Teign unaugmented, STA – South Teign augmented, RC – reference catchments. All species are larval unless otherwise stated as adult (A). FFG codes: G/C = gatherer/collector, S/D = shredder/detritivore, F/C = filterer/ collector, P/P/E = piercer/predator/engulfer, S = scraper.

Table 3. General linear model results for individual abundance, species richness, Hill-Shannon numbers, Hill-Simpson numbers and associated pairwise comparisons. Asterisks (*) indicate level of significance ($p < 0.05 = *$, $p < 0.01 = **$, $p < 0.001 = ***$). The code (u) indicates higher values in unaugmented reaches.

Table 4. Type 1 sums of squares PERMANCOVA with PhysChemPC (representing the first axis of a PCA of physiochemical data).

Table 5. Leaf pack installation information.

Table 6. General linear model results for total mass loss of micro mesh leaf packs as the dependent variable with associated pairwise comparisons. Asterisks (*) indicate level of significance ($p < 0.05 = *$, $p < 0.01 = **$, $p < 0.001 = ***$). The code (a) indicates significantly higher mass loss in augmented reaches.

Table 7. Species list with assigned functional feeding group (FFG) and individual abundances in 5 mm leaf packs across all reaches/catchments (AU = River Avon unaugmented, AA = River Avon augmented, STU = South Teign unaugmented, STA = South Teign augmented). All species are larval unless otherwise listed as (Adult). FFG codes: G/C = gatherer/collector, S/D = shredder/detritivore, F/C = filterer/ collector, P/P/E = piercer/predator/engulfer, S = scraper.

Table 8. General linear model results for individual abundance, species richness, Hill-Shannon numbers, Hill-Simpson numbers as the dependent variable and associated pairwise comparisons. Asterisks (*) indicate level of significance ($p < 0.05 = *$, $p < 0.01 = **$, $p < 0.001 = ***$).

= ***). The codes (u) or (a) indicate significantly higher values in either unaugmented or augmented reaches.

Table 9. General linear model results with inter-pack mass loss as the dependent variable and individual abundance, species richness, Hill-Shannon diversity, and Hill-Simpson diversity as individual covariates in separate GLM models, along with associated pairwise comparisons. Asterisks (*) indicate level of significance ($p < 0.05 = *$, $p < 0.01 = **$, $p < 0.001 = ***$). The code (a) indicates significantly higher mass loss in augmented reaches.

Table 10. Type 1 sums of squares PERMANOVA for leaf pack macroinvertebrate assemblage composition

Introduction

Restoration of riverine systems is a prominent area of research in the science of applied water resources (Wohl et al. 2005). 'River restoration' refers to a large variety of ecological, physical, spatial and management measures and practices that attempt to restore a natural state and functioning of a river system to support biodiversity, recreation, flood management and landscape development. The science of riverine restoration is focussed on identifying fundamental knowledge gaps needed for successful restorations (Wohl et al. 2015). The importance of riverine restorations is driven by rising concerns about water sustainability and declining biodiversity in light of anthropogenic and environmental perturbations (Muhar et al. 2016, Lu et al. 2019). The need to fully analyse the science of restorations is important, as truly effective restorations rely on not only short-term successes (such as initial habitat for salmonids) (Taylor et al. 2019), but also on long-term overall ecological success such as increased ecosystem functioning and service provision (Palmer et al. 2005). Due to the ongoing degradation of riverine ecosystems the restoration of rivers is now seen as an essential component of any conservation effort (Wohl et al. 2005).

Riverine ecosystems are subject to many anthropogenic perturbations (Reid et al. 2019), resulting in habitat degradation and loss of water quality, which in turn lead to loss of biodiversity (Gleick 1998, Albertson et al. 2013). For example, of all the rivers over 1,000 km in length only 36 percent are free to flow from source to their end, and only 23 percent flow continuously to the sea (Grill et al. 2019). Anthropogenic perturbations can be evident at small scales, such as input of sediments and nutrients from agriculture, and large scales, for example river regulation or dam construction (Vörösmarty and Sahagian 2000). As a result, somewhat unsurprisingly, extensive legislation has been enacted and significant investment in the restoration of rivers around the globe has taken place (Karr and Chu 1998). Many restorations are, however, less than successful, and these so-called 'restored' ecosystems continue to degrade (Williams and Wolman 1984, Kondolf et al. 2007). The United Nations General Assembly resolution 58/217, proclaimed 2005 -2015 as 'Water for Life' an 'International Decade for Action'. This resolution called for a greater focus on issues of water at all levels (Dudgeon et al. 2006). Common restoration goals include: (a) aesthetics (e.g. appearance, fishing, education); (b) construction of fish passages (e.g. construction of passages for, or removal of barriers to, fish migration); (c) reconfiguration of channels (e.g.

alteration of thalweg, channel geometry, encouraging primary production by improved access to daylight); (d) adjacent land purchase (thereby decreasing pressure on riverine systems by taking land back from farmers and focussing on preservation, protection and creating riparian buffer strips); (e) instream managing of species (i.e. translocation or stocking various flora and/or fauna and removal of invasive species); (f) dam removal or mitigation (by addressing issues such as lack of bedload gravel (BLG), transport or build-up of fine sediment in spawning gravel); and (g) instream habitat creation (gravel augmentations undertaken to provide refugia and spawning material for salmonids) (Wood and Armitage 1997, Yarnell et al. 2006, Follstad Shah et al. 2007, Wharton and Gilvear 2007).

River restorations have now become more prevalent in a wider range of river forms. Restoration approaches once employed on typical larger mid-order rivers to encourage, for example, salmonid spawning by providing habitat for redds (Hendry and Cragg-Hine 1997) are now applied on small, dammed, headwater streams that have become starved of BLG (Downs et al. 2016). Not all works employed in larger rivers are possible on small headwater streams which are constricted by development and topography, and consequently, restricted by cost, from creating certain structures (for example to boost fluvial dynamics in the form of a flood corridor that can be exploited by the river to deposit sediment and encourage growth of riparian flora) (Kondolf et al. 2006, Beechie et al. 2010). Sediment loading and hydrographs including dam flow perturbation are now widely used when planning riverine restorations (Staentzel et al. 2019a).

Dams potentially cause longitudinal connection issues (including problems in transport of sediment, organic matter, nutrients and barring fish migrations) (Roni et al. 2002). Dams also impact lateral connectivity by restricting water overflow to floodplains. This can cause decreases in riparian vegetation, thereby affecting a decline in habitat and associated niches for riverine flora and fauna (Roni et al. 2008, Liu and Wang 2018). Dams may also impact vertical connectivity by the reduction of regular hydraulic gradients which flush BLG of fine riverine sediment (FRS), thereby reducing exchange with the hyporheic zone (Kondolf 2006). In some rivers, environmental flow requirements have been assessed and plans put in place to increase the number of flushing flows and thereby facilitate transport of sediment and prevent homogenisation (Poff et al. 2007), and in other instances the ecological responses to altered flow regimes have been monitored post-application (Poff and Zimmerman 2010).

Further suggestions included the development of full flow regimes (Richter et al. 2006, Staentzel et al. 2019b). One method to mitigate flow perturbations, and therefore restrictions to downstream sediment transport, is the augmentation of BLG.

Projects involving the augmentation of BLG into rivers and streams have been undertaken in the USA from the early 1970s, and increasingly since 1976 (Staentzel et al. 2019b). California rivers in the Sierra Nevada and Coastal Ranges have seen restoration efforts (Kondolf and Matthews 1991, Kondolf and Wolman 1993, Kondolf and Micheli 1995, Kondolf et al. 1996) with the main focus of these augmentations being to improve ecological habitat for Salmonidae (Merz et al. 2006, Sellheim et al. 2016). An increase in habitat heterogeneity can be gained in-channel by gravel bar production, thereby unlocking the potential for niche creation and encouraging elevated biodiversity (Escobar-Arias and Pasternack 2011, Ock et al. 2015). In some instances that the addition of BLG has not generated any biological response (McManamay et al. 2013), possibly because of the size or amount of sediment added. Augmentations have also been seen to raise water levels, allowing greater inundation of the alluvial zone (Elkins et al. 2007). In some cases, BLG has not been observed to increase colonisation by other organisms such as macroinvertebrates, with sites being found to be no different in density or biomass to unrestored sites within a 4-week period (Merz and Ochikubo Chan 2005). In other cases, macroinvertebrate assemblages have been shown to differ in rivers that have undergone augmentation, from elevated abundance (Merz and Ochikubo Chan 2005), to depressed abundance (Albertson et al. 2011) in California, and equivalent abundance in France (Sarriquet et al. 2007). Gravels have also been shown to be crucial for lithophilic organisms and their growth phases (Pulg et al. 2013). As salmonids prey upon macroinvertebrates (Diehl 1992), the effects of augmentation on macroinvertebrate assemblages is important (Weber et al. 2014).

Macroinvertebrates represent most of the biodiversity of riverine systems, and are crucial to ecosystem function (Wallace and Webster 1996). They are a key contributor to nutrient cycling of material either produced in the system or inflowing from the riparian region (Malmqvist 2002). Assemblages found at particular catchments/reaches are often a significant gauge of system health and have been used in programmes of management (Marchant et al. 1997, Hawkins et al. 2000, Malmqvist 2002). Macroinvertebrates are useful indicators of ecosystem health (Dufrêne and Legendre 1997, Stone and Wallace 1998,

Henshall et al. 2011), as they are relatively easy to sample quantitatively, in comparison to other organisms such as phytoplankton or zooplankton (Reynoldson and Metcalfe-Smith 1992). Macroinvertebrate responses to water quality and habitat change are well studied. Their assemblages are comparatively stable over time when compared to microbial or planktonic communities, and also requires less frequent sampling (Hynes 1970, Cummins and Wilzbach 1985, Reynoldson and Metcalfe-Smith 1992, Death and Winterbourn 1995, Friberg 2014, White et al. 2017a).

To quantify biodiversity and characterize ecosystem function, bio-assessments are utilised globally in lotic environments (Cummins et al. 2005). In streams and rivers two popular approaches are applied. Firstly, a taxonomic approach, which is usually focussed on measuring richness and/or diversity such as an Index of Biotic Integrity (IBI) (Resh and Rosenberg 1993). Secondly, a functional approach may be utilized to describe the state of an ecosystem. This is a less time consuming tactic with less taxonomic work required (Cummins et al. 2005). The use of taxonomic approaches to make fast, reliable evaluations of either toxicity (e.g., in the case of a chemical spill) or biodiversity (e.g., for conservation assessment) is hindered by the need to identify organisms to genus, preferably species. In contrast, the functional trait approach is based on characteristics (both behavioural and morphological) that relate to the specific organisms feeding strategy (Cummins and Lauff 1969, Cummins 1973, Cummins and Klug 1979, Cummins and Wilzbach 1985, Cummins et al. 2005). The use of functional traits as a proxy for ecosystem health is however frequently overlooked in restoration projects (Kail et al. 2015), despite data gleaned from their inclusion having the potential to increase our understanding of how these systems function (White et al. 2017a). For example, traditionally recorded taxonomic data have the potential to allow individual taxa to be studied (e.g. H' or species richness) whereas functional trait data have the further potential to highlight specific responses to augmentation (White et al. 2017b). This was seen in a study in Carolina, USA, undertaken specifically to assess the feasibility of the use of functional traits to monitor the effects of restoration on macroinvertebrate assemblages (Tullos et al. 2009). Some studies propose functional diversity to be the greatest predictor of ecosystem function (Cadotte et al. 2011, Gagic et al. 2015, Schmera et al. 2017). Small-scale studies have shown that species richness drives ecosystem functioning, for example in a study of the effect of substrate heterogeneity on biofilm metabolism (Cardinale et al. 2002), and in

another field experiment in northern Sweden (Frainer et al. 2014). However, it has been suggested that ecosystem functioning (and its associated biodiversity) may rely on a 'cascade effect' between species, interactions between and among species, the sequence of species loss, species traits, and the environmental context (Schmera et al. 2017).

The study of organisms that feed on allochthonously inputted organic matter can be an excellent proxy for overall ecosystem health as they are the primary link to higher trophic levels (Marks 2019). Litter in the form of branches, twigs and leaves that fall into streams from the riparian environment is generally the primary energy input of most streams (Marcarelli et al. 2011). Research to date on leaf litter breakdown in streams has focussed mainly on rates of decomposition (Marks 2019). The study of macroinvertebrate functional traits and use of leaf litter as a proxy for functional diversity has been a growing field for decades (Petersen and Cummins 1974, Boling Jr et al. 1975, Suberkropp et al. 1976, Ward and Cummins 1979, Newbold et al. 1982, Webster and Benfield 1986, Richardson 1992, Wallace et al. 1997, Jonsson and Malmqvist 2000, Bergfur 2007, Péru and Dolédec 2010, Classen-Rodríguez et al. 2019).

The most prevalent macroinvertebrate taxa in stream systems are Ephemeroptera (Mayflies), Plecoptera (Stoneflies), Odonata (Dragonflies), Diptera (Flies) and Trichoptera (Caddisflies) (Graça 2001). Macroinvertebrates are generally classified functionally by the way they feed, not by what they eat (Wallace and Webster 1996): (1) Predators feed on other organisms; (2) Grazers-scrapers feed on biofilm on submerged structures like rocks and plants (Cummins et al. 1984); (3) Collector-filterers feed on fine particulate organic matter (FPOM) filtered from the water column; (4) collector-gatherers take FPOM directly from the substrate (Cummins et al. 2005); and (5) shredders feed on coarse particulate organic matter (CPOM), for instance leaf litter. Most of these functional groups, other than predators, can potentially function as detritivores (Graça 2001). In temperate zones, litter fall and therefore litter input into streams is seasonal (Graça 2001). This seasonality may cause shortages of detritus at certain times of year, or between seasons, consequently limiting food availability (Petersen Jr et al. 1989). There is a strong relationship between leaf litter input and macroinvertebrate assemblage. Studies have shown that the exclusion of leaf litter reduced both biomass and abundance of benthic macroinvertebrates (Wallace et al. 1997, Wallace et al. 1999). In particular, the exclusion of litter impacts shredders, gatherers and predators, which in turn reduces

secondary production (Graça 2001). To date, few studies have investigated the impacts of gravel augmentation on leaf litter breakdown and associated macroinvertebrate assemblages.

With the ongoing anthropogenic changes to riparian zones, rivers and streams and associated subsequent loss of habitat, restoration projects that involve investigating the relationship between biodiversity and ecosystem function are of particular importance (Hooper et al. 2012). Leaves of different riparian species decompose at different rates providing food for macroinvertebrates over a time-continuum from first leaf fall to later in the season (Ferreira et al. 2016, Siders et al. 2018). Mixed leaf pack studies have shown that richness of litter species entering a stream increases decomposition rates (Handa et al. 2014). However, if global change continues to homogenise our waterways and riparian zones, and with the influx of invasive riparian species of flora changing allochthonous input levels and breakdown rates, macroinvertebrate assemblages may suffer lowering species richness and overall biodiversity. This weakening of overall ecosystem interactions, has the potential to have deleterious knock-on effects for other trophic levels - including salmonids (Rosenfeld and Hatfield 2006, Lapointe et al. 2014), particularly as it appears larger bodied macroinvertebrates (the most important for decomposition) are also the most likely to become extinct (Duffy 2003).

Aims

This thesis aims to characterise the macroinvertebrate assemblage compositions and potential impacts of gravel augmentation on leaf litter breakdown and thereby ecosystem functioning of two dammed, sediment-starved, low-order streams on Dartmoor, Devon, UK: the River Avon and the South Teign. Chapter Two uses survey techniques to explore macroinvertebrate assemblage composition, and Chapter Three utilizes leaf litter pack experiments to explore the effect of gravel augmentation on a key ecosystem process and characterises litter pack macroinvertebrate assemblage composition and functionality.

The main objectives of this thesis were to:

- a) characterise macroinvertebrate assemblage composition across and between two dammed, sediment-starved, low-order augmented streams on Dartmoor, Devon, UK (River Avon and South Teign), and place these in context through comparison with other undammed systems in the region; and
- b) identify differences in leaf litter breakdown rates and associated community structure and functional diversity across and between both catchments at both macro and meso-scales, to identify possible changes in ecosystem function, and therefore potential impacts on higher trophic levels.

Chapter Two: Macroinvertebrate communities of two gravel-augmented Dartmoor rivers

Introduction

Stream ecosystems are increasingly subjected to anthropogenic perturbations, which result in habitat degradation, reduction of water quality, and associated losses of biodiversity (Gleick 1998, Vörösmarty and Sahagian 2000, Albertson et al. 2011). These perturbations result from actions operating at both large (e.g., climate change, river regulation, dam construction) and small scales (e.g., sediment and nutrient input from agriculture). Dams have the potential to affect entire watersheds (Boon 1988, Brooks et al. 2002) by disrupting fluxes of water, nutrients and sediment in riverine systems, which in turn has the potential to significantly impact stream biota (Cairns Jr 1995, Kondolf and Micheli 1995, Graf 2001). In some instances dams may completely block downstream transport of benthic sediment, leading to simplification of habitat, incision of channels and an imbalance between bedload gravel (BLG) (Gaeuman 2012) and fine riverine sediment (FRS) on the downstream channel bed (Williams and Wolman 1984, Ligon et al. 1995).

BLG is an important component of riverine systems for macroinvertebrates (Rice et al. 2001). It provides an important surface within the total makeup of a stream's complement of sediment on which macroinvertebrates move, shelter, rest and feed (Rice et al. 2001). BLG also defines channel slope and roughness, which in turn impacts macroinvertebrates through the hydraulic stresses they tolerate (Cummins and Lauff 1969, Minshall 1984, Rice et al. 2001, Compin and Céréghino 2007). Relatively stable substrates are attractive to benthic macroinvertebrates as they provide refugia when floods occur, and therefore aid subsequent recolonization (Lancaster and Hildrew 1993b, a, Rice et al. 2001), which in turn promotes community diversity, stability and abundance (Death and Winterbourn 1994, 1995, Sellheim et al. 2016). Roughness of substrate is a factor in determining near-bed hydraulic environments (e.g., turbulence, shear and flow separation). It determines an organism's ability to feed, move, or maintain position (Walton Jr et al. 1977, Statzner et al. 1988, Rice et al. 2001). This same roughness is an important element in the growth of periphyton and substrate holding of organic detritus (McAuliffe 1983, Ward 1992), which effects higher trophic levels in the form of herbivorous macroinvertebrates, and then in turn their predators

(e.g. salmonids) (Rempel et al. 2000, Rice et al. 2001). In addition, BLG characteristics affect the stability and connectivity of interstitial spaces that make up the in-channel hyporheic environment, controlling hyporheic (Stanford and Ward 1988, Boulton et al. 1998) fluxes of nutrients and water (Claret et al. 1997) including availability as refugia (Dole-Olivier et al. 1997, Rice et al. 2001). Availability of BLG is also directly required for salmonid spawning (Barlaup et al. 2008). Females typically dig pits in gravel by beating their tails, and the eggs are then deposited into the pit and fertilized by one or more males (Dalley et al. 1983, Gibson 1993, Saura et al. 2008). When fertilization is complete the female passages upstream and conceals the eggs by digging a new pit. This gravel construction is commonly called a redd (White 1942).

River restoration has become more widespread over the last few decades, with methods employed that attempt to recreate various abiotic and biotic factors that may have once been present naturally in riverine systems before human disturbance, thereby encouraging recovery of threatened biodiversity, and recolonization by historical assemblages (Kondolf and Micheli 1995, Dobson et al. 1997). Clearly, any strategy for riverine rehabilitation and/or management should be based on fundamental knowledge of ecosystem structure and function, and their likely responses (Cummins 1973). Methods for restoration include channel realignment or insertion of mid-stream structures to increase habitat heterogeneity (Rabeni and Minshall 1977, Nickelson et al. 1992, Brooks et al. 2002), removal of barriers to fish movement, repairs to bank erosion (Brookes and Shields Jr 1996, Albertson et al. 2011, Arnaud et al. 2017), and the augmentation of gravels to re-introduce BLG, which is particularly important in reaches downstream of dams (Bernhardt et al. 2005). Commonly these habitat enhancements focus on fish species (e.g. salmonids) (Nickelson et al. 1992, Rabeni and Jacobson 1993, Kondolf and Micheli 1995, Schälchli et al. 2010), in part due to their commercial value (Weber et al. 2014). Thus far, the impacts of restoration on other organisms have received little, if any, consideration (Albertson et al. 2011). The first gravel augmentations were conducted in the 1960's in the USA (Wheaton et al. 2004, Merz et al. 2006, Arnaud et al. 2017), on dammed rivers to re-create habitat suitable for salmonids. In Europe, gravel augmentation has been employed to mitigate sediment starvation downstream (Schälchli et al. 2010, Klösch et al. 2011), and in Japan gravel augmentation has been used to mitigate sediment deficits (Ock et al. 2013). In a study on the Danube

(Liedermann et al. 2013), gravel tracer studies appeared to be a good means for monitoring sediment transportation in rivers, and in turn could be useful for designing future models of sediment movement downstream.

Biological assessments are utilised worldwide in both lentic and lotic environments to assess biodiversity and characterize ecosystem function (Cummins et al. 2005). In the lotic environment of streams and rivers two general approaches are utilized; first, a taxonomic approach, which is usually focussed on measuring richness and/or diversity such as an Index of Biotic Integrity or IBI (Resh and Rosenberg 1993). Second, a functional approach may be adopted; this approach is generally used to characterize the condition of an ecosystem and is a far quicker method with less taxonomic work required (Cummins et al. 2005). The use of taxonomic approaches to make fast, reliable evaluations of either toxicity (in the case of a chemical spill) or biodiversity (for conservation assessment for example) is hampered by the need to identify organisms down to genus and preferably species, whereas the functional group approach is based on characteristics (both behavioural and morphological) that relate to an organism's feeding strategy (Cummins and Lauff 1969, Cummins 1973, Cummins and Klug 1979, Cummins and Wilzbach 1985, Cummins et al. 2005). Macroinvertebrates are useful indicators of an ecosystem health (Dufrêne and Legendre 1997, Stone and Wallace 1998, Henshall et al. 2011), as they are relatively easy to sample quantitatively in comparison to other organisms such as phytoplankton or zooplankton (Reynoldson and Metcalfe-Smith 1992). Macroinvertebrate responses to water quality and habitat change are well studied, and their assemblages are relatively stable over time when compared to microbial or planktonic communities, and they require less frequent sampling (Hynes 1970, Cummins and Wilzbach 1985, Reynoldson and Metcalfe-Smith 1992, Death and Winterbourn 1995, Friberg 2014, White et al. 2017a).

Macroinvertebrates represent a significant proportion of the biodiversity of riverine systems, and are crucial to ecosystem function (Wallace and Webster 1996). They are a key contributor to nutrient cycling of material either produced in the system or inflowing from the riparian region (Malmqvist 2002). Furthermore, assemblages found at reaches/catchments (depending on the context of the study) are often a significant gauge of system health and have been used in programmes of management (Marchant et al. 1997, Hawkins et al. 2000, Malmqvist 2002). Macroinvertebrate assemblages have been shown to differ in rivers that

have undergone augmentation; from elevated abundance (Merz and Ochikubo Chan 2005) to depressed (Albertson et al. 2011) in California, and equivalent abundances in France (Sarriquet et al. 2007). Given that salmonids prey upon macroinvertebrates (Diehl 1992), the consequences of augmentation upon their assemblages is therefore important (Weber et al. 2014). The augmentation of gravels to encourage salmonid spawning may be valuable, but knowledge of how this augmentation impacts macroinvertebrates is limited, particularly in the UK (Boon 1988). This study employs both taxonomic and functional group approaches to investigate the responses of macroinvertebrate assemblages to gravel augmentation in two dammed, sediment-starved rivers in Devon, Dartmoor, UK (River Avon and South Teign); the first time this has been examined in comparable upland watercourses of the type used by many breeding salmonid populations in western Europe. We explore the impact of gravel augmentation on macroinvertebrate abundance, species richness and diversity, as well as assemblage and functional feeding group composition.

Materials and methods

Study catchments

Sampling was conducted at Dartmoor National Park in Devon, UK, in augmented and unaugmented reaches of the River Avon and the South Teign. These two catchments were subject to a series of planned gravel augmentations of mixed gravel size (4 – 100mm), undertaken over a six-year period from 2014 – 2019 by Westcountry Rivers Trust. As well as at five ‘natural’ control reaches which were sampled as undammed reference catchments in line with the BACI (Before/After and Control/Impact) principle (Underwood 1992) (Figure 1). The River Avon rises 460 m above sea level on the Aune Head mires, south Dartmoor. Its catchment extends over 110.5 km² and it flows 40 km from source to sea. The river is dammed by the Avon Reservoir, which was constructed in 1957 (Bogle et al. 1959). The River Avon’s major tributaries include Bala Brook and Glaze Brook, both of which have sources on the moor itself (Environment Agency 2003). The South Teign rises near Grey Wethers on north Dartmoor, and then feeds Fernworthy Reservoir 19 km from the Avon Dam. The five control reaches selected were the East Dart at Bellever Forrest, Cherry Brook west of Postbridge, the River Walkham at Merrivale, the Blackbrook River to the east of Princetown, and the River

Meavy above Burrator Reservoir. The beds of the River Avon and the South Teign mainly consist of large cobbles and boulders, with sizable areas of exposed bedrock and scattered BLG deposits. The uplands of Dartmoor do produce low levels of BLG, however, it is assumed that the River Avon and Fernworthy Dams have reduced sediment supply to downstream reaches, with the potential for deleterious impacts on aquatic life (Downs et al. 2016).

Sampling methods

Samples were collected over five days from 6th July 2020 – 10th July 2020 from reaches with and without augmented gravels on the River Avon and South Teign (Figure 1, Table 1).

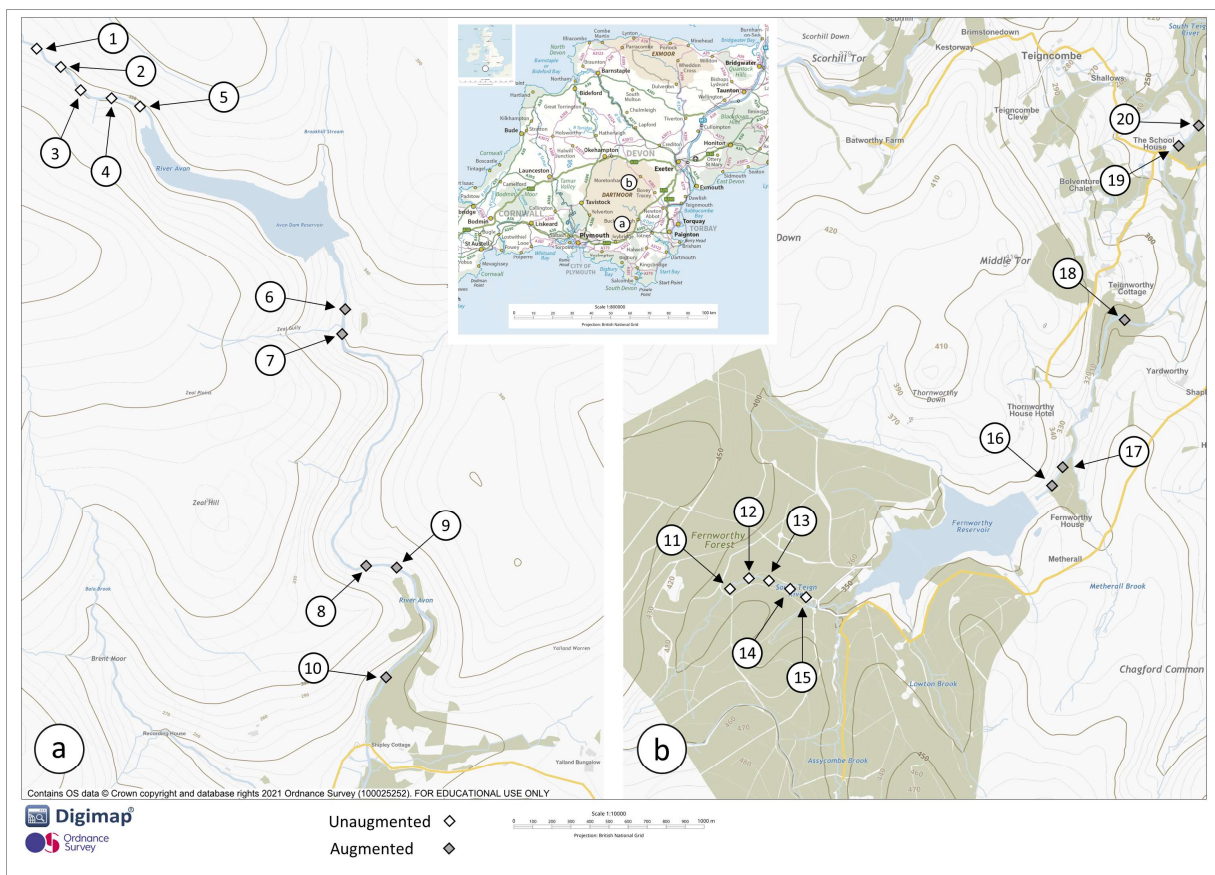


Figure 1. The location of Dartmoor National Park unaugmented/augmented gravel study reaches. The inset shows catchments within the British Isles: a) River Avon catchment, b) South Teign catchment. Individual sample reaches are marked on the map and coloured white/grey to distinguish augmentation state (Digimap 2021).

Table 1. Surber sample and reference catchment information.

Catchment	Reach	Augmentation state	Lat/long	Elevation
River Avon	1	unaugmented	50°28'45.8"N 3°52'54.2"W	351m
River Avon	2	unaugmented	50°28'44.3"N 3°52'49.9"W	350m
River Avon	3	unaugmented	50°28'41.1"N 3°52'45.9"W	349m
River Avon	4	unaugmented	50°28'39.6"N 3°52'38.9"W	347m
River Avon	5	unaugmented	50°28'38.4"N 3°52'31.8"W	345m
River Avon	6	augmented	50°28'08.5"N 3°51'41.5"W	306m
River Avon	7	augmented	50°28'06.9"N 3°51'41.7"W	303m
River Avon	8	augmented	50°27'29.2"N 3°51'37.2"W	268m
River Avon	9	augmented	50°27'29.5"N 3°51'35.1"W	266m
River Avon	10	augmented	50°27'11.4"N 3°51'31.2"W	230m
South Teign	11	unaugmented	50°38'19.8"N 3°54'19.6"W	383m
South Teign	12	unaugmented	50°38'18.7"N 3°54'16.3"W	381m
South Teign	13	unaugmented	50°38'18.4"N 3°54'13.5"W	379m
South Teign	14	unaugmented	50°38'17.6"N 3°54'09.3"W	373m
South Teign	15	unaugmented	50°38'16.7"N 3°54'07.4"W	365m
South Teign	16	augmented	50°38'38.6"N 3°52'48.6"W	331m
South Teign	17	augmented	50°38'39.1"N 3°52'47.6"W	329m
South Teign	18	augmented	50°39'15.0"N 3°52'13.2"W	281m
South Teign	19	augmented	50°39'50.1"N 3°52'08.6"W	245m
South Teign	20	augmented	50°39'52.4"N 3°52'04.7"W	243m
East Dart River	21	natural	50°34'49.8"N 3°53'47.2"W	309m
Cherry Brook	22	natural	50°34'35.4"N 3°55'48.2"W	354m
River Walkham	23	natural	50°33'27.2"N 4°02'53.7"W	281m
Blackbrook River	24	natural	50°33'28.0"N 3°59'40.9"W	391m
River Meavy	25	natural	50°30'24.7"N 4°01'16.2"W	263m

At each reach, five replicate surber (Surber 1937) samples were taken from riffle areas employing a sampler with an area of 0.1 m² and a 500 µm nylon mesh. Samples were washed through *in situ* to concentrate material in the bottom of the net, drained and then placed directly into labelled pots, to which 80% ethanol was added. Physical and chemical data were also recorded in association with each sample. As well as augmentation state these comprised Depth (cm), flow (m/s) with GEOPACKS MFP126-S Flow meter (Okehampton, UK) and turbidity (NTU) with a LaMotte 2020We turbidity meter (Baltimore, USA). Dissolved oxygen (DO) was recorded with a YSI Pro20 (Ohio, USA). Temperature (°C), pH, and conductivity (µs) readings were gathered with a YSI Pro1030 multimeter (Ohio, USA). Percentage cover of gravel, cobble, boulder, bedrock, and moss were visually estimated per reach.

In the laboratory, samples were rinsed through a 500 µm sieve with fresh water, then picked in a plastic tray marked with a 5 cm grid. Samples were sieved, and then picked several times to ensure no organisms were missed. Organisms were identified to species level where possible. Simuliidae were identified to family level, most Chironomidae to sub-family level, and to genus in the case of *Rheotanytarsus* spp. Organisms were examined using a Meiji Techno binocular microscope (10-75x magnification) with a Phototonic A1160 light source. An Olympus G72110 compound microscope (x100 magnification) was used when closer examination was required (e.g., *Baetis* spp. gill plates).

Data analyses

Linear mixed models were employed to examine the effect of catchment, reach and augmentation state on total number of individuals (Ind), number of species (S), Hill-Shannon diversity index, and Hill-Simpson diversity index using nested linear mixed models = state * catch + reach (state*catch) in IBM SPSS for Windows, version 24.0 (IBM Corp 2016), with planned pairwise comparisons between augmentation states using estimated marginal means. Conformity to assumptions of glm was determined using plots of fits and residuals. Hill-Shannon and Hill-Simpson numbers were calculated and used in place of Shannon's and Simpsons diversity indices as this conversion produces the 'effective number of species' and is therefore a more accurate representation of assemblage composition (Hill 1973, Chao et al. 2014). Permutational multivariate analysis of variance (PERMANOVA) undertaken in PRIMER version.7 (Clarke et al. 2014) was employed to test for the effects of augmentation, catchment and reach (nested within both catchment and augmentation state) on assemblage composition. In addition, multiple control reaches were included in qualitative analysis to determine typical between-reach variability *sensu* Underwood (1992). Physicochemistry measures were recorded for each individual sample, comprising temperature, pH, conductivity, dissolved oxygen, turbidity, flow speed, and depth, as well as percentage cover of gravel, cobbles, boulders, moss and bedrock. These data were then summarised using principle component analysis (PCA), and first axis scores based on normalised variables were incorporated in the PERMANOVA as a covariate, employing a type 1 SS PERMANCOVA model. SIMPER analysis was undertaken using the *vegan* package (Oksanen 2013) in R version. 3.4.2 (Team 2016) to examine which species contributed most to the dissimilarity between reaches

and catchments. To visualize patterns in assemblage composition across catchments, reaches and augmentation states, 2-dimensional multidimensional scaling (nMDS) was conducted using the Bray-Curtis similarity index based upon \log_{10} transformed abundances in the routine metaMDS in the *vegan* package, with either physicochemical vectors and species overlain, or the addition of samples from control reaches. Finally, organisms were assigned to functional feeding groups (FFGs) following (Merritt and Cummins 1996), with FFG frequencies generated from individual abundance data. These data were then analysed in Excel using a goodness of fit *G*-test to explore possible differences in functional composition between unaugmented and augmented reaches.

Results

Univariate analyses

A total of 3833 individuals were recorded, representing 44 taxa of aquatic macroinvertebrata (Table 2). Univariate GLMs indicated strong spatial variability for individual abundance ($p < 0.05$), species richness ($p < 0.01$), Hill-Shannon diversity ($p < 0.001$) and Hill-Simpson diversity ($p < 0.001$) at the level of reach but showed no significant effects for augmentation state or catchment sampled (Table 3). A significant difference was found ($p < 0.01$) in number of individuals between the River Avon augmentation states, with higher numbers recorded in unaugmented reaches (Table 3).

Table 2. Species list with assigned functional feeding group (FFG) and individual abundances across all reaches/catchments (AU – River Avon unaugmented, AA – River Avon augmented, STU – South Teign unaugmented, STA – South Teign augmented, RC – reference catchments. All species are larval unless otherwise stated as adult (A). FFG codes: G/C = gatherer/collector, S/D = shredder/detritivore, F/C = filterer/collector, P/P/E = piercer/predator/engulfer, S = scraper.

Order	Species	FFG	AU	AA	STU	STA	RC
Odonata (dragon/damselflies)	<i>Cordulegaster boltonii</i> (Donovan, 1807)	P/P/E	0	1	0	0	0
Trichoptera (Caddisflies)	<i>Hydropsyche siltalai</i> Döhler, 1964	F/C	5	4	43	12	16
	<i>Rhyacophila munda</i> McLachlan, 1862	P/P/E	2	0	6	0	6

	<i>Rhyacophila dorsalis</i> (Curtis, 1834)	P/P/ E	15	21	10	20	5
	<i>Polycentropus flavomaculatus</i> (Pictet, 1834)	F/C	35	64	9	21	10
Ephemeroptera (Mayflies)	<i>Baetis rhodani</i> Pictet, 1845	G/C	27	75	85	65	75
	<i>Serratella ignita</i> (Poda, 1761)	G/C	60	50	35	54	226
	<i>Heptagenia sulphurea</i> (Müller, 1776)	S	0	4	0	0	0
	<i>Electrogena lateralis</i> (Curtis, 1834)	S	1	6	0	0	0
	<i>Caenis rivulorum</i> Eaton, 1884	S	0	0	0	0	2
	<i>Ecdyonurus torrentis</i> Kimmins, 1942	S	0	1	0	0	0
Plecoptera (Stoneflies)	<i>Leuctra inermis</i> Kempny, 1899	S/D	128	53	15	356	183
	<i>Leuctra moselyi</i> Morton, 1929	S/D	0	0	0	0	4
	<i>Chloroperla torrentium</i> (Pictet, 1841)	S/D	0	0	60	43	3
	<i>Amphinemura sulcicollis</i> (Stephens, 1836)	S/D	0	4	0	0	0
	<i>Dinocras cephalotes</i> (Curtis, 1827)	P/P/ E	0	0	0	0	3
	<i>Protonemura meyeri</i> (Pictet, 1841)	S/D	147	4	22	2	54
	<i>Isoperla grammatica</i> (Poda, 1761)	P/P/ E	24	2	35	4	6
Coleoptera (Beetles)	<i>Elmis aenea</i> (Müller, P.W.J., 1806)	G/C	155	1	233	5	129
	<i>Oulimnius tuberculatus</i> (Müller, P.W.J., 1806)	G/C	110	9	5	0	23
	<i>Limnius volckmari</i> (Panzer, 1793)	G/C	28	12	3	28	49
	<i>Esolus parallelepipedus</i> (Müller, P.W.J., 1806)	G/C	0	0	0	0	2
	<i>Elmis aenea</i> (A)	S	18	0	35	0	14
	<i>Oulimnius tuberculatus</i> (A)	S	2	1	5	0	0
	<i>Limnius volckmari</i> (A)	S	4	2	0	2	1
	<i>Helophorus brevipalpis</i> Bedel, 1881	S/D	0	0	4	0	1
	<i>Hydrophilidae</i> sp. Latreille, 1802	G/C	0	1	0	0	1
	<i>Elodes</i> sp. Latreille, 1796	G/C	0	0	16	1	0
Amphipoda	<i>Gammarus pulex</i> Linnaeus, 1758	S	0	0	0	6	0
Diptera (Flies)	<i>Ibis marginata</i> (Fabricius, 1781)	P/P/ E	0	3	0	0	8
	<i>Dictenidia bimaculata</i> (Linnaeus, 1761)	P/P/ E	10	0	14	11	17
	<i>Tipulidae</i> spp.	P/P/ E	0	1	0	7	0
	<i>Rheotanytarsus</i> spp. Thienemann & Bause, 1913	G/C	0	86	0	6	26
	<i>Chironominae</i> spp.	G/C	0	31	0	13	4
	<i>Tanypodinae</i> sp.	G/C	4	64	1	34	18
	<i>Orthoclaadiinae</i> spp.	G/C	69	20	2	13	5
	<i>Simuliidae</i> spp.	F/C	32	76	28	63	38

Table 3. General linear model results for individual abundance, species richness, Hill-Shannon numbers, Hill-Simpson numbers and associated pairwise comparisons. Asterisks (*) indicate level of significance ($p < 0.05 = *$, $p < 0.01 = **$, $p < 0.001 = ***$). The code (u) indicates higher values in unaugmented reaches.

Source	Individual abundance	Species richness	Hill-Shannon	Hill-Simpson
state	ns	ns	ns	ns
catch	ns	ns	ns	ns
state*catch	ns	ns	ns	ns
reach(state*catch)	*	**	***	***
Avon state	(u)**	ns	ns	ns
South Teign state	ns	ns	ns	ns

Multivariate analyses

Type 1 sums of squares PERMANCOVA indicated a significant effect of augmentation ($p = 0.001$) upon assemblage composition after accounting for the strong influence of physicochemistry ($p = 0.008$) as represented by the first axis PCA scores. This latter accounted for 62% of the variation in physiochemical variables, being mainly correlated with depth (0.862), conductivity (-0.427) and temperature (0.135). Furthermore, in the PERMANCOVA, a strong catchment effect indicated a high spatial variability in assemblage composition ($p < 0.001$), which is also reflected at the level of reach ($p < 0.001$) (Table 4).

Table 4. Type 1 sums of squares PERMANCOVA with PhysChemPC (representing the first axis of a PCA of physiochemical data).

Source	df	MS	Pseudo-F	P(perm)
PhysChemPC	1	6192.1	2.6445	0.008
state	1	45787	13.65	0.001
catch	1	12404	4.4328	0.001
state*catch	1	14849	4.4828	0.001
reach(state*catch)	16	3322.2	2.4129	0.001
Residual	79	1376.8		

SIMPER analysis showed differences in species assemblages to be largely due to the dominance of the riffle beetles *Elmis aenea* and *Oulimnius tuberculatus*, and the stonefly *Protonemura meyeri* in unaugmented reaches of both the River Avon and South Teign, these taxa being present in relatively small numbers, if at all, in augmented reaches of either catchment. The stonefly *Leuctra inermis* was found in far greater numbers in the South Teign augmented reaches, an interesting contrast to the River Avon catchment where it was instead observed in higher abundance in unaugmented reaches. nMDS Ordination illustrates the distinction between augmented and unaugmented reaches in both catchments (Figure 2). Additionally, when added to the ordination, control reach fauna appeared to be more similar to unaugmented than augmented reaches (Figure 3).

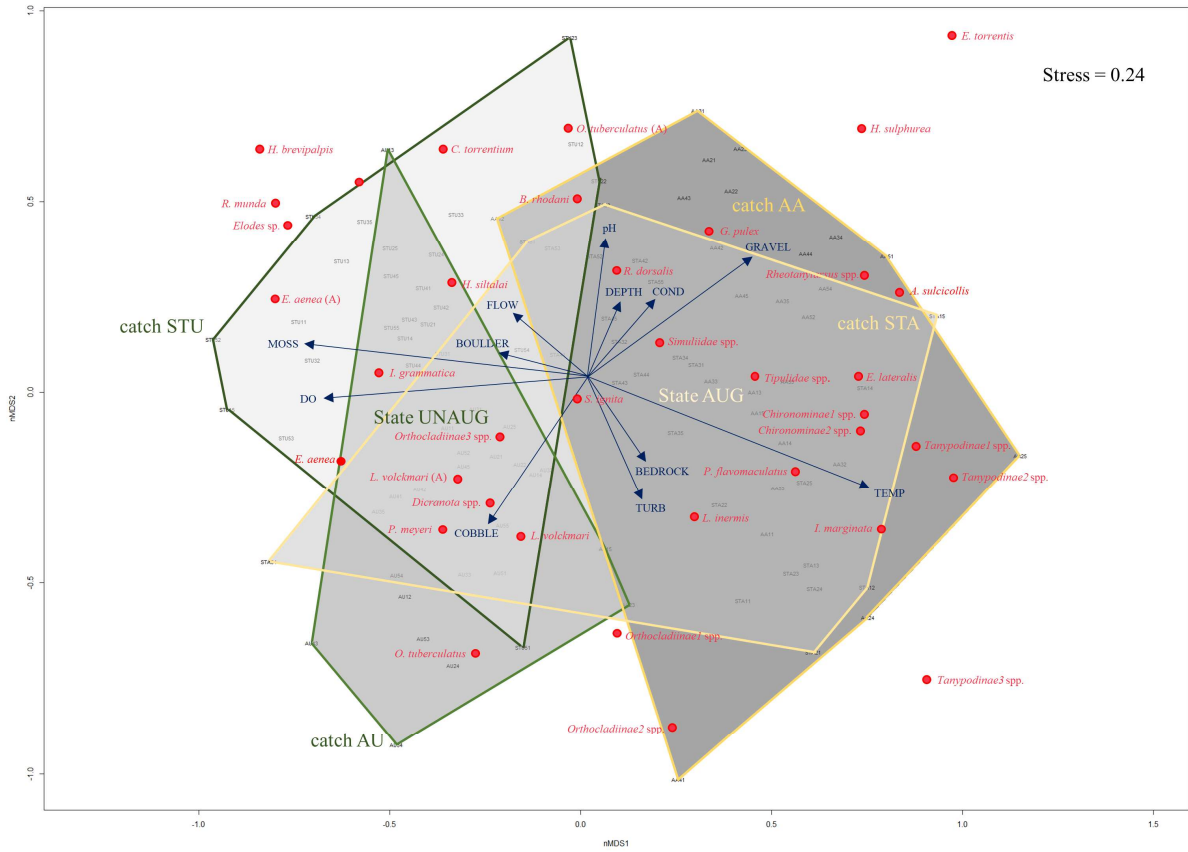


Figure 2. Non-metric multidimensional scaling (nMDS) ordination of macroinvertebrate abundance across unaugmented and augmented reaches of the two study catchments. Convex hulls (shaded polygons) are overlain to clarify groupings according to catchment and augmentation state, where A = River Avon, ST = South Teign, U = unaugmented and AUG = augmented, respectively. Sample codes indicated in small black letters; species indicated in red, (A) = indicates adult forms for taxa which occurred as both adult and larvae; for full taxonomic classification see Table 2. Blue arrows represent vectors of environmental variables related to nMDS axes.

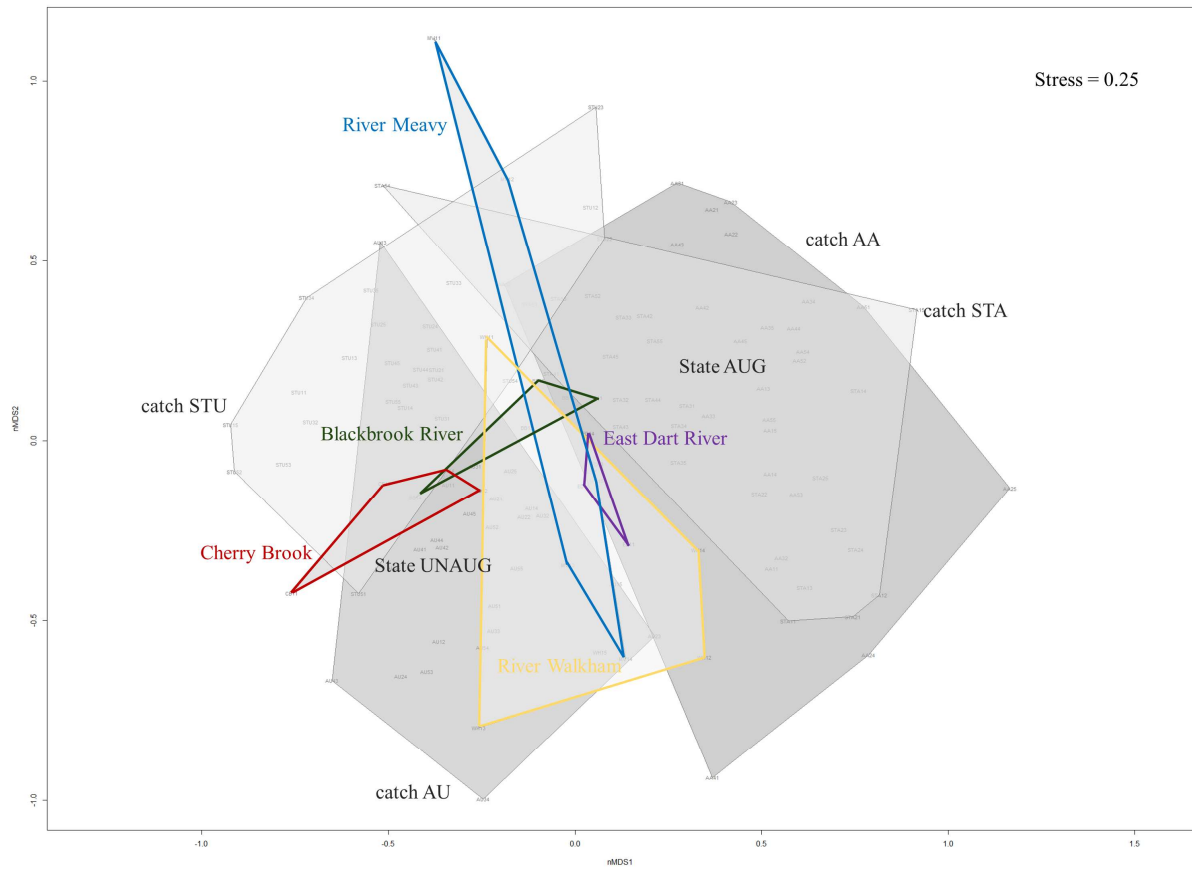
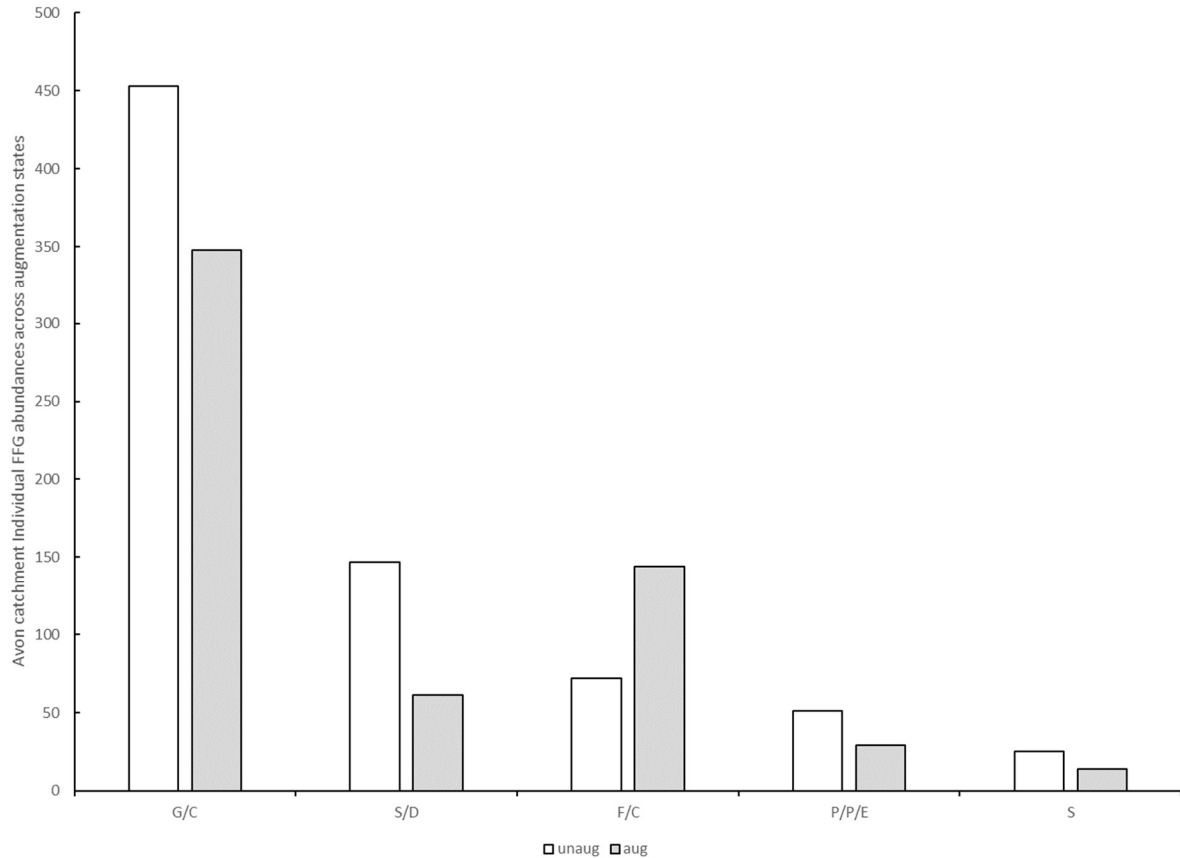


Figure 3. Non-metric multidimensional scaling (nMDS) ordination of macroinvertebrate abundance across unaugmented and augmented reaches of the two study catchments, together with control reaches sampled (labelled and coloured convex hulls), Where A = River Avon, ST = South Teign, U = unaugmented and AUG = augmented, respectively. Sample codes indicated in small black letters.

Functional feeding group analysis

There were significant differences in functional feeding group composition between unaugmented and augmented reaches of both the River Avon ($G=66.96$, 4 d.f., $p < 0.001$), and South Teign ($G=232.86$, 4 d.f., $p < 0.001$). Gatherer collectors were found in higher abundances in unaugmented reaches in both catchments (e.g., larval *Elmis aenea* in both catchments and *Oulimnius tuberculatus* in the River Avon). This trend followed with predator/piercer/engulfers (e.g., *Isoperla grammatica*, both catchments) and scrapers (e.g., adult *E. aenea*). However, shredder/detritivores showed a different pattern between catchments: unaugmented reaches of the River Avon supported more than augmented reaches, whereas in the South Teign shredder/detritivores were more abundant in augmented reaches. Interestingly, this juxtaposition of dominance across catchments seems to be driven by larvae of the stonefly *Leuctra inermis*. (see Figure 4 and Table 2 for species functional group classifications).

(a)



(b)

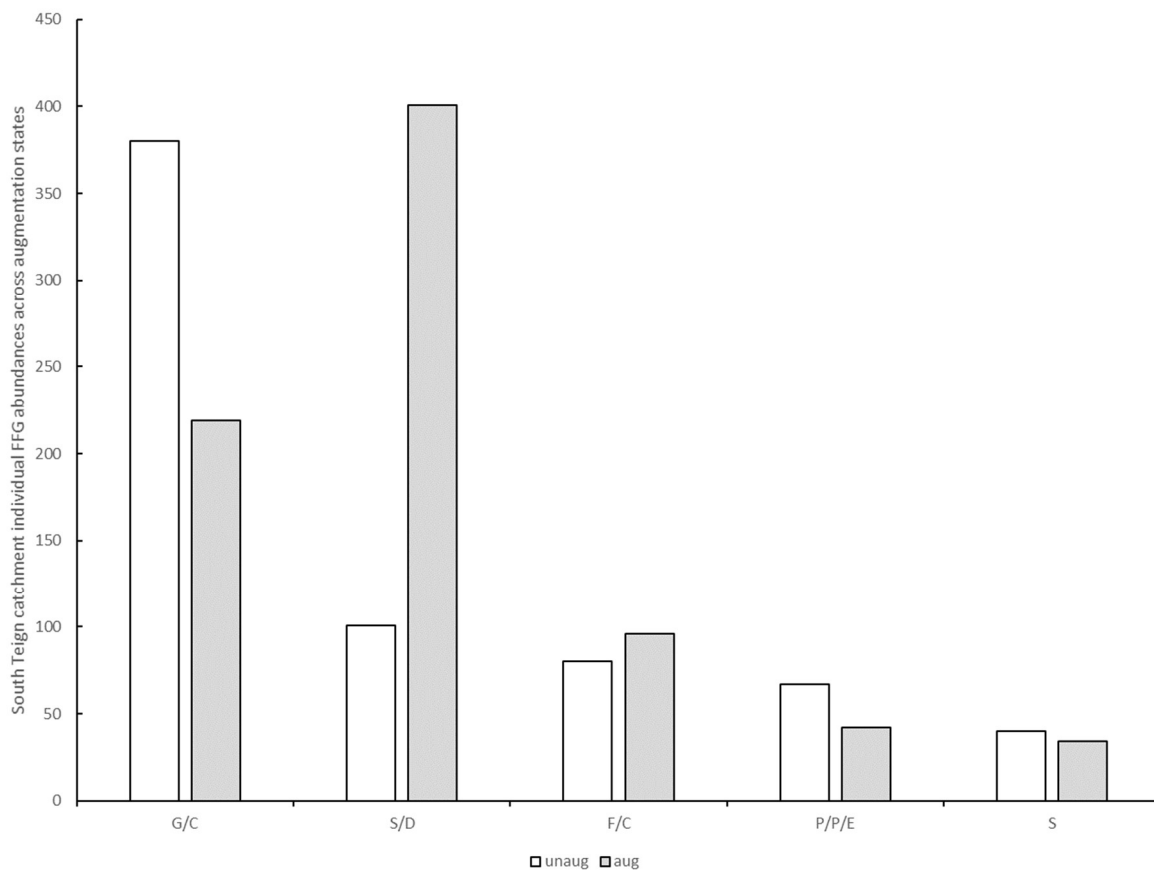


Figure 4. Individual functional feeding group abundances across catchments and augmentation states; (a) River Avon catchment and (b) South Teign catchment. Graph codes: G/C = gatherer/collector, S/D = shredder/detritivore, F/C = filterer/collector, P/P/E = piercer/predator/engulfer, S = scraper.

Discussion

This study explored the effects of augmentation of gravels on macroinvertebrates, and is the first time that such a study has been undertaken on upland watercourses of this type. The impact of gravel augmentation on macroinvertebrate assemblages has been investigated with varying and sometimes inconsistent results (Merz and Ochikubo Chan 2005, Sarriquet et al. 2007, Albertson et al. 2011). In this study, control reach faunas appeared to be more similar in assemblage composition to unaugmented reaches on the two study rivers, which would seem to make sense considering the River Avon and the South Teign are, to all intents and purposes, 'natural' (at least from a flow and riffle perspective - not taking into account riparian input) before they flow into their respective reservoirs. In augmented catchments however, augmentation led to small-scale significant differences in macroinvertebrate assemblages at

the level of reach for individual abundance, species richness, Hill-Shannon and Hill-Simpson diversity. Augmentation was also observed to have a significant effect on macroinvertebrate assemblage composition: unaugmented reaches in both catchments were found to be dominated by the riffle beetles *E. aenea* and *O. tuberculatus*, and at the River Avon, by the stonefly *P. meyeri*. An interesting contrast between catchments was seen with *L. inermis* however, with higher densities found in unaugmented reaches of the River Avon, and in contrast, augmented reaches of the South Teign. In addition, across catchments, augmented reaches supported higher densities of Simuliidae and Chironomidae, in particular *Rheotanytarsus* spp. Functional group composition was mainly comprised of gatherer/collectors and predator/piercer/engulfers in unaugmented reaches, with shredder/detritivores (largely *L. inermis*), and filterer/collectors dominating augmented reaches.

The macro and meso-scale spatial invertebrate assemblage variabilities revealed in this study could in part be attributed to the fact that most ecosystems are heterogeneous at varying scales; from microhabitats, to whole landscapes and ecoregions (Heino et al. 2004). Systems are hierarchically organised, comprising river systems, stream segments, reach systems, sequences of riffle-pool and their component microhabitats (Rabeni and Jacobson 1993, Heino et al. 2004). At each scale, environmental conditions differ considerably, and this variability is in turn reflected in the heterogeneity of macroinvertebrate assemblages (Hildrew and Giller 1994, Poff 1997). Spatial variation in benthic macroinvertebrates has generally been related to in-stream factors (e.g. intra or interspecific interactions, sediment type or flow speed). This variation has also been studied within riffles and streams; for example, one study found that flow velocity was the most influential factor in predicting macroinvertebrate assemblages, with size of sediment being the least influential factor (Barmuta 1990). It is interesting to note that at small-scales (e.g. a patch of pebbles) colonisation dynamics was found likely to be a mixture of species and location-specific dispersal and selection mechanisms, with larger spatial scales being more predictable (e.g. riffles and pools differing substantially).

The hyporheic zone, the interface between flow and sediment, might be another factor determining small-scale reach level macroinvertebrate assemblages observed in this study (Stanford and Ward 1988). Saturated subsurface sediments of the hyporheic zone contain

proportions of groundwater and surface water. This water is thought to be a major store of detritus which in turn influences surface stream functioning through hydrological exchange (Valett et al. 1994) and heterotrophic metabolism (Mulholland et al. 1997). The hyporheic zone has been shown to provide refugia (Lancaster and Hildrew 1993b, a, Rice et al. 2001) for macroinvertebrates in times of disturbance (e.g. flood) (Wood et al. 2010), or as a resource patch (Bretschko 1991). Macroinvertebrates have been shown to use the hyporheic zone in early instars, and smaller-bodied taxa with shorter generation times have the ability to colonise new resources (e.g. augmented gravels) faster due to high mobility (Marzluff and Dial 1991).

Strong spatial variability between catchments and reaches could also indicate small scale differences in colonisation patterns. In natural streams, colonisation and subsequent changes in dominance of species (succession) are common, particularly where subject to seasonal and unpredictable disturbance (e.g. floods) (Peckarsky 1986). The world of riffle dwelling invertebrates has been described as “an everchanging mosaic of environments in which elements arise, vanish, and reappear with different periodicities and predictabilities” (Sheldon 1977). These varying disturbances may well play a pivotal role in community assemblage; for instance a recently augmented reach may be kept in a nonequilibrium state and therefore be prevented from attaining ecological saturation and the tight species packing that should theoretically characterize a stable, resource limited and niche controlled system (Resh et al. 1988, Townsend 1989, Mackay 1992). One method of colonisation is known as ‘invertebrate drift’, which refers to down-stream dispersal of benthic macroinvertebrates that live in or amongst the substratum of rivers and streams (Elliott 2008a). It has been claimed that drift is the main distributor of benthic organisms in lotic systems (Minshall 1985), and it has been shown in several studies that downstream dispersal follows a diel rhythmic pattern (e.g. most organisms drift at night) (Elliott 2008a). This rapid colonisation and movement of taxa from patch to patch has been deemed a key component of macroinvertebrate assemblages (Humphries 2002), and is another possible driver of both small-scale (reach level) and meso-scale (catchment level) variability.

Variability between reaches may also be governed in part by FRS availability and its small-scale interactions with BLG. FRS comprises both organic and inorganic particles finer than 1 mm in diameter (Kemp et al. 2011), and when at natural levels, is an essential component of

habitat heterogeneity and ecosystem functioning in fluvial systems (Yarnell et al. 2006, Kemp et al. 2011). However, as a result of altered flow regimes caused by dams, increased deposition of FRS may occur (Wood and Armitage 1997, Kemp et al. 2011). FRS increases can have a major impact on macroinvertebrate communities; by smothering (Kefford et al. 2010, Kemp et al. 2011), and through limitation of oxygen and reduction of periphyton, zooplankton and other macrophyte and bryophyte sources of food that could alter the food chain (Palmer et al. 1997, Theurer et al. 1998). FRS may also fill interstitial spaces, reducing habitat availability for some invertebrate species (Wood and Armitage 1997, Theurer et al. 1998) and potentially disconnecting the hyporheic zone from benthic substrata (Mathers et al. 2022).

Assemblage composition between unaugmented and augmented reaches differed as perhaps would be expected: unaugmented reaches had therefore more exposed bedrock and therefore supported higher levels of moss cover and were more heterogenic in structure than augmented reaches. This heterogeneity encouraged higher species richness and abundance of shredder/detritivores such as *P. meyeri*; probably due to the abundance of bryophytes (e.g. the moss *Fontinalis*) as they have been shown to provide sites of refuge for macroinvertebrates (Cummins and Klug 1979). The passive capture of detritus particles by bryophytes also encourages gatherers/collectors of fine particulate organic matter. For example larvae of *E. aenea*, *O. tuberculatus* and *L. volckmari* can be seen in relative abundance in unaugmented reaches, along with their associated adult forms (designated as scrapers for this study due to differing opinions and confounding evidence as to feeding preferences) (Elliott 2006, 2008a, Elliott 2008b). The relatively poor dispersal abilities of *L. volckmari* may help explain its relatively low abundance overall in unaugmented and augmented reaches (Friberg et al. 1998). Predators/engulfers/piercers were also marginally more abundant (*R. munda* and *I. grammatica*), presumably due to relatively higher abundance of prey, and macrophytic predatory concealment. Interestingly, *R. dorsalis* was found in higher abundance in augmented reaches.

Augmented reaches held more gatherer/collectors than unaugmented reaches but of differing species: the net-spinning caddisfly *P. flavomaculatus*, members of the family Chironomidae (*Rheotanytarsus*, *Orthocaldiinae*, *Tanypodinae*) and the filterer/collectors Simuliidae. These colonisers may have drifted to the augmentation reaches or been laid as eggs randomly (Ogbeibu and Oribhabor 2002). *P. flavomaculatus* is a net-spinning predator

(Edington and Hildrew 1981), and has been shown to prey upon copepods, ostracods, *Gammarus*, *Baetis*, *Ecdyonurus*, *Amphenemura*, Chironomidae and Simuliidae (Dudgeon 1987). The presence of *P. flavomaculatus* has been shown to increase densities of chironomids (Diamond 1986, Englund 1993). It could be that increased *P. flavomaculatus* and their associated predatory net structures provide refuge for chironomids from other predators and passively trap food resources (e.g. drifting particulates, *P. flavomaculatus* faeces or periphyton) and therefore decrease emigration (Englund and Evander 1999). In another study, it was found that 62 percent of chironomids were able to crawl out of *Neureclipsis bimaculata* (Polycentropodidae) nets and escape, therefore increasing immigration (Richardson 1984). It would be interesting to explore the possibility that *P. flavomaculatus* is found in augmented reaches in direct response to the presence of Chironomids, or if the reverse is true as evidence would seem to suggest (Richardson 1984, Diamond 1986, Englund 1993, Englund and Evander 1999). The nets of caddisfly larvae may not just benefit chironomids: they may increase spatial complexity, and this complexity of habitat characteristically has positive impacts on many different aquatic macroinvertebrates (Englund and Evander 1999, Beisel et al. 2000, Cardinale et al. 2002, Death 2003, Compin and Céréghino 2007) Further study here may be warranted as increased heterogeneity could have an impact on small-scale ecosystem functioning and food availability for salmonids in reaches of gravel augmentation (Gurski et al. 2014). The mayfly larvae *H. sulphurea* was found exclusively in augmented reaches, and as a species normally associated with coarse stones and substrates this is unsurprising (Friberg et al. 1998). Another mayfly, *B. rhodani*, a species with good dispersal abilities, was found at both catchments and in all augmentation states (Rondorf et al. 1990, Friberg et al. 1998, Albertson et al. 2011).

Potential impacts for fish species

Macroinvertebrates provide a crucial source of food for fish species, and changes in their composition and quality could directly influence fish growth and community structure (Williams and Wolman 1984, Kemp et al. 2011). The decline in species richness and individual abundance observed between unaugmented and augmented reaches in this study could have major consequences for fish. Young salmon have been observed to prey switch in line with relative abundance and profitability (Thonney and Gibson 1989). However, availability of prey

and carbon content have been shown to limit their survivability (Gibson 1993), with several studies showing correlations with salmonid size and prey availability (Egglshaw 1967, Gibson and Galbraith 1975, Gibson 1993). There is some evidence that young salmonids feed on *Baetis* spp. due to its abundance in stream drift (Sagar and Glova 1988, Rader 1997, Albertson et al. 2011), and also on relatively large invertebrate prey such as *Hydropsyche* spp. even though little time is spent in the drift (Rondorf et al. 1990, Amundsen et al. 2001, Albertson et al. 2011). Therefore, if preferential feeding is seen in juveniles, then relative abundances of preferred prey could influence predation effectiveness and capture rates (MacArthur and Pianka 1966, Strauss 1979, Albertson et al. 2011). This dominance shift could therefore have implications for fish when macroinvertebrates recolonise augmented gravels by methods such as drift. FRS have been shown to have multiple effects on fish when either suspended or after deposition; including elevated stress responses (Redding and Schreck 1982, Lake and Hinch 1999), or depletion of oxygen in the water column (Bruton 1985). FRS may also infiltrate the interstitial spaces between BLG impacting oxygen supply to developing eggs, and embryonic stages of excavating fish (e.g. salmonids), which can lead to weight reductions, morphological changes, and hypoxia (Kemp et al. 2011). All of these factors will impact salmonid growth and therefore availability on the commercial market (Weber et al. 2014).

Chapter Three: The effects of gravel augmentation on leaf litter breakdown and the composition of leaf pack invertebrate assemblages

Introduction

Riverine ecosystems have the potential to transform, store, and transfer organic matter, sediments, inorganic nutrients and metabolites to adjacent ecosystems (e.g., the sea or riparian zones). Therefore, they can be considered bioreactors, fuelled and managed by the ecological communities they support (Peralta-Maraver et al. 2021). Alluvial aquifers, floodplains, streambeds and surface waters all contribute to make up the matrix of riverine ecosystems, which are connected by fluxes of matter and energy across ecohydrological interfaces or 'control points' (Hedin et al. 1998). These interfaces are comprised of interactions of hydrological, biogeochemical, and ecological processes (Krause et al. 2011b, Krause et al. 2017). Ecohydrological interfaces are generally non-stationary, spatially heterogeneous, temporally dynamic and vary in size from the micro to the macro (Kennedy et al. 2009, Krause et al. 2011a, Roskosch et al. 2012). Riverine ecohydrological interfaces provide key ecosystem services, including purification of water, maintenance of biodiversity and thermal regulation (Krause et al. 2011a, Krause et al. 2011b), as well as increasing resilience of biota to perturbations and providing zones for potential recolonization (Stubbington 2012, Krause et al. 2017).

Within all ecosystems food webs depict the impacts of community structure and ecosystem function on resident biota (MacArthur 1955, Woodward and Hildrew 2002). Food webs are spatially heterogeneous and differ between habitats, which in turn, differ in productivity, abundance of resources, and composition of community (Polis and Strong 1996, Doi 2009). In a riverine ecosystem, two classes of resource that contribute to the riverine food web and therefore the overall health of an ecosystem are autochthonous (e.g. phytoplankton) and allochthonous (e.g. leaf litter) inputs, and in the riverine ecosystem form the major part of the food web (Polis and Strong 1996, Doi 2009). The relative contribution of these inputs to the overall ecosystem will depend on the relative amounts of autochthonous production and allochthonous subsidies (leaf litter for example) (Lidman et al. 2017, Wymore et al. 2018, Ding and Wang 2019, Santonja et al. 2019). In stream ecosystems, riffles and pools are examples of different forms of ecohydrological interface, which then lead into larger rivers and form

the lower part of the catchment, which in turn continues into brackish estuary, and then on and into the sea (Vannote et al. 1980, Doretto et al. 2020).

Leaf litter is a key contributor to the allochthonous quotient of energy of many riverine ecosystems (Cummins et al. 1973, Petersen and Cummins 1974, Shieh et al. 2008, Pozo et al. 2011). The breakdown and decomposition of leaf litter in riverine ecosystems is generally driven by extrinsic factors e.g. environment or water characteristics (Woodward et al. 2012, Zhang et al. 2018) and intrinsic factors e.g. the traits of litter (Schindler and Gessner 2009, Walpola et al. 2011, Pettit et al. 2012). In temperate zones litter fall and therefore litter input into streams is seasonal (Graça 2001), and this seasonality may cause shortages of detritus at certain times of year, or between seasons, consequently restricting food availability (Petersen Jr et al. 1989). The river continuum concept (RCC) (Vannote et al. 1980, Green et al. 2022) was developed for rivers and streams in the U.S. where many of the headlands of river systems are forested, and posits that headwaters (orders 1- 3) have large inputs of riparian subsidies as they flow through forested areas, which lowers autotrophic production by shading and producing relatively large quantities of allochthonous input. As a result, benthic microalgal food sources and macroinvertebrate food sources potentially shift to subsidized terrestrial matter (Hill and Knight 1988, Hill et al. 1995). However, anthropogenic perturbation of natural riparian landscapes (e.g. deforestation) may reduce allochthony and thereby increase autochthony (Jonsson and Stenroth 2016).

Riverine macroinvertebrates utilize riparian vegetation in a variety of ways throughout their lifecycle inhabiting different zones throughout ontogeny (Cummins et al. 1989a, Cummins et al. 1989b). As terrestrial adults they may use riverine riparian vegetation for mating, feeding, dispersal and for refuge (Brown 1987, Jackson and Resh 1989, Sweeney 1993, Reinhart and VandeVoort 2006), whereas as aquatic larvae, they may use leaf litter as a food source or as refuges (Oester et al. 2022). The most prevalent macroinvertebrate taxa in stream ecosystems are Odonata (Dragonflies), Plecoptera (Stoneflies), Ephemeroptera (Mayflies), Diptera (Flies) and Trichoptera (Caddisflies) (Graça 2001). Macroinvertebrates are generally classified functionally by the way they feed, as opposed to food source (Wallace and Webster 1996). Key functional feeding groups (FFG) are: (1) *Piercer/Predator/Engulfers* (P/P/E) which feed on other organisms; (2) *Grazers-scrapers* (S) which feed on biofilm on submerged structures (Cummins et al. 1984); (3) *Filterer/Collectors* (F/C) which feed on fine particulate

organic matter (FPOM) filtered from the water column: (4) *Gatherer/Collectors* (G/C) which take FPOM directly from the substrate (Cummins et al. 2005); and (5) *Shredder/Detritivores* (S/D) which feed on coarse particulate organic matter (CPOM), including leaf litter (Ruetz et al. 2002). Most of these functional groups other than predators can function as detritivores (Graça 2001).

Research to date on leaf litter breakdown in streams has focussed primarily on rates of decomposition, often without reference to macroinvertebrate involvement (Marks 2019). However, a body of work has investigated macroinvertebrate functional traits and subsequent utilization of leaf litter as a proxy for functional diversity. (Petersen and Cummins 1974, Boling Jr et al. 1975, Suberkropp et al. 1976, Ward and Cummins 1979, Newbold et al. 1982, Webster and Benfield 1986, Richardson 1992, Wallace et al. 1997, Jonsson and Malmqvist 2000, Bergfur 2007, Péru and Dolédec 2010, Classen-Rodríguez et al. 2019). The exclusion of leaf litter results in reduction of both biomass and abundance of benthic macroinvertebrates (Wallace et al. 1997, Wallace et al. 1999). In particular, the exclusion of litter may impact S/D, G/C and P/P/E which in turn reduces secondary production (Graça 2001). Potential impacts on leaf litter production include anthropogenic perturbations such as deforestation and dam creation.

Potentially significant impacts on leaf litter production and supply include anthropogenic perturbations such as deforestation and dam creation, and Dartmoor National Park, like much of northern Europe, is believed to of once had a fully wooded upland, but has a long (in anthropogenic terms) history of human settlement, gradual deforestation (Simmonds 1970) and other anthropogenic perturbations (Thorndycraft et al. 1999, Thorndycraft et al. 2004). In addition to such factors, the creation of dams will clearly impact leaf litter supply and breakdown directly and indirectly, by changing the physical environment downstream; these changes having impacts on litter supply and retention and macroinvertebrate assemblages. This study expands on the work described in Chapter 2 by examining the impact of gravel augmentation on leaf litter breakdown and macroinvertebrate biodiversity. Specifically, it compares rates of leaf mass loss and the composition of colonizing macroinvertebrate assemblages between gravel augmented and unaugmented reaches in the River Avon and South Teign, two dammed, sediment-starved catchments on Dartmoor, Devon, UK, the first time this has been examined in upland watercourses of this type.

Materials and methods

Study catchments

Leaf packs were installed in Dartmoor National Park, Devon, UK in unaugmented and augmented reaches of the Rivers Avon and the South Teign (Figure 5 and Table 5). These two catchments were subject to a series of planned gravel augmentations of mixed gravel size (4 – 100mm), undertaken over a six-year period from 2014 – 2019 by Westcountry Rivers Trust. The River Avon rises 460 m above sea level on the Aune Head mires, south Dartmoor. Its catchment extends over 110.5 km² and flows 40 km from source to sea. The River Avon is dammed by the Avon Reservoir, which was constructed in 1957 (Bogle et al. 1959). The River Avon's major tributaries include Bala Brook and Glaze Brook, both of which have sources on the moor itself (Environment Agency 2003). The South Teign rises near Grey Wethers on north Dartmoor, which then feeds Fernworthy reservoir 19 km from the Avon Dam. The beds of the River Avon and the South Teign mainly consist of large cobbles and boulders, with sizable areas of exposed bedrock and bed load gravel deposits. The uplands of Dartmoor produce relatively low levels of BLG. However, it is believed that the River Avon and Fernworthy Dams have reduced sediment supply to downstream reaches, with the potential for deleterious impacts on aquatic life (Downs et al. 2016).

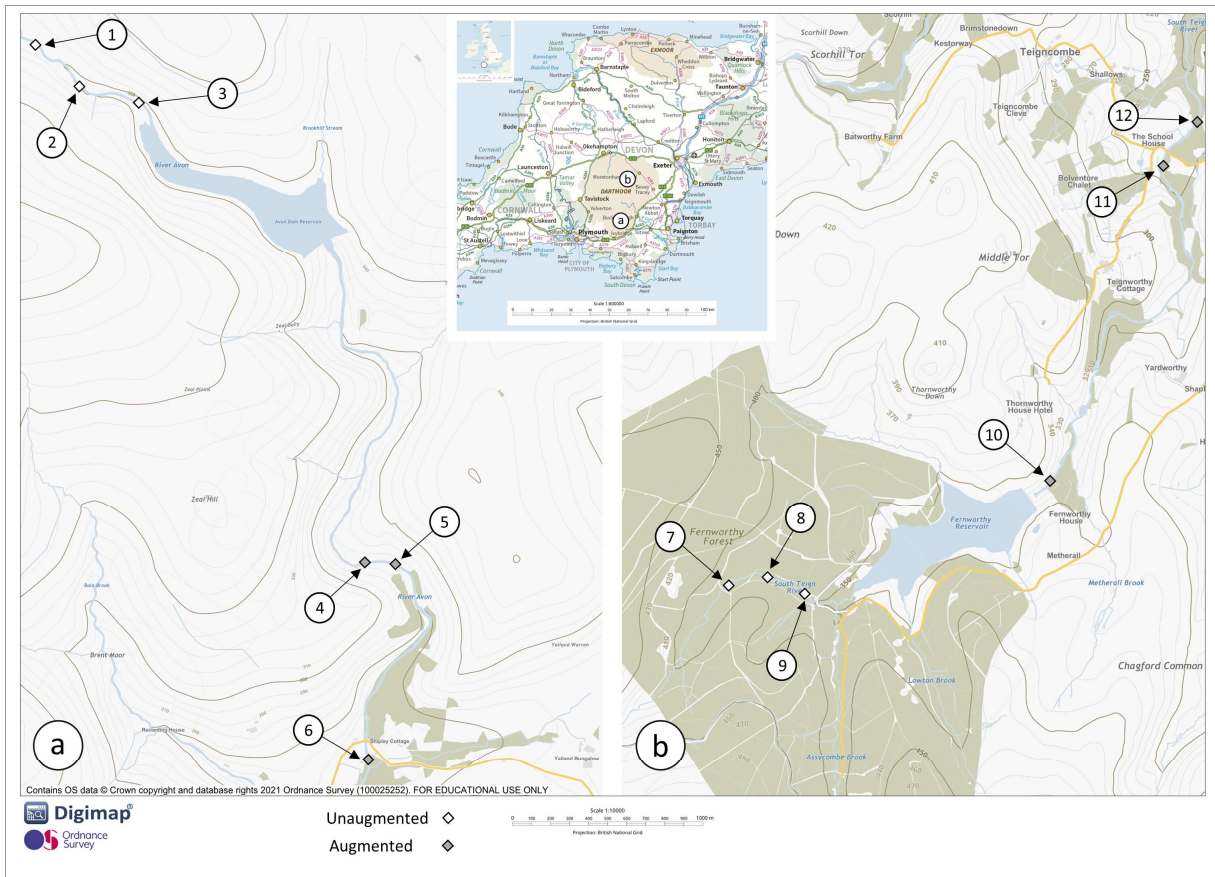


Figure 5. Location of Dartmoor National Park leaf pack study reaches. The inset shows catchments within the British Isles: a) River Avon catchment, b) South Teign catchment. Individual leaf pack installation reaches are marked on the map and coloured white/grey to distinguish augmentation state (Digimap 2021).

Table 5. Leaf pack installation information.

Catchment	Reach	Augmentation state	Lat/long	Elevation
River Avon	1	unaugmented	50°28'45.8"N 3°52'54.2"W	351m
River Avon	2	unaugmented	50°28'41.1"N 3°52'45.9"W	349m
River Avon	3	unaugmented	50°28'38.4"N 3°52'31.8"W	345m
River Avon	4	augmented	50°27'29.2"N 3°51'37.2"W	268m
River Avon	5	augmented	50°27'29.5"N 3°51'35.1"W	266m
River Avon	6	augmented	50°27'01.4"N 3°51'27.2"W	218m
South Teign	7	unaugmented	50°38'19.8"N 3°54'19.6"W	383m
South Teign	8	unaugmented	50°38'18.4"N 3°54'13.5"W	379m
South Teign	9	unaugmented	50°38'16.7"N 3°54'07.4"W	365m
South Teign	10	augmented	50°38'38.6"N 3°52'48.6"W	331m
South Teign	11	augmented	50°39'46.7"N 3°52'05.4"W	244m
South Teign	12	augmented	50°39'49.6"N 3°51'59.6"W	243m

Leaf pack experiments

Leaf pack construction, collection and processing followed the method outlined in (Benfield et al. 2017). Oak (*Quercus robur*) leaves were collected from trees local to the study catchments shortly after abscission, and air dried in the laboratory for three weeks until they reached constant dry mass (CDM), this dried matter was then used to construct leaf packs. 120 mesh bags (10 cm x 17 cm) were constructed; 60 bags from 5 mm mesh fabric (to allow ingress of macroinvertebrates), and 60 from 0.25 mm (hereafter micro) mesh fabric (to control for microbial mass loss). All bags were filled with 7 g of dried leaf matter (± 0.1 g). Packs were inserted into both catchments, fastened to large rocks in riffle areas with either unaugmented or augmented gravels (5 x 5mm mesh and 5 x micro mesh packs per reach, 3 reaches per augmentation state). Each rock had both a 5 mm bag and a micro mesh bag attached. Rocks were strung together with strong wire and tied to a bankside feature to minimize loss in the event of spates/flooding. Leaf packs were positioned on rocks to attempt to imitate natural leaf packs (i.e., upstream of the rock they were attached to). Due to the relatively slow breakdown of oak species leaves (Petersen and Cummins 1974) and to allow colonisation by macroinvertebrates, leaf packs were inserted between 27th – 30th July 2020 and collected 21st – 24th September 2020 after 56 days of immersion. Leaf packs were retrieved from reaches, numbered and placed in individual plastic pots with 80% ethanol for subsequent processing. In the laboratory, leaf packs were removed from pots and macroinvertebrates identified in a plastic tray marked with a 5 cm grid, prior to washing and sieving the remaining leaf matter of silt and mineral deposits in a 250 μ m sieve. Retained leaf matter was air-dried in pre-weighed brown paper bags for three weeks to return material to CDM and then re-weighed. Organisms were identified to species level where possible, except for Simuliidae (family level), Chironomidae (sub-family), *Rheotanytarsus spp.* and *Elodes spp.* (genus). Organisms were examined using a Meiji Techno binocular microscope (10-75x magnification) with a Phototonic A1160 light source. An Olympus G72110 compound microscope (x100 magnification) was used when closer examination was required (e.g., *Baetis spp.* gill plates).

Data analyses

A general linear model was run with total mass loss of micro bags as the dependant variable to interrogate the possible effects of *state*, *catch*, and *reach* on micro mesh pack mass loss. Linear mixed models = state * catch + reach (state * catch) were employed to examine the effect of augmentation state, catchment and reach on total number of individuals (Ind), number of species (S), Hill-Shannon diversity index, and Hill-Simpson diversity index found in 5 mm mesh leaf packs. Hill-Shannon and Hill-Simpson numbers were calculated and used in place of Shannon's and Simpsons diversity indices, as this conversion produces the effective number of species and is therefore a more accurate representation of assemblage composition (Hill 1973, Chao et al. 2014). The difference in mass between micro and 5mm mesh packs of each leaf pack sample pair (inter-pack mass loss) was calculated and used as the dependent variable in the same model with (Ind), (S), Hill-Shannon diversity index, and Hill-Simpson diversity index as covariates, to explore the influence of both catchment/state/reach and macroinvertebrate assemblage parameters on leaf litter breakdown. Univariate analyses were undertaken in IBM SPSS for Windows, version 24.0 (IBM Corp 2016).

Organisms were assigned to functional feeding groups (FFGs) following (Merritt and Cummins 1996), and FFG frequencies generated from abundance data. These data were then analysed using a goodness of fit G-test to explore possible differences in functional assemblage composition between unaugmented and augmented reaches.

Permutational multivariate analysis of variance (PERMANOVA) undertaken in PRIMER version.7 (Clarke et al. 2014) was employed to test for the effects of augmentation state, catchment and reach (nested within both catchment and augmentation state) on 5 mm leaf pack macroinvertebrate assemblage composition. SIMPER analysis was undertaken using the *vegan* package (Oksanen 2013) in R version. 3.4.2 (Team 2016) to examine which species contributed most to the dissimilarity between reaches and catchments. To visualize patterns in assemblage composition across sites and augmentation states, 2-dimensional multidimensional scaling (nMDS) was conducted using the Bray-Curtis similarity index based upon \log_{10} transformed abundances in the routine metaMDS in the *vegan* package.

Results

Univariate analyses

A GLM using micro mesh mass loss as the dependent variable showed a significant effect of state on mass loss but at no other level, with higher mass loss found in augmented reaches for pairwise comparisons at both the River Avon ($p < 0.01$) and South Teign ($p < 0.05$) (Figure 6, Table 6). In total, 1808 individual organisms from 28 taxa were recorded across all 5 mm leaf packs (Table 7). General linear mixed models indicated significant effects of state on individual abundance ($p < 0.01$) and Hill-Shannon diversity ($p < 0.05$), with significant effects being found at the level of state*catch for species richness ($p < 0.01$), Hill-Shannon diversity ($p < 0.001$) and Hill-Simpson diversity ($p < 0.001$). In addition, reach (state*catch) was shown to have a significant impact on individual abundance ($p < 0.01$) (Figure 7, Table 8). Pairwise comparisons for the effect of state yielded significant results across all dependent variables, with unaugmented reaches showing greater faunal abundance for five out of 8 pairwise tests (Table 8). GLM analyses with inter-pack differences in mass loss as the dependent variable and individual abundance, species richness, Hill-Shannon diversity and Hill-Simpson diversity as covariates, revealed that differences in macroinvertebrate abundance and diversity did not appear to significantly affect leaf mass loss (Table 9). There was also no significant overall effect of state on the rate of leaf litter breakdown by macroinvertebrates, but significant differences in leaf mass loss were observed at the level of reach (Table 9). Pairwise comparisons between augmentation states within catchments, however, showed significant interactions between state and all four covariates in the South Teign catchment, with significantly more mass lost in augmented reaches (Table 9).

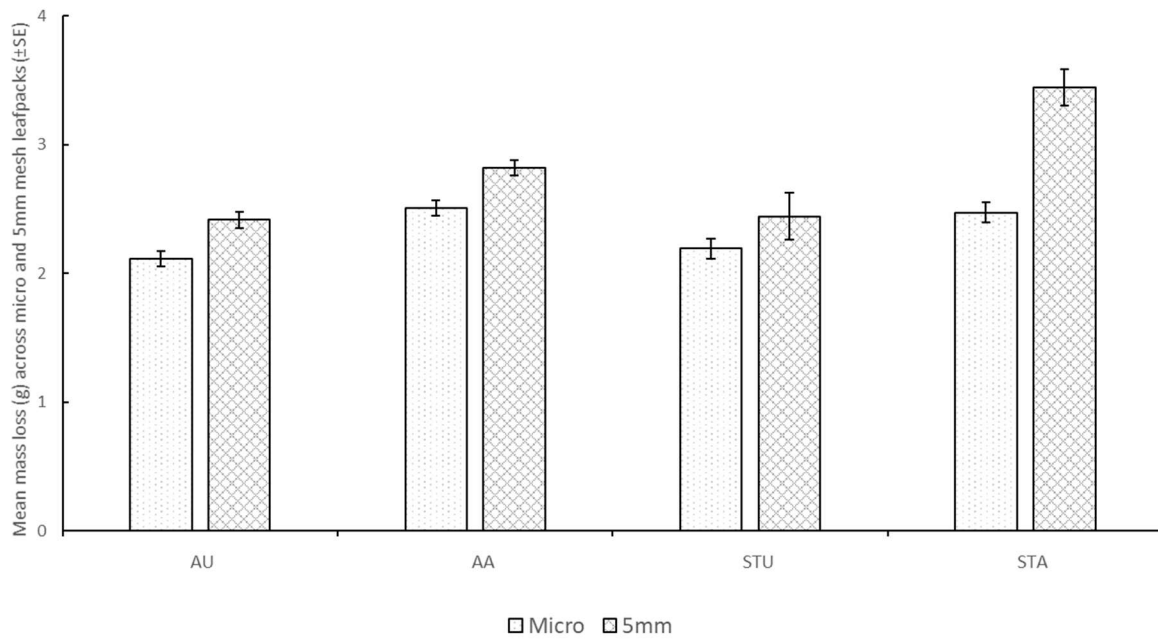


Figure 6. Mean total mass loss across micro and 5mm mesh leaf packs at catchments: River Avon unaugmented (AU), River Avon augmented (AA), South Teign unaugmented (STU) and South Teign augmented (STA). Error bars represent standard error (SE) of the mean.

Table 6. General linear model results for total mass loss of micro mesh leaf packs as the dependent variable with associated pairwise comparisons. Asterisks (*) indicate level of significance ($p < 0.05 = *$, $p < 0.01 = **$, $p < 0.001 = ***$). The code (a) indicates significantly higher mass loss in augmented reaches.

Source	df	MS	F	Sig.
state	1	1.690	10.721	0.01
catch	1	.010	.063	0.809
state*catch	1	.049	.309	0.593
reach(state*catch)	8	.158	1.385	0.227
Avon state	(a) **			
South Teign state	(a) *			

Table 7. Species list with assigned functional feeding group (FFG) and individual abundances in 5 mm leaf packs across all reaches/catchments (AU = River Avon unaugmented, AA = River Avon augmented, STU = South Teign unaugmented, STA = South Teign augmented). All species are larval unless otherwise listed as (Adult). FFG codes: G/C = gatherer/collector, S/D = shredder/detritivore, F/C = filterer/ collector, P/P/E = piercer/predator/engulfer, S = scraper.

Order	Species	FFG	AU	AA	STU	STA
Trichoptera (Caddisflies)	<i>Hydropsyche siltalai</i> Döhler, 1964	F/C	21	15	0	33
	<i>Rhyacophila munda</i> McLachlan, 1862	P/P/E	11	0	0	5
	<i>Rhyacophila dorsalis</i> (Curtis, 1834)	P/P/E	21	0	5	13
	<i>Polycentropus flavomaculatus</i> (Pictet, 1834)	F/C	32	10	2	27
Ephemeroptera (Mayflies)	<i>Baetis rhodani</i> Pictet, 1845	G/C	59	0	40	0
Plecoptera (Stoneflies)	<i>Leuctra inermis</i> Kempny, 1899	S/D	199	71	132	82
	<i>Leuctra moselyi</i> Morton, 1907	S/D	20	0	0	0
	<i>Amphinemura sulcicollis</i> (Stephens, 1836)	S/D	0	0	0	4
	<i>Protonemura meyeri</i> (Pictet, 1841)	S/D	81	127	146	28
	<i>Isoperla grammatica</i> (Poda, 1761)	P/P/E	0	0	0	2
Coleoptera (Beetles)	<i>Elmis aenea</i> (Müller, P.W.J., 1806)	G/C	190	17	68	5
	<i>Oulimnius tuberculatus</i> (Müller, P.W.J., 1806)	G/C	51	16	0	4
	<i>Limnius volckmari</i> (Panzer, 1793)	G/C	57	1	0	3
	<i>Esolus parallelepipedus</i> (Müller, P.W.J., 1806)	G/C	4	0	2	0
	<i>Elmis aenea</i> (Adult)	S	15	0	8	2
	<i>Oulimnius tuberculatus</i> (Adult)	S	5	0	0	0
	<i>Limnius volckmari</i> (Adult)	S	11	0	0	1
	<i>Elodes</i> sp. Latreille, 1796	G/C	5	2	21	3
Amphipoda (Amphipods)	<i>Gammarus pulex</i> Linnaeus, 1758	S	0	0	0	32
Diptera (Flies)	<i>Ibisia marginata</i> (Fabricius, 1781)	P/P/E	6	14	2	6
	<i>Dictenidia bimaculata</i> (Linnaeus, 1761)	P/P/E	6	0	0	4
	<i>Tipulidae</i> sp. Latreille, 1802	P/P/E	0	0	1	0
	<i>Chironominae</i> spp.	G/C	7	1	5	12
	<i>Tanypodinae</i> spp.	G/C	6	3	12	6
	<i>Orthoclaadiinae</i> spp. (Lenz, 1921)	G/C	0	0	0	8

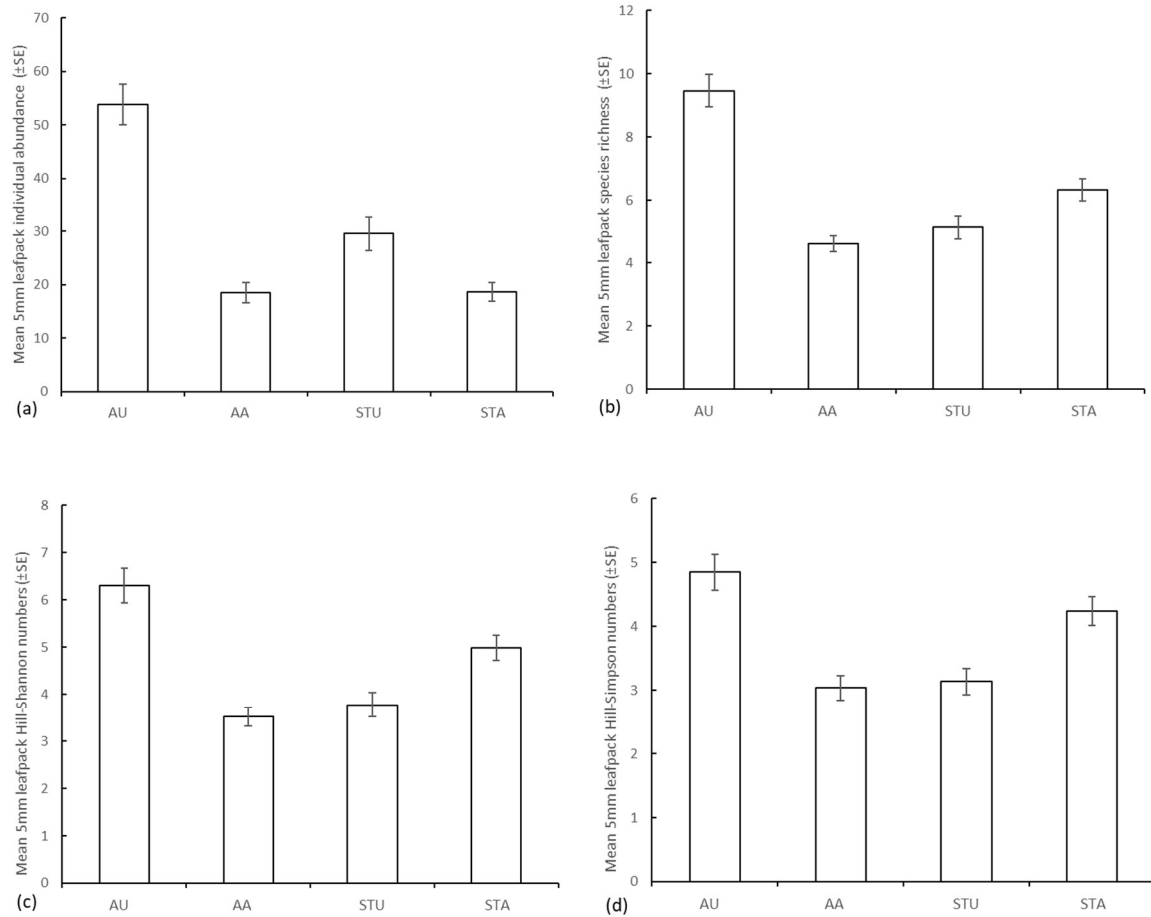


Figure 7. Mean number of (a) individual abundance, (b) species richness, (c) Hill-Shannon numbers and (d) Hill-Simpson numbers found in 5mm mesh leaf packs at catchments: River Avon unaugmented (AU), River Avon augmented (AA), South Teign unaugmented (STU) and South Teign augmented (STA). Error bars represent standard error (SE) of the mean.

Table 8. General linear model results for individual abundance, species richness, Hill-Shannon numbers, Hill-Simpson numbers as the dependent variable and associated pairwise comparisons. Asterisks (*) indicate level of significance ($p < 0.05 = *$, $p < 0.01 = **$, $p < 0.001 = ***$). The codes (u) or (a) indicate significantly higher values in either unaugmented or augmented reaches.

Source	Individual abundance	Species richness	Hill-Shannon	Hill-Simpson
state	**	ns	*	ns
catch	ns	ns	ns	ns
state*catch	ns	**	***	***
reach(state*catch)	**	ns	ns	ns

Avon state	(u)***	(a)***	(u)***	(u)***
South Teign state	(u)**	(u)*	(a)*	(a)**

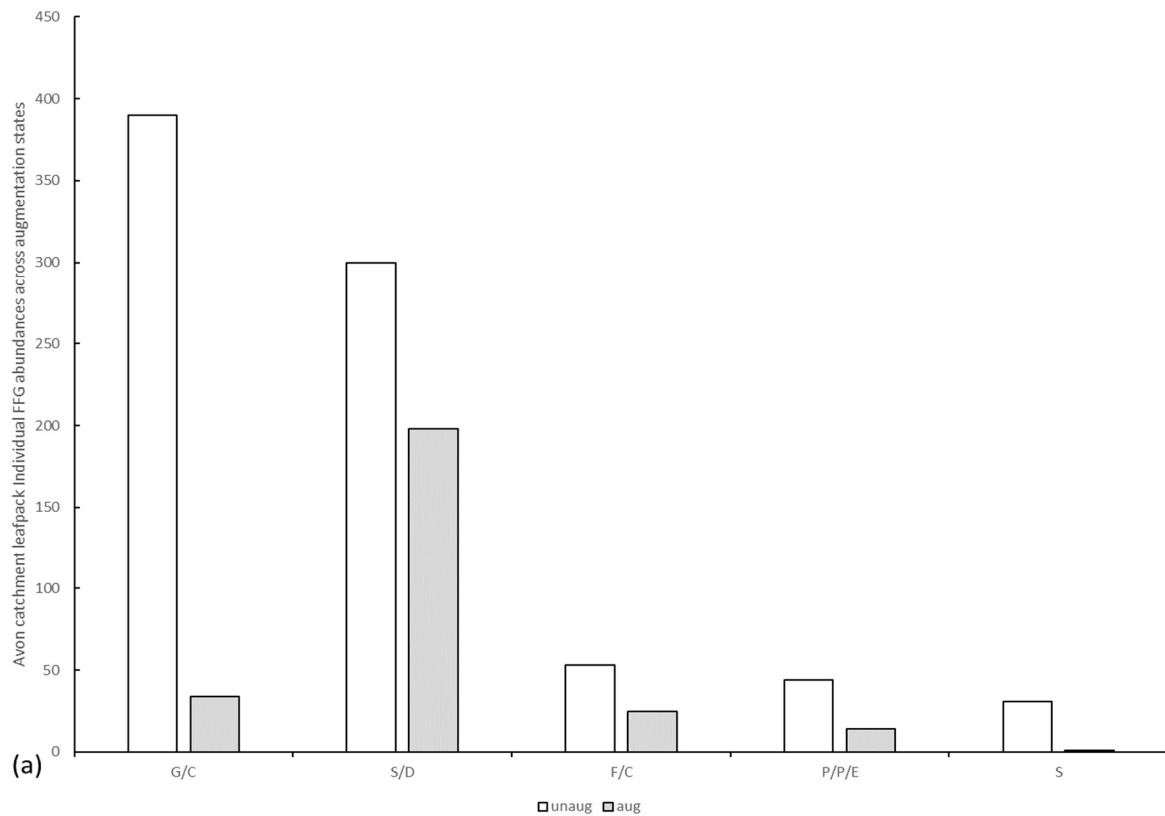
Table 9. General linear model results with inter-pack mass loss as the dependent variable and individual abundance, species richness, Hill-Shannon diversity, and Hill-Simpson diversity as individual covariates in separate GLM models, along with associated pairwise comparisons. Asterisks (*) indicate level of significance ($p < 0.05 = *$, $p < 0.01 = **$, $p < 0.001 = ***$). The code (a) indicates significantly higher mass loss in augmented reaches.

Source	Individual abundance	Species richness	Hill-Shannon	Hill-Simpson
covariate	ns	ns	ns	ns
state	ns	ns	ns	ns
catch	ns	ns	ns	ns
state*catch	ns	ns	ns	ns
reach(state*catch)	*	*	*	*
Avon state	ns	ns	ns	ns
South Teign state	(a)**	(a)**	(a)**	(a)**

Functional feeding group analysis

Functional feeding group analysis showed significant differences between unaugmented and augmented reaches at both the River Avon ($G=147.80$, 4 d.f., $p < 0.001$), and South Teign catchments ($G=212.78$, 4 d.f., $p < 0.001$) (Figure 8.). G/C and S/D were found in higher abundance in unaugmented reaches. This was driven by the S/D stonefly *Leuctra inermis*, and the G/C mayfly *Baetis rhodani* and the riffle beetle *Elmis aenea*. Leaf packs from Avon unaugmented reaches also held *Oulimnius tuberculatus* and *Limnius volckmari*, which were not found in those from unaugmented reaches of the South Teign. F/C, P/P/E and S showed contrasting patterns of abundance in leaf packs between the two catchments, with more being observed in unaugmented reaches of the River Avon, and in augmented reaches of the South Teign. This was largely driven by the Trichopteran F/C *Hydropsyche siltalai* and

Polycentropus flavomaculatus, and the P/P/E *Rhyacophila munda* and *Rhyacophila dorsalis*. In addition, the stonefly S/D *Protonemura meyeri*, was found in relatively high abundance in augmented reaches of the River Avon catchment, and in contrast, in relatively higher abundance in unaugmented reaches of the South Teign.



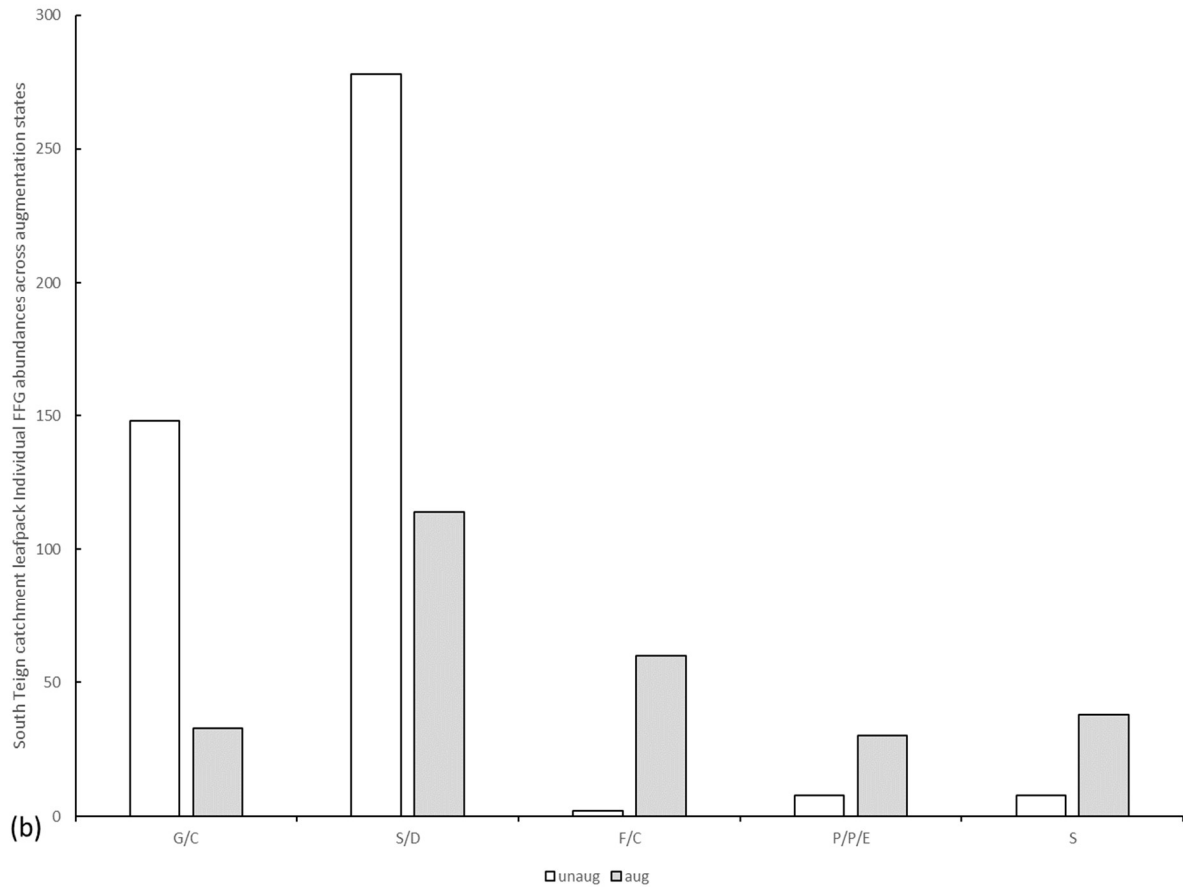


Figure 8. Individual functional feeding group abundances across catchments and augmentation states: (a) River Avon catchment and (b) South Teign catchment. Graph codes: G/C = gatherer/collector, S/D = shredder/detritivore, F/C = filterer/collector, P/P/E = piercer/predator/engulfer, S = scraper.

Multivariate analyses

Type 1 sums of squares PERMANOVA indicated a significant effect of augmentation state on leaf pack macroinvertebrate assemblage composition ($p < 0.01$), which was reflected at catchment level ($p < 0.05$), state*catchment level ($p < 0.01$) and at the level of reach ($p < 0.001$) (Table 10).

Table 10. Type 1 sums of squares PERMANOVA for leaf pack macroinvertebrate assemblage composition

Source	df	MS	Pseudo-F	P(perm)
state	1	14857	4.602	0.004
catch	1	7193.5	2.2282	0.024
state*catch	1	19602	6.072	0.003

<i>reach(catch*state)</i>	8	228.3	3.1627	0.001
Res	48	1020.8		

nMDS ordination (Figure 9) indicated separation of unaugmented and augmented reaches in both catchments. However, there was considerable overlap between River Avon augmented and South Teign unaugmented leaf packs, driven by the presence of *Protonemura meyeri*, *Ibisia marginata* and *Elodes* sp. at South Teign unaugmented sites.

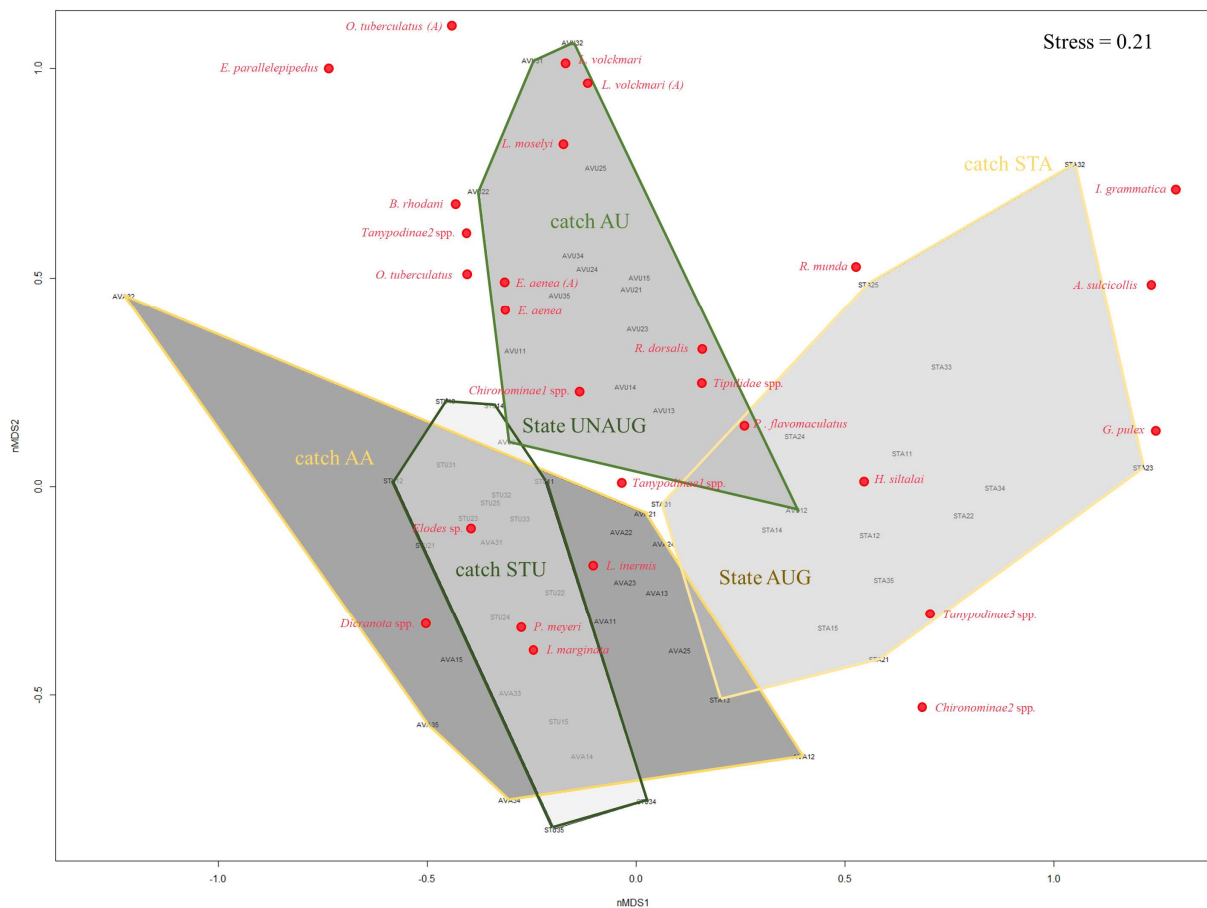


Figure 9. Non-metric multidimensional scaling (nMDS) ordination of macroinvertebrate abundance across unaugmented and augmented reaches of the two study catchments. Convex hulls (shaded polygons) are overlain and coloured to clarify groupings according to catchment and augmentation state, where AA = River Avon augmented, AU = River Avon unaugmented, STA = South Teign augmented, STU = South Teign unaugmented and states AUG and UNAUG respectively. Sample codes indicated in small black letters; species indicated in red, (A) = adult forms for taxa which occurred as both larvae and adults; for full taxonomic classifications see Table 6.

Discussion

This study explores, for the first time, the impact of augmented gravels on leaf litter breakdown and associated colonizing macroinvertebrate assemblages in sediment starved upland watercourses. The influence of gravel augmentation on macroinvertebrate assemblages has been studied with varying and sometimes inconsistent results (Merz and Ochikubo Chan 2005, Sarriquet et al. 2007, Albertson et al. 2011). Similar varying results have been seen for leaf litter breakdown and associated macroinvertebrate assemblages, with work to date mainly focussing on decomposition rates (Marks 2019). Macroinvertebrate functional traits and the utilization of leaf litter breakdown and loss as a surrogate for functional diversity and therefore ecosystem function has been a developing field for decades (Petersen and Cummins 1974, Boling Jr et al. 1975, Suberkropp et al. 1976, Ward and Cummins 1979, Newbold et al. 1982, Webster and Benfield 1986, Richardson 1992, Wallace et al. 1997, Jonsson and Malmqvist 2000, Bergfur 2007, Péru and Dolédec 2010, Classen-Rodríguez et al. 2019, Fornaroli et al. 2019, López-Rojo et al. 2019, Walpola et al. 2019, Oester et al. 2022). The study of riverine microbial decomposition is similarly well documented (Cummins 1973, Kaplan and Bott 1983, Findlay and Arsuffi 1989, Petersen et al. 1989, Meyer 1994, Jansson et al. 1999, Gulis and Suberkropp 2003, Yoshimura et al. 2008, Marks et al. 2009, Kominoski et al. 2011, Besemer et al. 2013, Newman et al. 2015, Bastias et al. 2018, Santonja et al. 2018, Lin et al. 2019, Vander Vorste et al. 2019). This study combines these distinct fields of research to investigate how leaf litter and corresponding macroinvertebrate functional assemblages respond to gravel augmentation.

In summary, gravel augmentation had no consistent effect on inter-pack mass loss. There were however, small but significant differences in mass loss at reach scale in both rivers, indicating high spatial variability within the catchments studied. Inter-pack mass loss in the South Teign was significantly higher in augmented reaches. In contrast, this was not borne out on the River Avon, where augmentation did not have a consistent impact. Augmentation state had an impact on micro leaf pack mass loss, with a weak effect at the South Teign, but a stronger effect at the River Avon. More mass was lost at both catchments for both augmentation states in 5mm leaf packs than micro leaf packs, with the largest differential in mass loss observed at South Teign augmented reaches.

This study revealed significant small and large-scale differences in the composition of macroinvertebrate assemblages colonizing 5 mm leaf packs. Augmentation yielded significant differences both within and between catchments. Within catchments, augmentation led to lower abundance, species richness and diversity overall at River Avon unaugmented reaches. In contrast, in the South Teign, other than for species abundance, augmented reaches were richer and more diverse. Augmentation led to significant differences in assemblage composition for individual abundance, as well as Hill-Shannon diversity, with species richness, Hill-Shannon and Hill-Simpson diversity significantly different at catchment level. At reach level, augmentation had a significant impact on individual abundance, with unaugmented catchments yielding higher scores in 5 out of 8 pairwise tests. Functionally, the River Avon held higher abundances of G/C and S/D in unaugmented reaches, with the same pattern seen at the South Teign. However, F/C, P/P/E and S were found in higher abundances in the South Teign augmented reaches, in contrast to the River Avon, indicating potential small-scale reach effects of augmentation. Large-scale differences were seen in macroinvertebrate composition between and within catchments at all levels and augmentation states, indicating high spatial variability.

The small scale differences in colonisation patterns and associated mass loss of leaf packs observed both between catchments, reaches and augmentation states may be driven, in part, by succession, especially if the catchment is subject to seasonal or unpredictable perturbations (Peckarsky 1986, Resh et al. 1988, Bergfur 2007). One process of colonisation, known as drift, is the downstream movement of macroinvertebrates (Elliott 2008a, Naman et al. 2016). 'Active drift' (where taxa leave the substrate and drift on purpose) has been observed to be one of the main dispersal methods utilized by benthic organisms in lotic environments, and likely follows a diel rhythmic pattern (Elliott 1965, 1967, 1968, Radford and Hartland.R 1971). However, 'passive drift' (where taxa are dislodged and travel downstream by environmental stress e.g. flooding) may be caused by disturbances, and therefore disturbances have the potential to play pivotal roles in macroinvertebrate assemblages (Naman et al. 2016). It is possible that disturbances, in combination with dams, impoundment, and associated gravel augmentations (Staentzel et al. 2019b, Wang et al. 2021, Wang et al. 2023) may keep reaches in a state of non-equilibrium, preventing the attainment of ecological saturation, and species packing that denotes a stable, niche controlled

ecosystem (Suberkropp and Klug 1980, Resh et al. 1988, Townsend 1989, Choné and Biron 2016).

The overall 'patchiness' of macroinvertebrate assemblages within leaf packs may also be due to the riparian structure of the catchments: the River Avon above the dam has no tree cover whereas the South Teign above the dam is partially forested with mixed woodland. Both have been subject to anthropogenic perturbations (Jukes-Browne 1904, Bogle et al. 1959, Simmonds 1970, Thorndycraft et al. 1999, Thorndycraft et al. 2004). Large lakes and rivers are generally believed to be autochthonous, whereas upland headwaters are generally believed to mainly rely on allochthonous inputs from riparian vegetation (Webster et al. 1999, Jonsson and Stenroth 2016). However, with a lack of riparian vegetation and woodland at the River Avon catchment above the dam, it seems likely that it relies on autochthonous inputs (for example benthic algae) due to higher light intensity than would otherwise be expected in a forested upland riverine ecosystem. This has the potential to impact macroinvertebrate assemblages (Doi 2009, Jonsson et al. 2018). The lack of riparian input may account for the relative domination of River Avon unaugmented reach leaf packs by riffle beetle species (e.g. *Elmis aenea*) (G/C) or (S) and their relative absence in augmented reaches. This could be potentially due to adults having been found to feed on periphytic algae and detritus, or if adults and larvae had yet to enter the drift (Brown 1987, Elliott 2006, Elliott 2008b). The distribution of S/D *Protonemura meyeri* seemed to follow this pattern in the River Avon and the South Teign, with higher abundances observed in augmented reaches of the River Avon, and unaugmented reaches of the South Teign, which would be expected due to either an absence, or presence, of allochthonous riparian inputs respectively (Kaushik and Hynes 1971, Cummins et al. 1973, Oester et al. 2022). The S/D *Leuctra inermis* was found in relatively high abundance in River Avon and South Teign unaugmented reaches, and in lesser abundance in augmented reaches. As *Leuctra inermis* is considered functionally similar to *Protonemura meyeri*, this is an unexpected difference (Wantzen and Wagner 2006, Vitecek et al. 2017).

The differences in macroinvertebrate colonisation and leaf litter breakdown may be related to aquatic hyphomycetes, which have been shown to increase the rate of consumption of leaf litter by aquatic macroinvertebrates both through conditioning of the litter, and by their presence as a macroinvertebrate food source. This allows further breakdown and availability within riverine ecosystems (Cummins and Klug 1979, Ferreira et al. 2016). Ingoldian fungi are

aquatic hyphomycetes first encountered and published in the UK in 1940 (Ingold 1942), which upon colonisation of aquatic leaf litter convert leaf matter from coarse to fine particulates causing loss of mass (Barlocher 1979, Bärlocher 1982). Aquatic hyphomycetes are likely to have a role in the breakdown of study leaf packs at both micro and 5mm sizes. As 5mm leaf packs lost more mass overall than micro mesh packs, it is possible that leaf matter was not only consumed and conditioned by aquatic fungi, but that their presence also facilitated macroinvertebrate feeding interactions e.g. *S/D Protonemura meyeri* at the River Avon augmented reaches and in both states at the South Teign, and *S/D Leuctra inermis* at South Teign unaugmented reaches. The presence of aquatic hyphomycetes has been shown to increase with higher riparian leaf input which they consume (Srivastava and Lawton 1998, Ferreira et al. 2016). Therefore, at catchments such as the River Avon above the dam where deforestation has occurred, a potential lack of fungal biomass and diversity may contribute to a lack of aquatic macroinvertebrate biodiversity, potentially impacting the entire food web. It is notable that more mass was lost in augmented reaches of both catchments (of both micro and 5mm leaf packs), with the overall highest inter-pack difference in South Teign augmented reaches. The South Teign catchment is forested throughout its length as discussed, therefore potentially an accumulation of leaf litter and detritous may have facilitated a larger accumulation of aquatic hyphomycetes. However, the South Teign in the reaches above the dam is made up of mixed woodland including pine, which has been observed to inhibit fungal growth (Bärlocher and Oertli 1978). This may explain why the greatest inter-pack mass loss was seen in augmented reaches of the South Teign where there could be relatively less inhibition to microbial activity.

Overall, damming of streams and rivers has the potential to impact entire riverine ecosystems, altering flow, temperature and production, by changing macroinvertebrate assemblage structures and thereby altering functional diversity and food webs (Vannote et al. 1980, Vannote and Sweeney 1980, O'Sullivan et al. 2022, Oester et al. 2022). The current findings support these conclusions in regard to macroinvertebrate distributions, particularly of *S/D* and *G/C*, and inter-pack and overall mass loss. Species found in leaf packs were in general functionally different between catchments depending on 'normal' riparian subsidies and augmentation state. Further studies of this relationship could potentially include macroinvertebrate biomass and the quantification and functionality of assemblages of

aquatic hyphomycetes present to discern a relationship (if any) between unforested/forest reaches and relationships with augmentation. The findings in this study suggest that the augmentation of gravels in perturbed catchments may have an impact on ecosystem functioning and macroinvertebrate assemblages. However, this seems to largely depend on small-scale reach level in-river conditions and local availability of riparian input.

Chapter Four: Conclusion

This thesis investigated potential impacts of gravel augmentation on macroinvertebrate assemblage composition, functional diversity and leaf litter breakdown at both macro and meso-scale across two low-order, sediment-starved streams on Dartmoor, UK. It aimed to provide insight on potential changes to ecosystem functioning caused by gravel augmentation and consequential drivers of the down-stream deleterious impacts of gravel augmentation on higher trophic levels (e.g., salmonids). The exclusion of leaf litter may potentially restrict macroinvertebrate functionality, in particular G/C, S/D and P/P/E's, thereby reducing secondary production (Graça 2001, Wang et al. 2023).

In total, 5641 individuals from 44 taxa were recorded across both studies and catchments. Evidence was found that augmentation led to both small and large-scale differences in assemblage composition and functioning in both studies. This highlights the potential of augmentation to impact assemblages at varying scales, and therefore perturb ecosystem functionality, potentially also influencing higher trophic levels. Leaf litter breakdown across both catchments was higher in augmented reaches for both micro and 5mm leaf packs, with small-scale variation within catchments for inter-pack mass loss. Whether the differences in macroinvertebrate assemblage, diversity and functionality, and leaf pack mass loss are due solely to the effects of augmentation, or to a combination of augmentation and various other biological or environmental factors (including historical perturbations) remains unclear and merits further investigation.

Looking at the differences in individual abundance patterns between studies more closely, it appears that only certain species were found across both survey and leaf pack studies, with only a certain subset of taxa colonising leaf packs. *B. rhodani* (G/C) (Ephemeroptera) was the only mayfly species to be found in both studies. It was found for all augmentation states for the survey study. In contrast, it was found only in unaugmented reaches of both catchments in the leaf pack study. *R. munda* (P/P/E), *R. dorsalis* (P/P/E) and *P. flavomaculatus* (F/C) (Trichoptera) showed varying individual abundances between studies and augmentation states. *P. flavomaculatus* was found in both studies, in both catchments, for both augmentation states. Although the high abundance of chironomids is not reflected in the leaf pack study as it is in the survey, this may be an example of *P. flavomaculatus*' adaptability in

habitat choice and feeding strategies. For example the use of spun-nets on benthic gravels, boulders or rocks, or free roaming inside leaf packs demonstrates the potentially wide niche breadth of *P. flavomaculatus*' (Reiso and Brittain 2000) in particular as the cost of net building has been demonstrated to detrimentally impact biota weight, and therefore fitness (Dudgeon 1987). Of the Plecoptera, two species are worth noting. Each of *L. inermis* (S/D) and *P. meyeri* (S/D), were found for both augmentation states at both catchments and in both studies. However, for the survey study, there was a higher abundance of *L. inermis* in unaugmented reaches of the River Avon, whereas at the South Teign, a higher abundance was found in augmented reaches. This is in contrast to the leaf pack study, where a higher abundance of *L. inermis* were observed in unaugmented reach leaf packs of both catchments. For *P. meyeri*, the survey study found higher abundances in augmented reaches for both catchments. However, the leaf pack study found higher abundances in augmented reaches of the River Avon, which, given the relative lack of riparian input above the dam at the River Avon is not surprising. In contrast, unaugmented reaches of the South Teign held higher abundances of *P. meyeri*. Coleoptera showed similar patterns across both studies, with higher abundances generally found in unaugmented reaches, the most abundant being *E. aenea* for both larval (G/C) and adult (S) forms. Diptera were found in higher abundances in the survey study, in particular *Simuliidae* spp. (F/C). which were seen between both catchments, and for both augmentation states. Chironomids were, however, generally found in higher abundance in augmented reaches. The presence of *I. marginata* (P/P/E) in higher abundances in the leaf pack study was particularly notable, likely due to the relative concentration of macroinvertebrate prey items in leaf packs (Benson and Pearson, McArthur and Barnes 1988, Paul and Meyer 1996).

Functionally, G/C's were found in higher abundances for both studies in unaugmented reaches, which would be expected. Abundances of S/D's were higher in unaugmented reaches of the River Avon for both studies, and in unaugmented reaches of the South Teign catchment for the leaf pack study only. In contrast, the survey study showed higher S/D abundance in augmented reaches of the South Teign catchment. However, the S/D *Chloroperla torrentium*, although found in the South Teign survey study, was absent from leaf packs in the leaf litter study, which is noteworthy due to its functionality. F/C distributions between studies differed, with F/C's being more abundant in augmented reaches of both

catchments in the survey study, and also in South Teign leaf pack study. F/C's were however found in higher abundance in unaugmented reaches of the River Avon for the leaf pack study. P/P/E and S distributions for both catchments in the survey study showed higher macroinvertebrate abundances in unaugmented reaches, with the same pattern being seen at the River Avon in the leaf pack study, however. This trend was not maintained for the South Teign, where more P/P/E and S were found in augmented reaches, and in greater abundance than seen in the survey study, as could be expected.

In regard to the potential impact that anthropogenic perturbations such as damming, deforestation or channelisation can have on riverine ecosystems, and therefore overall ecosystem functionality and health, the patterns seen here may begin to highlight possible issues within catchments. For example, deforestation above the dam at the River Avon may cause a switch to an unnatural autochthonous state, and thereby, through reduction of available leaf litter, a perturbation of the food web. In addition, the spatial variability of macroinvertebrate assemblages found in both studies have the potential to impact salmonids by providing more suitable habitat for early colonisers (e.g., chironomids) of lower dietary quality. Where reaches below a dam have been treated with augmented gravels, there may be a lack of prey biomass availability for juvenile salmonids. The presence of a dam also prevents salmonid movement upstream to unaugmented areas to potentially access reaches with more 'natural' assemblages of biota.

Suggestions for further study include: (a) quantification of macroinvertebrate biomass and gut contents (Hieber and Gessner 2002), thereby giving a more accurate insight on food availability and quality for fish species; (b) further investigation of macroinvertebrate feeding functionality and potential down-stream impacts on the riverine food web and ecosystem health; and (c) sampling and identification of aquatic hyphomycetes from leaf litter and in-stream, having regard to the role Ingoldian fungi play in both the breakdown of leaf litter, and as a food source for macroinvertebrates (Bärlocher 1982, Marks 2019).

Concerning conservation and management, the reference to gravel augmentation as 'restoration' may conceal a potential problem. Augmentation of perturbed streams with gravel to encourage salmonid spawning is considered a positive measure. However, without considering the whole food web and whole-system nature of riverine ecosystems, this type of 'restoration' could be ultimately more detrimental to ecosystem health, at least in the short

term, if not implemented with caution. At the least, gravel augmentation may be a technique that requires careful consideration before implementation in order to properly address the declining state of our freshwater aquatic ecosystems. Pre-augmentation macroinvertebrate surveys might be carried out in addition to fish surveys to characterise macroinvertebrate assemblages and diversity prior to augmentation, thereby creating a baseline. In addition, yearly post-augmentation macroinvertebrate surveys could be employed to assess the effectiveness of augmentations. Yearly post-augmentation surveys have the potential to monitor macroinvertebrate colonisations, characterising communities and recording potential changes in taxa over time, thereby providing community assemblage data to stakeholders on food availability for the fish they seek to encourage, as well as providing an overall snapshot of ecosystem health. Furthermore, long-term records of macroinvertebrate communities are critical for understanding how changes in climate may impact not only macroinvertebrates and ecosystem functioning (Baranov et al. 2020, Correa-Araneda et al. 2020, Mouton et al. 2020), but salmonids (Reeder et al. 2021). Gravel augmentation is a disturbance in itself, therefore, the injection of gravels into a riverine system with the intention of creating habitat for salmonids that has a stable macroinvertebrate community has the potential to be detrimental to biodiversity, and consequently, ecosystem functioning.

References

- Albertson, L., L. Koenig, B. Lewis, S. Zeug, L. Harrison, and B. Cardinale. 2013. How does restored habitat for Chinook salmon (*Oncorhynchus tshawytscha*) in the Merced River in California compare with other Chinook streams? *River Research and Applications* **29**:469-482.
- Albertson, L. K., B. J. Cardinale, S. C. Zeug, L. R. Harrison, H. S. Lenihan, and M. A. Wydzga. 2011. Impacts of channel reconstruction on invertebrate assemblages in a restored river. *Restoration Ecology* **19**:627-638.
- Amundsen, P.-A., H.-M. Gabler, and L. S. Riise. 2001. Intraspecific food resource partitioning in Atlantic salmon (*Salmo salar*) parr in a subarctic river. *Aquatic Living Resources* **14**:257-265.
- Arnaud, F., H. Piégay, D. Béal, P. Collery, L. Vaudor, and A. J. Rollet. 2017. Monitoring gravel augmentation in a large regulated river and implications for process-based restoration. *Earth Surface Processes and Landforms* **42**:2147-2166.
- Baranov, V., J. Jourdan, F. Pilotto, R. Wagner, and P. Haase. 2020. Complex and nonlinear climate-driven changes in freshwater insect communities over 42 years. *Conservation Biology*.
- Barlaup, B. T., S. E. Gabrielsen, H. Skoglund, and T. Wiers. 2008. Addition of spawning gravel—a means to restore spawning habitat of atlantic salmon (*Salmo salar L.*), and Anadromous and resident brown trout (*Salmo trutta L.*) in regulated rivers. *River Research and Applications* **24**:543-550.
- Barlocher, F. 1979. On trophic interactions between microorganisms and animals. *The American Naturalist* **114**:147-148.
- Bärlocher, F. 1982. On the ecology of Ingoldian fungi. *BioScience* **32**:581-586.
- Bärlocher, F., and J. Oertli. 1978. Inhibitors of aquatic hyphomycetes in dead conifer needles. *Mycologia* **70**:964-974.
- Barmuta, L. A. 1990. Interaction between the effects of Substratum, Velocity and location on Stream Benthos: and experiment. *Marine and Freshwater Research* **41**:557-573.
- Bastias, E., M. Ribot, A. M. Romani, J. Mora-Gomez, F. Sabater, P. Lopez, and E. Marti. 2018. Responses of microbially driven leaf litter decomposition to stream nutrients depend on litter quality. *Hydrobiologia* **806**:333-346.

- Beechie, T. J., D. A. Sear, J. D. Olden, G. R. Pess, J. M. Buffington, H. Moir, P. Roni, and M. M. Pollock. 2010. Process-based Principles for Restoring River Ecosystems. *BioScience* **60**:209-222.
- Beisel, J.-N., P. Usseglio-Polatera, and J.-C. Moreteau. 2000. The spatial heterogeneity of a river bottom: a key factor determining macroinvertebrate communities. Pages 163-171 *Assessing the ecological integrity of running waters*. Springer.
- Benfield, E. F., K. M. Fritz, and S. D. Tiegs. 2017. Chapter 27 - Leaf-Litter Breakdown. Pages 71-82 *in* G. A. Lamberti and F. R. Hauer, editors. *Methods in Stream Ecology* (Third Edition). Academic Press.
- Benson, L. J., and R. G. Pearson. Dynamics of organic material and invertebrates in a tropical headwater stream. *Hydrobiologia*:1-16.
- Bergfur, J. 2007. Seasonal variation in leaf-litter breakdown in nine boreal streams: implications for assessing functional integrity. *Fundamental and Applied Limnology/Archiv für Hydrobiologie* **169**:319-329.
- Bernhardt, E. S., M. A. Palmer, J. Allan, G. Alexander, K. Barnas, S. Brooks, J. Carr, S. Clayton, C. Dahm, and J. Follstad-Shah. 2005. Synthesizing US river restoration efforts. American Association for the Advancement of Science.
- Besemer, K., G. Singer, C. Quince, E. Bertuzzo, W. Sloan, and T. J. Battin. 2013. Headwaters are critical reservoirs of microbial diversity for fluvial networks. *Proceedings of the Royal Society B: Biological Sciences* **280**:20131760.
- Bogle, J. M. L., R. Ross, and T. McMillan. 1959. The design and construction on the Avon Dam (including plates). *Proceedings of the Institution of Civil Engineers* **12**:83-106.
- Boling Jr, R. H., E. D. Goodman, J. A. Van Sickle, J. O. Zimmer, K. W. Cummings, R. C. Petersen, and S. R. Reice. 1975. Toward a model of detritus processing in a woodland stream. *Ecology* **56**:141-151.
- Boon, P. 1988. The impact of river regulation on invertebrate communities in the UK. *Regulated Rivers: Research & Management* **2**:389-409.
- Boulton, A. J., S. Findlay, P. Marmonier, E. H. Stanley, and H. M. Valett. 1998. The functional significance of the hyporheic zone in streams and rivers. *Annual review of ecology and systematics* **29**:59-81.

- Bretschko, G. 1991. The limnology of a low order alpine gravel stream (Ritrodat-Lunz study area, Austria). *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen* **24**:1908-1912.
- Brookes, A., and F. D. Shields Jr. 1996. River channel restoration: guiding principles for sustainable projects.
- Brooks, S. S., M. A. Palmer, B. J. Cardinale, C. M. Swan, and S. Ribblett. 2002. Assessing stream ecosystem rehabilitation: limitations of community structure data. *Restoration Ecology* **10**:156-168.
- Brown, H. P. 1987. Biology of riffle beetles. *Annual review of entomology* **32**:253-273.
- Bruton, M. 1985. The effects of suspensoids on fish. Pages 221-241 *Perspectives in Southern Hemisphere Limnology*. Springer.
- Cadotte, M. W., K. Carscadden, and N. Mirotchnick. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied ecology* **48**:1079-1087.
- Cairns Jr, J. 1995. Ecological integrity of aquatic systems. *Regulated Rivers: Research & Management* **11**:313-323.
- Cardinale, B. J., M. A. Palmer, C. M. Swan, S. Brooks, and N. L. Poff. 2002. The influence of substrate heterogeneity on biofilm metabolism in a stream ecosystem. *Ecology* **83**:412-422.
- Chao, A., C.-H. Chiu, and L. Jost. 2014. Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. *Annual Review of Ecology, Evolution, and Systematics* **45**:297-324.
- Choné, G., and P. Biron. 2016. Assessing the relationship between river mobility and habitat. *River Research and Applications* **32**:528-539.
- Claret, C., P. Marmonier, J. Boissier, Michel, D. Fontvieille, and P. Blanc. 1997. Nutrient transfer between parafluvial interstitial water and river water: influence of gravel bar heterogeneity. *Freshwater Biology* **37**:657-670.
- Clarke, K. R., R. Gorley, P. Somerfield, and R. Warwick. 2014. Change in marine communities: an approach to statistical analysis and interpretation. Primer-E Ltd.
- Classen-Rodríguez, L., P. E. Gutiérrez-Fonseca, and A. Ramírez. 2019. Leaf litter decomposition and macroinvertebrate assemblages along an urban stream gradient in Puerto Rico. *Biotropica*.

- Compin, A., and R. Céréghino. 2007. Spatial patterns of macroinvertebrate functional feeding groups in streams in relation to physical variables and land-cover in Southwestern France. *Landscape Ecology* **22**:1215-1225.
- Correa-Araneda, F., A. M. Tonin, J. Pérez, K. Álvarez, N. López-Rojo, A. Díaz, C. Esse, F. Encina-Montoya, R. Figueroa, and A. Cornejo. 2020. Extreme climate events can slow down litter breakdown in streams. *Aquatic sciences* **82**:1-7.
- Cummins, K., and M. Wilzbach. 1985. Field procedures for analysis of functional feeding groups of stream invertebrates. Appalachian Environmental Laboratory, University of Maryland, Frostburg, Contr.
- Cummins, K. W. 1973. Trophic relations of aquatic insects. *Annual review of entomology* **18**:183-206.
- Cummins, K. W., and M. J. Klug. 1979. Feeding ecology of stream invertebrates. *Annual review of ecology and systematics* **10**:147-172.
- Cummins, K. W., and G. H. Lauff. 1969. The influence of substrate particle size on the microdistribution of stream macrobenthos. *Hydrobiologia* **34**:145-181.
- Cummins, K. W., R. W. Merritt, and P. C. Andrade. 2005. The use of invertebrate functional groups to characterize ecosystem attributes in selected streams and rivers in south Brazil. *Studies on Neotropical Fauna and Environment* **40**:69-89.
- Cummins, K. W., G. Minshall, J. Sedell, C. Cushing, and R. Petersen. 1984. Stream ecosystem theory: With 1 figure and 6 tables in the text. *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen* **22**:1818-1827.
- Cummins, K. W., R. C. Petersen, F. O. Howard, J. C. Wuycheck, and V. I. Holt. 1973. Utilization of leaf litter by stream detritivores. *Ecology* **54**:336-345.
- Cummins, K. W., M. A. Wilzbach, D. M. Gates, J. B. Perry, and W. B. Taliaferro. 1989a. Shredders and riparian vegetation. *BioScience* **39**:24-30.
- Cummins, K. W., M. A. Wilzbach, D. M. Gates, J. B. Perry, and W. B. Taliferro. 1989b. Shredders and riparian vegetation - Leaf litter that falls into streams influences communities of stream invertebrates. *BioScience* **39**:24-30.
- Dalley, E., C. Andrews, and J. Green. 1983. Precocious male Atlantic salmon parr (*Salmo salar*) in insular Newfoundland. *Canadian Journal of Fisheries and Aquatic Sciences* **40**:647-652.

- Death, R. G. 2003. Spatial patterns in lotic invertebrate community composition: is substrate disturbance actually important? *Canadian Journal of Fisheries and Aquatic Sciences* **60**:603-611.
- Death, R. G., and M. J. Winterbourn. 1994. Environmental stability and community persistence: a multivariate perspective. *Journal of the North American Benthological Society* **13**:125-139.
- Death, R. G., and M. J. Winterbourn. 1995. Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. *Ecology* **76**:1446-1460.
- Diamond, J. M. 1986. Effects of larval retreats of the caddisfly *Cheumatopsyche* on macroinvertebrate colonization in piedmont, USA streams. *Oikos*:13-18.
- Diehl, S. 1992. Fish predation and benthic community structure: the role of omnivory and habitat complexity. *Ecology* **73**:1646-1661.
- Digimap, E. 2021. Digimap ordnance survey collection.
- Ding, S., and D. Wang. 2019. The effects of litter quality and living plants on the home-field advantage of aquatic macrophyte decomposition in a eutrophic urban lake, China. *Science of the Total Environment* **650**:1529-1536.
- Dobson, A. P., A. Bradshaw, and A. á. Baker. 1997. Hopes for the future: restoration ecology and conservation biology. *Science* **277**:515-522.
- Doi, H. 2009. Spatial patterns of autochthonous and allochthonous resources in aquatic food webs. *Population Ecology* **51**:57-64.
- Dole-Olivier, M. J., P. Marmonier, and J. L. Beffy. 1997. Response of invertebrates to lotic disturbance: is the hyporheic zone a patchy refugium? *Freshwater Biology* **37**:257-276.
- Doretto, A., E. Piano, and C. E. Larson. 2020. The River Continuum Concept: lessons from the past and perspectives for the future. *Canadian Journal of Fisheries and Aquatic Sciences* **77**:1853-1864.
- Downs, P. W., C. Bithell, V. E. Keele, and D. J. Gilvear. 2016. Dispersal of augmented gravel in a steep, boulder-bedded reach: Early implications for restoring salmonid habitat. Page 380 *in* 11th International Symposium on Ecohydraulics (ISE 2016). Engineers Australia.

- Dudgeon, D. 1987. A laboratory study of optimal behaviour and the costs of net construction by *Polycentropus Havomaculatus* (Insecta: Trichoptera: Polycentropodidae). *Journal of Zoology* **211**:121-141.
- Dudgeon, D., A. H. Arthington, M. O. Gessner, Z.-I. Kawabata, D. J. Knowler, C. Leveque, R. J. Naiman, A.-H. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* **81**:163-182.
- Duffy, J. E. 2003. Biodiversity loss, trophic skew and ecosystem functioning. *Ecology letters* **6**:680-687.
- Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological monographs* **67**:345-366.
- Edington, J. M., and A. G. Hildrew. 1981. A Key to the Caseless Caddis larvae of the British Isles: with notes on their ecology. Freshwater Biological Association.
- Egglishaw, H. J. 1967. The food, growth and population structure of salmon and trout in two streams in the Scottish Highlands. HM Stationery Office.
- Elkins, E. M., G. B. Pasternack, and J. E. Merz. 2007. Use of slope creation for rehabilitating incised, regulated, gravel bed rivers. *Water Resources Research* **43**.
- Elliott, J. 1965. Daily fluctuations of drift invertebrates in a Dartmoor stream. *Nature* **205**:1127-1129.
- Elliott, J. 1967. Invertebrate drift in a Dartmoor stream. *Arch. Hydrobiol* **63**:202-237.
- Elliott, J. 1968. The life histories and drifting of Trichoptera in a Dartmoor stream. *The Journal of Animal Ecology*:615-625.
- Elliott, J. 2006. Critical periods in the life cycle and the effects of a severe spate vary markedly between four species of elmids beetles in a small stream. *Freshwater Biology* **51**:1527-1542.
- Elliott, J. 2008a. Ontogenetic changes in the drifting of four species of elmids beetles elucidate the complexity of drift-benthos relationships in a small stream in Northwest England. *Freshwater Biology* **53**:159-170.
- Elliott, J. M. 2008b. The ecology of riffle beetles (Coleoptera: Elmidae). *Freshwater Reviews* **1**:189-204.
- Englund, G. 1993. Interactions in a lake outlet stream community: direct and indirect effects of net-spinning caddis larvae. *Oikos*:431-438.

- Englund, G., and D. Evander. 1999. Interactions between sculpins, net-spinning caddis larvae and midge larvae. *Oikos*:117-126.
- Environment Agency. 2003. The Rivers Avon and Erme Salmon Action Plan, Consultation Document. Environment Agency, Bristol, UK.
- Escobar-Arias, M. I., and G. B. Pasternack. 2011. Differences in river ecological functions due to rapid channel alteration processes in two California rivers using the functional flows model, part 2—model applications. *River Research and Applications* **27**:1-22.
- Ferreira, V., J. Castela, P. Rosa, A. M. Tonin, L. Boyero, and M. A. S. Graca. 2016. Aquatic hyphomycetes, benthic macroinvertebrates and leaf litter decomposition in streams naturally differing in riparian vegetation. *Aquatic ecology* **50**:711-725.
- Findlay, S. E. G., and T. L. Arsuffi. 1989. Microbial-growth and detritus transformations during decomposition of leaf litter in a stream. *Freshwater Biology* **21**:261-269.
- Follstad Shah, J. J., C. N. Dahm, S. P. Gloss, and E. S. Bernhardt. 2007. River and riparian restoration in the Southwest: results of the National River Restoration Science Synthesis Project. *Restoration Ecology* **15**:550-562.
- Fornaroli, R., S. Calabrese, F. Marazzi, S. Zaupa, and V. Mezzanotte. 2019. The influence of multiple controls on structural and functional characteristics of macroinvertebrate community in a regulated Alpine river. *Ecohydrology* **12**:e2069.
- Frainer, A., B. G. McKie, and B. Malmqvist. 2014. When does diversity matter? Species functional diversity and ecosystem functioning across habitats and seasons in a field experiment. *Journal of Animal Ecology* **83**:460-469.
- Friberg, N. 2014. Impacts and indicators of change in lotic ecosystems. *Wiley Interdisciplinary Reviews: Water* **1**:513-531.
- Friberg, N., B. Kronvang, H. Ole Hansen, and L. M. Svendsen. 1998. Long-term, habitat-specific response of a macroinvertebrate community to river restoration. *Aquatic Conservation: Marine and Freshwater Ecosystems* **8**:87-99.
- Gaeuman, D. 2012. Mitigating downstream effects of dams. *Gravel-Bed Rivers: Processes, Tools, Environments*:182-189.
- Gagic, V., I. Bartomeus, T. Jonsson, A. Taylor, C. Winqvist, C. Fischer, E. M. Slade, I. Steffan-Dewenter, M. Emmerson, S. G. Potts, T. Tschardtke, W. Weisser, and R. Bommarco. 2015. Functional identity and diversity of animals predict ecosystem functioning

- better than species-based indices. *Proceedings of the Royal Society B-Biological Sciences* **282**.
- Gibson, R. 1993. The Atlantic salmon in fresh water: spawning, rearing and production. *Reviews in fish biology and fisheries* **3**:39-73.
- Gibson, R. J., and D. Galbraith. 1975. The relationships between invertebrate drift and salmonid populations in the Matamek River, Quebec, below a lake. *Transactions of the American Fisheries Society* **104**:529-535.
- Gleick, P. H. 1998. Water in crisis: paths to sustainable water use. *Ecological Applications* **8**:571-579.
- Graça, M. A. 2001. The role of invertebrates on leaf litter decomposition in streams—a review. *International Review of Hydrobiology* **86**:383-393.
- Graf, W. L. 2001. Dam age control: restoring the physical integrity of America's rivers. *Annals of the Association of American Geographers* **91**:1-27.
- Green, M. D., K. E. Anderson, D. B. Herbst, and M. J. Spasojevic. 2022. Rethinking biodiversity patterns and processes in stream ecosystems. *Ecological monographs* **92**:e1520.
- Grill, G., B. Lehner, M. Thieme, B. Geenen, D. Tickner, F. Antonelli, S. Babu, P. Borrelli, L. Cheng, and H. Crochetiere. 2019. Mapping the world's free-flowing rivers. *Nature* **569**:215.
- Gulis, V., and K. Suberkropp. 2003. Leaf litter decomposition and microbial activity in nutrient-enriched and unaltered reaches of a headwater stream. *Freshwater Biology* **48**:123-134.
- Gurski, F. d. A., G. D. Pinha, Y. Moretto, A. M. Takeda, and N. C. Bueno. 2014. Effect of habitat heterogeneity in the composition and distribution of Chironomidae (Diptera) assemblage in different microhabitats of preserved streams in the Brazilian Atlantic Forest. *Acta Limnologica Brasiliensia* **26**:163-175.
- Handa, I. T., R. Aerts, F. Berendse, M. P. Berg, A. Bruder, O. Butenschoen, E. Chauvet, M. O. Gessner, J. Jabiol, M. Makkonen, B. G. McKie, B. Malmqvist, E. T. H. M. Peeters, S. Scheu, B. Schmid, J. van Ruijven, V. C. A. Vos, and S. Haettenschwiler. 2014. Consequences of biodiversity loss for litter decomposition across biomes. *Nature* **509**:218-+.

- Hawkins, C. P., R. H. Norris, J. N. Hogue, and J. W. Feminella. 2000. Development and evaluation of predictive models for measuring the biological integrity of streams. *Ecological Applications* **10**:1456-1477.
- Hedin, L. O., J. C. Von Fischer, N. E. Ostrom, B. P. Kennedy, M. G. Brown, and G. P. Robertson. 1998. Thermodynamic constraints on nitrogen transformations and other biogeochemical processes at soil–stream interfaces. *Ecology* **79**:684-703.
- Heino, J., P. Louhi, and T. Muotka. 2004. Identifying the scales of variability in stream macroinvertebrate abundance, functional composition and assemblage structure. *Freshwater Biology* **49**:1230-1239.
- Hendry, K., and D. Cragg-Hine. 1997. *Restoration of Riverine Salmon Habitats: A Guidance Manual*. Environment Agency.
- Henshall, S. E., J. P. Sadler, D. M. Hannah, and A. J. Bates. 2011. The role of microhabitat and food availability in determining riparian invertebrate distributions on gravel bars: a habitat manipulation experiment. *Ecohydrology* **4**:512-519.
- Hieber, M., and M. O. Gessner. 2002. Contribution of stream detritivores, fungi, and bacteria to leaf breakdown based on biomass estimates. *Ecology* **83**:1026-1038.
- Hildrew, A., and P. Giller. 1994. Patchiness, species interactions and disturbance in the stream benthos.
- Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* **54**:427-432.
- Hill, W. R., and A. W. Knight. 1988. Nutrient and light limitation of algae in two northern California streams 1. *Journal of Phycology* **24**:125-132.
- Hill, W. R., M. G. Ryon, and E. M. Schilling. 1995. Light limitation in a stream ecosystem: responses by primary producers and consumers. *Ecology* **76**:1297-1309.
- Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. K. Byrnes, B. A. Hungate, K. L. Matulich, A. Gonzalez, J. E. Duffy, L. Gamfeldt, and M. I. O'Connor. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* **486**:105-U129.
- Humphries, S. 2002. Dispersal in drift-prone macroinvertebrates: a case for density-independence. *Freshwater Biology* **47**:921-929.
- Hynes, H. 1970. The ecology of stream insects. *Annual review of entomology* **15**:25-42.
- IBM Corp. 2016. *IBM SPSS Statistics for Windows, Version 24.0*. Armonk, NY: IBM Corp.

- Ingold, C. 1942. Aquatic hyphomycetes of decaying alder leaves. *Transactions of the British Mycological Society* **25**:339-IN336.
- Jackson, J. K., and V. H. Resh. 1989. Activities and ecological role of adult aquatic insects in the riparian zone of streams. USDA Forest Service General Technical Report PSW-110:342-344.
- Jansson, M., A. K. Bergstrom, P. Blomqvist, A. Isaksson, and A. Jonsson. 1999. Impact of allochthonous organic carbon on microbial food web carbon dynamics and structure in Lake Ortrasket. *Archiv für Hydrobiologie* **144**:409-428.
- Jonsson, M., and B. Malmqvist. 2000. Ecosystem process rate increases with animal species richness: evidence from leaf-eating, aquatic insects. *Oikos* **89**:519-523.
- Jonsson, M., L. E. Polvi, R. A. Sponseller, and K. Stenroth. 2018. Catchment properties predict autochthony in stream filter feeders. *Hydrobiologia* **815**:83-95.
- Jonsson, M., and K. Stenroth. 2016. True autochthony and allochthony in aquatic–terrestrial resource fluxes along a landuse gradient. *Freshwater Science* **35**:882-894.
- Jukes-Browne, A. J. 1904. The valley of the Teign. *Quarterly Journal of the Geological Society* **60**:319-334.
- Kail, J., K. Brabec, M. Poppe, and K. Januschke. 2015. The effect of river restoration on fish, macroinvertebrates and aquatic macrophytes: a meta-analysis. *Ecological Indicators* **58**:311-321.
- Kaplan, L. A., and T. L. Bott. 1983. Microbial heterotrophic utilization of dissolved organic-matter in a Piedmont stream. *Freshwater Biology* **13**:363-377.
- Karr, J. R., and E. W. Chu. 1998. Restoring life in running waters: better biological monitoring. Island Press.
- Kaushik, N. K., and H. B. N. Hynes. 1971. Fate of dead leaves that fall into streams. *Archiv für Hydrobiologie* **68**:465-&.
- Kefford, B. J., L. Zaluzniak, J. E. Dunlop, D. Nugegoda, and S. C. Choy. 2010. How are macroinvertebrates of slow flowing lotic systems directly affected by suspended and deposited sediments? *Environmental Pollution* **158**:543-550.
- Kemp, P., D. Sear, A. Collins, P. Naden, and I. Jones. 2011. The impacts of fine sediment on riverine fish. *Hydrological Processes* **25**:1800-1821.

- Kennedy, C. D., D. P. Genereux, D. R. Corbett, and H. Mitasova. 2009. Relationships among groundwater age, denitrification, and the coupled groundwater and nitrogen fluxes through a streambed. *Water Resources Research* **45**.
- Klösch, M., R. Hornich, N. Baumann, G. Puchner, and H. Habersack. 2011. Mitigating channel incision via sediment input and self-initiated riverbank erosion at the Mur River, Austria. Washington DC American Geophysical Union Geophysical Monograph Series **194**:319-336.
- Kominoski, J. S., L. B. Marczak, and J. S. Richardson. 2011. Riparian forest composition affects stream litter decomposition despite similar microbial and invertebrate communities. *Ecology* **92**:151-159.
- Kondolf, G. M. 2006. River restoration and meanders. *Ecology and Society* **11**.
- Kondolf, G. M., S. Anderson, R. Lave, L. Pagano, A. Merenlender, and E. Bernhardt. 2007. Two decades of river restoration in California: What can we learn? *Restoration Ecology* **15**:516-523.
- Kondolf, G. M., A. J. Boulton, S. O'Daniel, G. C. Poole, F. J. Rahel, E. H. Stanley, E. Wohl, Å. Bång, J. Carlstrom, and C. Cristoni. 2006. Process-based ecological river restoration: visualizing three-dimensional connectivity and dynamic vectors to recover lost linkages. *Ecology & society* **11**:1-16.
- Kondolf, G. M., and W. Matthews. 1991. Management of coarse sediment in regulated rivers of California.
- Kondolf, G. M., and E. R. Micheli. 1995. Evaluating stream restoration projects. *Environmental Management* **19**:1-15.
- Kondolf, G. M., J. C. Vick, and T. M. Ramirez. 1996. Salmon spawning habitat rehabilitation on the Merced River, California: An evaluation of project planning and performance. *Transactions of the American Fisheries Society* **125**:899-912.
- Kondolf, G. M., and M. G. Wolman. 1993. The sizes of salmonid spawning gravels. *Water Resources Research* **29**:2275-2285.
- Krause, S., D. Hannah, P. Wood, and J. Sadler. 2011a. Hydrology and ecology interfaces: Processes and interactions in wetland, riparian and groundwater-based ecosystems. *Ecohydrology* **4**:476-480.

- Krause, S., D. M. Hannah, J. P. Sadler, and P. J. Wood. 2011b. Ecohydrology on the edge: interactions across the interfaces of wetland, riparian and groundwater-based ecosystems. *Ecohydrology* **4**:477-480.
- Krause, S., J. Lewandowski, N. B. Grimm, D. M. Hannah, G. Pinay, K. McDonald, E. Martí, A. Argerich, L. Pfister, and J. Klaus. 2017. Ecohydrological interfaces as hot spots of ecosystem processes. *Water Resources Research* **53**:6359-6376.
- Lake, R. G., and S. G. Hinch. 1999. Acute effects of suspended sediment angularity on juvenile coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* **56**:862-867.
- Lancaster, J., and A. G. Hildrew. 1993a. Characterizing in-stream flow refugia. *Canadian Journal of Fisheries and Aquatic Sciences* **50**:1663-1675.
- Lancaster, J., and A. G. Hildrew. 1993b. Flow refugia and the microdistribution of lotic macroinvertebrates. *Journal of the North American Benthological Society* **12**:385-393.
- Lapointe, N. W. R., S. J. Cooke, J. G. Imhof, D. Boisclair, J. M. Casselman, R. A. Curry, O. E. Langer, R. L. McLaughlin, C. K. Minns, J. R. Post, M. Power, J. B. Rasmussen, J. D. Reynolds, J. S. Richardson, and W. M. Tonn. 2014. Principles for ensuring healthy and productive freshwater ecosystems that support sustainable fisheries. *Environmental Reviews* **22**:110-134.
- Lidman, J., M. Jonsson, R. M. Burrows, M. Bundschuh, and R. A. Sponseller. 2017. Composition of riparian litter input regulates organic matter decomposition: Implications for headwater stream functioning in a managed forest landscape. *Ecology and evolution* **7**:1068-1077.
- Liedermann, M., M. Tritthart, and H. Habersack. 2013. Particle path characteristics at the large gravel-bed river Danube: results from a tracer study and numerical modelling. *Earth Surface Processes and Landforms* **38**:512-522.
- Ligon, F. K., W. E. Dietrich, and W. J. Trush. 1995. Downstream ecological effects of dams. *BioScience* **45**:183-192.
- Lin, Q., R. Sekar, R. Marrs, and Y. Zhang. 2019. Effect of River Ecological Restoration on Biofilm Microbial Community Composition. *Water* **11**:1244.
- Liu, X., and H. Wang. 2018. Effects of loss of lateral hydrological connectivity on fish functional diversity. *Conservation Biology* **32**:1336-1345.

- López-Rojo, N., J. Pozo, J. Pérez, A. Basaguren, A. Martínez, A. M. Tonin, F. Correa-Araneda, and L. Boyero. 2019. Plant diversity loss affects stream ecosystem multifunctionality. *Ecology*:e02847.
- Lu, W., R. A. Font, S. Cheng, J. Wang, and J. Kollmann. 2019. Assessing the context and ecological effects of river restoration—A meta-analysis. *Ecological Engineering* **136**:30-37.
- MacArthur, R. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology* **36**:533-536.
- MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. *The American Naturalist* **100**:603-609.
- Mackay, R. J. 1992. Colonization by lotic macroinvertebrates: a review of processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences* **49**:617-628.
- Malmqvist, B. 2002. Aquatic invertebrates in riverine landscapes. *Freshwater Biology* **47**:679-694.
- Marcarelli, A. M., C. V. Baxter, M. M. Mineau, and R. O. Hall, Jr. 2011. Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. *Ecology* **92**:1215-1225.
- Marchant, R., A. Hirst, R. Norris, R. Butcher, L. Metzeling, and D. Tiller. 1997. Classification and prediction of macroinvertebrate assemblages from running waters in Victoria, Australia. *Journal of the North American Benthological Society* **16**:664-681.
- Marks, J. C. 2019. Revisiting the Fates of Dead Leaves That Fall into Streams. *Annual Review of Ecology, Evolution, and Systematics* **50**.
- Marks, J. C., G. A. Haden, B. L. Harrop, E. G. Reese, J. L. Keams, M. E. Watwood, and T. G. Whitham. 2009. Genetic and environmental controls of microbial communities on leaf litter in streams. *Freshwater Biology* **54**:2616-2627.
- Marzluff, J. M., and K. P. Dial. 1991. Life history correlates of taxonomic diversity. *Ecology* **72**:428-439.
- Mathers, K. L., A. Doretto, S. Fenoglio, M. J. Hill, and P. J. Wood. 2022. Temporal effects of fine sediment deposition on benthic macroinvertebrate community structure, function and biodiversity likely reflects landscape setting. *Science of the Total Environment*:154612.

- McArthur, J. V., and J. R. Barnes. 1988. Community dynamics of leaf litter breakdown in a Utah USA alpine stream. *Journal of the North American Benthological Society* **7**:37-43.
- McAuliffe, J. R. 1983. Competition, colonization patterns, and disturbance in stream benthic communities. Pages 137-156 *Stream ecology*. Springer.
- McManamay, R. A., D. J. Orth, and C. A. Dolloff. 2013. Macroinvertebrate community responses to gravel addition in a southeastern regulated river. *Southeastern Naturalist* **12**:599-619.
- Merritt, R. W., and K. W. Cummins. 1996. *An introduction to the aquatic insects of North America*. Kendall Hunt.
- Merz, J. E., and L. K. Ochikubo Chan. 2005. Effects of gravel augmentation on macroinvertebrate assemblages in a regulated California river. *River Research and Applications* **21**:61-74.
- Merz, J. E., G. B. Pasternack, and J. M. Wheaton. 2006. Sediment budget for salmonid spawning habitat rehabilitation in a regulated river. *Geomorphology* **76**:207-228.
- Meyer, J. L. 1994. The microbial loop in flowing waters. *Microbial Ecology* **28**:195-199.
- Minshall, G. 1984. Aquatic insect-substratum relationships. In 'The Ecology of Aquatic Insects'. (Eds V.H. Resh and D. M. Rosenberg.) pp. 358-400. Praeger: New York.
- Minshall, G. W. 1985. Towards a theory of macroinvertebrate community structure in stream ecosystems. *Archiv für Hydrobiologie* **104**:49-76.
- Mouton, T. L., J. D. Tonkin, F. Stephenson, P. Verburg, and M. Flourey. 2020. Increasing climate-driven taxonomic homogenization but functional differentiation among river macroinvertebrate assemblages. *Global change biology* **26**:6904-6915.
- Muhar, S., K. Januschke, J. Kail, M. Poppe, S. Schmutz, D. Hering, and A. Buijse. 2016. Evaluating good-practice cases for river restoration across Europe: context, methodological framework, selected results and recommendations. *Hydrobiologia* **769**:3-19.
- Mulholland, P. J., E. R. Marzolf, J. R. Webster, D. R. Hart, and S. P. Hendricks. 1997. Evidence that hyporheic zones increase heterotrophic metabolism and phosphorus uptake in forest streams. *Limnology and Oceanography* **42**:443-451.

- Naman, S. M., J. S. Rosenfeld, and J. S. Richardson. 2016. Causes and consequences of invertebrate drift in running waters: from individuals to populations and trophic fluxes. *Canadian Journal of Fisheries and Aquatic Sciences* **73**:1292-1305.
- Newbold, J., R. O'Neill, J. Elwood, and W. Van Winkle. 1982. Nutrient spiralling in streams: implications for nutrient limitation and invertebrate activity. *The American Naturalist* **120**:628-652.
- Newman, M. M., M. R. Liles, and J. W. Feminella. 2015. Litter Breakdown and Microbial Succession on Two Submerged Leaf Species in a Small Forested Stream. *PLoS One* **10**.
- Nickelson, T. E., M. F. Solazzi, S. L. Johnson, and J. D. Rodgers. 1992. Effectiveness of selected stream improvement techniques to create suitable summer and winter rearing habitat for juvenile coho salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. *Canadian Journal of Fisheries and Aquatic Sciences* **49**:790-794.
- O'Sullivan, A. M., K. J. Devito, L. D'Orangeville, and R. A. Curry. 2022. The waterscape continuum concept: Rethinking boundaries in ecosystems. *Wiley Interdisciplinary Reviews: Water* **9**:e1598.
- Ock, G., D. Gaeuman, J. McSloy, and G. M. Kondolf. 2015. Ecological functions of restored gravel bars, the Trinity River, California. *Ecological Engineering* **83**:49-60.
- Ock, G., T. Sumi, and Y. Takemon. 2013. Sediment replenishment to downstream reaches below dams: implementation perspectives. *Hydrological Research Letters* **7**:54-59.
- Oester, R., P. C. dos Reis Oliveira, M. S. Moretti, F. Altermatt, and A. Bruder. 2022. Leaf-associated macroinvertebrate assemblage and leaf litter breakdown in headwater streams depend on local riparian vegetation. *Hydrobiologia*:1-16.
- Ogbeibu, A., and B. Oribhabor. 2002. Ecological impact of river impoundment using benthic macro-invertebrates as indicators. *Water Research* **36**:2427-2436.
- Oksanen, J. 2013. *Vegan: ecological diversity*. R Project **368**.
- Palmer, M. A., R. F. Ambrose, and N. L. Poff. 1997. Ecological theory and community restoration ecology. *Restoration Ecology* **5**:291-300.
- Palmer, M. A., E. Bernhardt, J. Allan, P. Lake, G. Alexander, S. Brooks, J. Carr, S. Clayton, C. Dahm, and J. F. Shah. 2005. Standards for ecologically successful river restoration. *Journal of Applied ecology* **42**:208-217.

- Paul, M. J., and J. L. Meyer. 1996. Fungal biomass of 3 leaf litter species during decay in an Appalachian stream. *Journal of the North American Benthological Society* **15**:421-432.
- Peckarsky, B. L. 1986. Colonization of natural substrates by stream benthos. *Canadian Journal of Fisheries and Aquatic Sciences* **43**:700-709.
- Peralta-Maraver, I., R. Stubbington, S. Arnon, P. Kratina, S. Krause, V. de Mello Cionek, N. K. Leite, A. L. L. da Silva, S. M. Thomaz, and M. Posselt. 2021. The riverine bioreactor: An integrative perspective on biological decomposition of organic matter across riverine habitats. *Science of the Total Environment* **772**:145494.
- Péru, N., and S. Dolédec. 2010. From compositional to functional biodiversity metrics in bioassessment: a case study using stream macroinvertebrate communities. *Ecological Indicators* **10**:1025-1036.
- Petersen Jr, R. C., K. W. Cummins, and G. M. Ward. 1989. Microbial and animal processing of detritus in a woodland stream. *Ecological monographs* **59**:21-39.
- Petersen, R. C., and K. W. Cummins. 1974. Leaf processing in a woodland stream. *Freshwater Biology* **4**:343-368.
- Petersen, R. C., K. W. Cummins, and G. M. Ward. 1989. Microbial and animal processing of detritus in a woodland stream. *Ecological monographs* **59**:21-39.
- Pettit, N. E., T. Davies, J. B. Fellman, P. F. Grierson, D. M. Warfe, and P. M. Davies. 2012. Leaf litter chemistry, decomposition and assimilation by macroinvertebrates in two tropical streams. *Hydrobiologia* **680**:63-77.
- Poff, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* **16**:391-409.
- Poff, N. L., J. D. Olden, D. M. Merritt, and D. M. Pepin. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences of the United States of America* **104**:5732-5737.
- Poff, N. L., and J. K. Zimmerman. 2010. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology* **55**:194-205.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *The American Naturalist* **147**:813-846.

- Pozo, J., J. Casas, M. Menéndez, S. Mollá, I. Arostegui, A. Basaguren, C. Casado, E. Descals, J. García-Avilés, and J. M. González. 2011. Leaf-litter decomposition in headwater streams: a comparison of the process among four climatic regions. *Journal of the North American Benthological Society* **30**:935-950.
- Pulg, U., B. T. Barlaup, K. Sternecker, L. Trepl, and G. Unfer. 2013. Restoration of spawning habitats of brown trout (*Salmo trutta*) in a regulated chalk stream. *River Research and Applications* **29**:172-182.
- Rabeni, C., and G. Minshall. 1977. Factors affecting microdistribution of stream benthic insects. *Oikos*:33-43.
- Rabeni, C. F., and R. B. Jacobson. 1993. The importance of fluvial hydraulics to fish-habitat restoration in low-gradient alluvial streams. *Freshwater Biology* **29**:211-220.
- Rader, R. B. 1997. A functional classification of the drift: traits that influence invertebrate availability to salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:1211-1234.
- Radford, D. S., and Hartland, R. 1971. Preliminary investigation of bottom fauna and invertebrate drift in an unregulated and a regulated stream in Alberta. *Journal of Applied Ecology* **8**:883-&.
- Redding, J. M., and C. Schreck. 1982. Mount St. Helens ash causes sublethal stress responses in steelhead trout. Mt. St. Helens: effects on water resources. Washington State University, Washington Water Research Center, Report **41**.
- Reeder, W. J., F. Gariglio, R. Carnie, C. Tang, D. Isaak, Q. Chen, Z. Yu, J. A. McKean, and D. Tonina. 2021. Some (fish might) like it hot: Habitat quality and fish growth from past to future climates. *Science of the Total Environment* **787**:147532.
- Reid, A. J., A. K. Carlson, I. F. Creed, E. J. Eliason, P. A. Gell, P. T. Johnson, K. A. Kidd, T. J. MacCormack, J. D. Olden, and S. J. Ormerod. 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews* **94**:849-873.
- Reinhart, K. O., and R. VandeVoort. 2006. Effect of native and exotic leaf litter on macroinvertebrate communities and decomposition in a western Montana stream. *Diversity and distributions* **12**:776-781.
- Reiso, S., and J. E. Brittain. 2000. Life cycle, diet and habitat of *Polycentropus flavomaculatus*, *Plectrocnemia conspersa* and *Rhyacophila nubila* (Trichoptera) in

- Øvre Heimdalen, Jotunheimen Mountains, Norway. *Norwegian Journal of Entomology* **47**:113-124.
- Rempel, L. L., J. S. Richardson, and M. C. Healey. 2000. Macroinvertebrate community structure along gradients of hydraulic and sedimentary conditions in a large gravel-bed river. *Freshwater Biology* **45**:57-73.
- Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* **7**:433-455.
- Resh, V. H., and D. M. Rosenberg. 1993. Freshwater biomonitoring and benthic macroinvertebrates.
- Reynoldson, T. B., and J. L. Metcalfe-Smith. 1992. An overview of the assessment of aquatic ecosystem health using benthic invertebrates. *Journal of Aquatic Ecosystem Health* **1**:295-308.
- Rice, S. P., M. T. Greenwood, and C. B. Joyce. 2001. Macroinvertebrate community changes at coarse sediment recruitment points along two gravel bed rivers. *Water Resources Research* **37**:2793-2803.
- Richardson, J. 1992. Food, microhabitat, or both? Macroinvertebrate use of leaf accumulations in a montane stream. *Freshwater Biology* **27**:169-176.
- Richardson, J. S. 1984. Prey selection and distribution of a predaceous, net-spinning caddisfly, *Neureclipsis bimaculata* (Polycentropodidae). *Canadian Journal of Zoology* **62**:1561-1565.
- Richter, B. D., A. T. Warner, J. L. Meyer, and K. Lutz. 2006. A collaborative and adaptive process for developing environmental flow recommendations. *River Research and Applications* **22**:297-318.
- Rondorf, D. W., G. A. Gray, and R. B. Fairley. 1990. Feeding ecology of subyearling chinook salmon in riverine and reservoir habitats of the Columbia River. *Transactions of the American Fisheries Society* **119**:16-24.
- Roni, P., T. J. Beechie, R. E. Bilby, F. E. Leonetti, M. M. Pollock, and G. R. Pess. 2002. A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest watersheds. *North American Journal of Fisheries Management* **22**:1-20.

- Roni, P., K. Hanson, and T. Beechie. 2008. Global review of the physical and biological effectiveness of stream habitat rehabilitation techniques. *North American Journal of Fisheries Management* **28**:856-890.
- Rosenfeld, J. S., and T. Hatfield. 2006. Information needs for assessing critical habitat of freshwater fish. *Canadian Journal of Fisheries and Aquatic Sciences* **63**:683-698.
- Roskosch, A., N. Hette, M. Hupfer, and J. Lewandowski. 2012. Alteration of *Chironomus plumosus* ventilation activity and bioirrigation-mediated benthic fluxes by changes in temperature, oxygen concentration, and seasonal variations. *Freshwater Science* **31**:269-281.
- Ruetz, C. R., R. M. Newman, and B. Vondracek. 2002. Top-down control in a detritus-based food web: fish, shredders, and leaf breakdown. *Oecologia* **132**:307-315.
- Sagar, P., and G. Glova. 1988. Diel feeding periodicity, daily ration and prey selection of a riverine population of juvenile chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). *Journal of Fish Biology* **33**:643-653.
- Santonja, M., L. Pellan, and C. Piscart. 2018. Macroinvertebrate identity mediates the effects of litter quality and microbial conditioning on leaf litter recycling in temperate streams. *Ecology and evolution* **8**:2542-2553.
- Santonja, M., H. Rodríguez-Pérez, N. Le Bris, and C. Piscart. 2019. Leaf Nutrients and Macroinvertebrates Control Litter Mixing Effects on Decomposition in Temperate Streams. *Ecosystems*:1-17.
- Sarriquet, P.-E., P. Bordenave, and P. Marmonier. 2007. Effects of bottom sediment restoration on interstitial habitat characteristics and benthic macroinvertebrate assemblages in a headwater stream. *River Research and Applications* **23**:815-828.
- Saura, M., A. Caballero, P. Caballero, and P. Moran. 2008. Impact of precocious male parr on the effective size of a wild population of Atlantic salmon. *Freshwater Biology* **53**:2375-2384.
- Schälchli, U., M. Breitenstein, and A. Kirchhofer. 2010. Restoring sediment transport and fish spawning habitat of the Aare River. *Wasser Energie Luft* **102**:209-213.
- Schindler, M. H., and M. O. Gessner. 2009. Functional leaf traits and biodiversity effects on litter decomposition in a stream. *Ecology* **90**:1641-1649.

- Schmera, D., J. Heino, J. Podani, T. Erős, and S. Dolédec. 2017. Functional diversity: a review of methodology and current knowledge in freshwater macroinvertebrate research. *Hydrobiologia* **787**:27-44.
- Sellheim, K. L., C. B. Watry, B. Rook, S. C. Zeug, J. Hannon, J. Zimmerman, K. Dove, and J. E. Merz. 2016. Juvenile Salmonid Utilization of Floodplain Rearing Habitat After Gravel Augmentation in a Regulated River. *River Research and Applications* **32**:610-621.
- Sheldon, A. 1977. Colonization curves: application to stream insects on semi-natural substrates. *Oikos*:256-261.
- Shieh, S.-H., C.-P. Wang, C.-B. Hsu, and P.-S. Yang. 2008. Leaf breakdown in a subtropical stream: nutrient release patterns. *Fundamental and Applied Limnology* **171**:273-284.
- Siders, A. C., Z. G. Compson, B. A. Hungate, P. Dijkstra, G. W. Koch, A. S. Wymore, A. S. Grandy, and J. C. Marks. 2018. Litter identity affects assimilation of carbon and nitrogen by a shredding caddisfly. *Ecosphere* **9**.
- Simmonds, I. 1970. Environment and early man on Dartmoor, Devon, England. *Proceedings, Prehistoric Society, Cambridge* **35**:203-219.
- Srivastava, D. S., and J. H. Lawton. 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. *The American Naturalist* **152**:510-529.
- Staentzel, C., I. Combroux, A. Barillier, C. Grac, E. Chanez, and J.-N. Beisel. 2019a. Effects of a river restoration project along the Old Rhine River (France-Germany): Response of macroinvertebrate communities. *Ecological Engineering* **127**:114-124.
- Staentzel, C., G. M. Kondolf, L. Schmitt, I. Combroux, A. Barillier, and J.-N. Beisel. 2019b. Restoring fluvial forms and processes by gravel augmentation or bank erosion below dams: A systematic review of ecological responses. *Science of the Total Environment*:135743.
- Stanford, J., and J. Ward. 1988. The hyporheic habitat of river ecosystems. *Nature* **335**:64.
- Statzner, B., J. A. Gore, and V. H. Resh. 1988. Hydraulic stream ecology: observed patterns and potential applications. *Journal of the North American Benthological Society* **7**:307-360.
- Stone, M. K., and J. B. Wallace. 1998. Long-term recovery of a mountain stream from clear-cut logging: the effects of forest succession on benthic invertebrate community structure. *Freshwater Biology* **39**:151-169.

- Strauss, R. E. 1979. Reliability Estimates for Ivlev's Electivity Index, the Forage Ratio, and a Proposed Linear Index of Food Selection. *Transactions of the American Fisheries Society* **108**:344-352.
- Stubbington, R. 2012. The hyporheic zone as an invertebrate refuge: a review of variability in space, time, taxa and behaviour. *Marine and Freshwater Research* **63**:293-311.
- Suberkropp, K., G. Godshalk, and M. Klug. 1976. Changes in the chemical composition of leaves during processing in a woodland stream. *Ecology* **57**:720-727.
- Suberkropp, K., and M. J. Klug. 1980. The maceration of deciduous leaf litter by aquatic hyphomycetes. *Canadian Journal of Botany-Revue Canadienne De Botanique* **58**:1025-1031.
- Surber, E. W. 1937. Rainbow trout and bottom fauna production in one mile of stream. *Transactions of the American Fisheries Society* **66**:193-202.
- Sweeney, B. W. 1993. Effects of streamside vegetation on macroinvertebrate communities of White Clay Creek in eastern North America. *Proceedings of the Academy of Natural Sciences of Philadelphia*:291-340.
- Taylor, J. J., T. Rytwinski, J. R. Bennett, K. E. Smokorowski, N. W. Lapointe, R. Janusz, K. Clarke, B. Tonn, J. C. Walsh, and S. J. Cooke. 2019. The effectiveness of spawning habitat creation or enhancement for substrate-spawning temperate fish: a systematic review. *Environmental Evidence* **8**:19.
- Team, R. 2016. RStudio: Integrated development for R [Computer software]. RStudio, Inc. Boston, MA. URL: <http://www.rstudio.com>.
- Theurer, F., T. Harrod, and M. Theurer. 1998. Sedimentation and salmonids in England and Wales. Environment Agency.
- Thonney, J.-P., and R. Gibson. 1989. Feeding strategies of brook trout, *Salvelinus fontinalis*, and juvenile Atlantic salmon, *Salmo salar*, in a Newfoundland river. *Canadian field-naturalist*. Ottawa ON **103**:48-56.
- Thorndycraft, V. R., D. Pirrie, and A. G. Brown. 1999. Tracing the record of early alluvial tin mining on Dartmoor, UK. Geological Society, London, Special Publications **165**:91-102.
- Thorndycraft, V. R., D. Pirrie, and A. G. Brown. 2004. Alluvial records of medieval and prehistoric tin mining on Dartmoor, southwest England. *Geoarchaeology: An International Journal* **19**:219-236.

- Townsend, C. R. 1989. The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society* **8**:36-50.
- Tullos, D. D., D. L. Penrose, G. D. Jennings, and W. G. Cope. 2009. Analysis of functional traits in reconfigured channels: implications for the bioassessment and disturbance of river restoration. *Journal of the North American Benthological Society* **28**:80-92.
- Underwood, A. 1992. Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. *Journal of Experimental Marine Biology and Ecology* **161**:145-178.
- Valett, H. M., S. G. Fisher, N. B. Grimm, and P. Camill. 1994. Vertical hydrologic exchange and ecological stability of a desert stream ecosystem. *Ecology* **75**:548-560.
- Vander Vorste, R., A. J. Timpano, C. Cappellin, B. D. Badgley, C. E. Zipper, and S. H. Schoenholtz. 2019. Microbial and macroinvertebrate communities, but not leaf decomposition, change along a mining-induced salinity gradient. *Freshwater Biology* **64**:671-684.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**:130-137.
- Vannote, R. L., and B. W. Sweeney. 1980. Geographic analysis of thermal equilibria - A conceptual-model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *American Naturalist* **115**:667-695.
- Vitecek, S., G. Vinçon, W. Graf, and S. Pauls. 2017. High cryptic diversity in aquatic insects: an integrative approach to study the enigmatic *Leuctra inermis* species group (Plecoptera). *Arthropod Systematics & Phylogeny* **75**:497-521.
- Vörösmarty, C. J., and D. Sahagian. 2000. Anthropogenic disturbance of the terrestrial water cycle. *BioScience* **50**:753-765.
- Wallace, J. B., S. Eggert, J. L. Meyer, and J. Webster. 1999. Effects of resource limitation on a detrital-based ecosystem. *Ecological monographs* **69**:409-442.
- Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* **277**:102-104.
- Wallace, J. B., and J. R. Webster. 1996. The role of macroinvertebrates in stream ecosystem function. *Annual review of entomology* **41**:115-139.
- Walpola, H., M. Leichtfried, M. Amarasinghe, and L. Fuereder. 2011. Leaf Litter Decomposition of Three Riparian Tree Species and Associated Macroinvertebrates of

- Eswathu Oya, a Low Order Tropical Stream in Sri Lanka. *International Review of Hydrobiology* **96**:90-104.
- Walpole, H., M. Leichtfried, and L. Füreder. 2019. Natural leaf packs and invertebrates in a tropical stream: Is there a functional relationship? *Sri Lanka Journal of Aquatic Sciences* **24**.
- Walton Jr, O., S. Reice, and R. Andrews. 1977. The effects of density, sediment particle size and velocity on drift of *Acroneuria abnormis* (Plecoptera). *Oikos*:291-298.
- Wang, J., S. Bao, K. Zhang, J. Heino, X. Jiang, Z. Liu, and J. Tao. 2023. Responses of macroinvertebrate functional trait structure to river damming: From within-river to basin-scale patterns. *Environmental Research*:115255.
- Wang, J., C. Ding, J. Tao, X. Jiang, J. Heino, L. Ding, W. Su, M. Chen, K. Zhang, and D. He. 2021. Damming affects riverine macroinvertebrate metacommunity dynamics: Insights from taxonomic and functional beta diversity. *Science of the Total Environment* **763**:142945.
- Wantzen, K. M., and R. Wagner. 2006. Detritus processing by invertebrate shredders: a neotropical–temperate comparison. *Journal of the North American Benthological Society* **25**:216-232.
- Ward, G. M., and K. W. Cummins. 1979. Effects of food quality on growth of a stream detritivore, *Paratendipes albimanus* (Meigen)(Diptera: Chironomidae). *Ecology* **60**:57-64.
- Ward, J. V. 1992. *Aquatic insect ecology*. 1. Ecology and habitat. John Wiley & Sons, Inc.
- Weber, N., N. Bouwes, and C. E. Jordan. 2014. Estimation of salmonid habitat growth potential through measurements of invertebrate food abundance and temperature. *Canadian Journal of Fisheries and Aquatic Sciences* **71**:1158-1170.
- Webster, J., and E. Benfield. 1986. Vascular plant breakdown in freshwater ecosystems. *Annual review of ecology and systematics* **17**:567-594.
- Webster, J. R., E. F. Benfield, T. P. Ehrman, M. A. Schaeffer, J. L. Tank, J. J. Hutchens, and D. J. D'Angelo. 1999. What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta. *Freshwater Biology* **41**:687-705.

- Wharton, G., and D. J. Gilvear. 2007. River restoration in the UK: Meeting the dual needs of the European Union Water Framework Directive and flood defence? *International Journal of River Basin Management* **5**:143-154.
- Wheaton, J. M., G. B. Pasternack, and J. E. Merz. 2004. Spawning habitat rehabilitation-II. Using hypothesis development and testing in design, Mokelumne river, California, USA. *International Journal of River Basin Management* **2**:21-37.
- White, H. 1942. Atlantic salmon redds and artificial spawning beds. *Journal of the Fisheries Board of Canada* **6**:37-44.
- White, J., M. J. Hill, M. Bickerton, and P. J. Wood. 2017a. Macroinvertebrate taxonomic and functional trait compositions within lotic habitats affected by river restoration practices. *Environmental Management* **60**:513-525.
- White, J. C., D. M. Hannah, A. House, S. J. V. Beatson, A. Martin, and P. J. Wood. 2017b. Macroinvertebrate responses to flow and stream temperature variability across regulated and non-regulated rivers. *Ecohydrology* **10**.
- Williams, G. P., and M. G. Wolman. 1984. Downstream effects of dams on alluvial rivers.
- Wohl, E., P. L. Angermeier, B. Bledsoe, G. M. Kondolf, L. MacDonnell, D. M. Merritt, M. A. Palmer, N. L. Poff, and D. Tarboton. 2005. River restoration. *Water Resources Research* **41**.
- Wohl, E., S. N. Lane, and A. C. Wilcox. 2015. The science and practice of river restoration. *Water Resources Research* **51**:5974-5997.
- Wood, P. J., and P. D. Armitage. 1997. Biological effects of fine sediment in the lotic environment. *Environmental Management* **21**:203-217.
- Wood, P. J., A. Boulton, S. Little, and R. Stubbington. 2010. Is the hyporheic zone a refugium for aquatic macroinvertebrates during severe low flow conditions? *Fundamental and Applied Limnology/Archiv für Hydrobiologie* **176**:377-390.
- Woodward, G., M. O. Gessner, P. S. Giller, V. Gulis, S. Hladyz, A. Lecerf, B. Malmqvist, B. G. McKie, S. D. Tiegs, and H. Cariss. 2012. Continental-scale effects of nutrient pollution on stream ecosystem functioning. *Science* **336**:1438-1440.
- Woodward, G., and A. G. Hildrew. 2002. Food web structure in riverine landscapes. *Freshwater Biology* **47**:777-798.

- Wymore, A. S., E. Salpas, G. Casaburi, C. M. Liu, L. B. Price, B. A. Hungate, W. H. McDowell, and J. C. Marks. 2018. Effects of plant species on stream bacterial communities via leachate from leaf litter. *Hydrobiologia* **807**:131-144.
- Yarnell, S. M., J. F. Mount, and E. W. Larsen. 2006. The influence of relative sediment supply on riverine habitat heterogeneity. *Geomorphology* **80**:310-324.
- Yoshimura, C., M. O. Gessner, K. Tockner, and H. Furumai. 2008. Chemical properties, microbial respiration, and decomposition of coarse and fine particulate organic matter. *Journal of the North American Benthological Society* **27**:664-673.
- Zhang, T. a., Y. Luo, H. Y. H. Chen, and H. Ruan. 2018. Responses of litter decomposition and nutrient release to N addition: A meta-analysis of terrestrial ecosystems. *Applied Soil Ecology* **128**:35-42.