The form and stability of alluvial riverbeds, and their effects on macroinvertebrate communities across Great Britain

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Thesis summary

The sustainable functioning of macroinvertebrate communities forms the basis of many of the vital ecosystem services provided by rivers, yet these communities are amongst the most stressed on the planet and predictions show these stresses increasing in the future. At a conceptual level, macroinvertebrate community composition is inextricably linked to the riverbed sediment in which they reside, although evidence of these links is largely confined to descriptive or small-scale studies. Robust predictions of the response of these communities to future change are urgently needed but this first requires a better understanding of the interaction between physical and ecological processes across larger spatial and temporal scales.

Using national scale monitoring data for rivers across Great Britain, this study tested the ability of simple process-based models to predict physical habitat features (e.g. bars), before investigating their ability to describe spatial and temporal trends of invertebrate community function, composition and response to physical perturbation. The simple nature of the approaches used in this study, which combine basic geomorphological models with traditional ecological metrics and functional traits, presents an opportunity to develop tools that allow river managers to base decisions on quantifiable measures of physical process instead of expert opinion.

Overall, the results provided evidence of an implicit link between freshwater community composition, function, and the spatial variation in physical processes. Traditional and functional measures of community diversity showed a response to changing bed material calibre and stability across large spatial scales, consistent with other studies of habitat stability in rivers and other ecosystems. Despite this, there was limited evidence of temporal variability in communities due to riverbed disturbance, perhaps because water quality continued to suppress the physical habitat signal. Further work is required to isolate the effect of riverbed disturbance from other controlling mechanisms.

1 General Introduction

Freshwaters, including rivers, are amongst the most biodiverse ecosystems, supporting an estimated 6% of all known species, despite covering only 0.8% of the Earth's surface (Dudgeon *et al*., 2006). At the same time, rivers provide hugely valued ecosystem services to humans, such as drinking water, irrigation, recreation and transport (Cotanza *et al*., 1997; Cotanza *et al*., 2014; Maltby *et al*., 2011). Human activities have directly (e.g. through impoundment, abstraction and flood control) and indirectly (e.g. through climate change and land use change) made rivers amongst the most impacted and threatened ecosystems (Sala *et al*., 2000; Dudgeon *et al*., 2006), and their long-term prognosis is poor as population growth and urbanisation exacerbate these pressures on river systems (Palmer *et al*., 2008*;* Vorosmarty *et al*., 2010). To address the consequences of these pressures, and improve river management and restoration, a better understanding is required of the factors shaping riverine biodiversity, species distributions and community structure (Petts, 2009). This cuts across traditional research disciplines including freshwater ecology, geomorphology and hydrology, and emphasises the urgent need for more multidisciplinary research (Dollar *et al*., 2007; Vaughan *et al*., 2009).

Physical habitat is considered to be one of the major drivers of biodiversity patterns in rivers (Vannote *et al*, 1980; Townsend and Hildrew, 1994; Benda *et al*, 2004). Yet despite its recognised importance and long history of research (e.g. Riley, 1921; Percival and Whitehead, 1929), it has been comparatively understudied, primarily due to a focus on water quality (Vaughan *et al*., 2009). In rivers, physical habitat is shaped by the local movement of sediment, which in turn is largely controlled by four key elements; sediment supply, sediment calibre, discharge and channel slope (Knighton, 1998). These parameters can be viewed as driving forces (discharge and slope) and resisting forces (sediment calibre and supply) and they define the channel morphology, the threshold at which sediment transport occurs and how the sediment is transported through the channel. These processes create and redistribute the habitats familiar to river ecologists e.g. riffles, areas of fine sediment or those suitable for macrophyte colonisation (Demars *et al*., 2012). In theory, it should be possible to predict how a river functions at a location based on an understanding of these key parameters, creating scope for relatively simple process-based models that could be linked to the ecology. Furthermore, capturing the dynamics of sediment transport should help to describe the disturbance regime to which organisms are exposed

(Death and Winterbourn, 1995; Death, 2002; Schwendel *et al*., 2010a), which may play an important role in determining community structure (Connell, 1978; Miller *et al*. 2010). These events alter the physical attributes of the channel and its instream and riparian habitats, in turn impacting on the biota that reside in this altered habitat (Death and Winterbourn, 1995; Death, 2002; Schwendel *et al*., 2010a), the subject of this thesis.

Three major factors have contributed to a surge of interest in physical habitat over recent years. Firstly, conservation and restoration efforts have successfully focussed on improving water quality and have resultantly promoted the issues caused by physical modifications and poor habitat quality to the fore of river restoration efforts (Collins *et al*., 2012). Secondly, policy drivers such as the Water Framework Directive (2000) have emphasised the importance of hydromorphology by placing it alongside the traditional measures of riverine health, biological and water quality (Griffiths, 2002). Whilst this policy change has led to the consideration of hydromorphology by the statutory bodies and other river managers, interdisciplinary research has been slow to react and as such there is a lack of tools to pinpoint where ecology-hydromorphology interactions can be improved (Vaughan *et al*., 2009). The third factor is climate change, with predictions of changes in the timing, intensity and overall magnitude of rainfall (Murphy *et al*., 2009; Kendon *et al*., 2014), with potential ramifications for physical habitat. Climate is a major control on the flow regime of the stream network (Poff *et al*, 1997), the production and delivery of sediment (e.g. by triggering landslides; Parker *et al*., 2016) and land use (e.g. by controlling the distribution of vegetation; Bachelet *et al*, 2001), which in turn control smaller scale variations including reach-scale morphology (Buffington and Montgomery, 1997) and water temperature (van Vliet *et al*., 2013). Climate is a major control on sediment supply to the fluvial network over long timescales, especially in regions with little tectonic activity such as the UK, with both the frequency and intensity of storm events influencing rates of sediment delivery to river channels via hillslope processes (Wilby *et al*., 1997). General predictions of more frequent and intense storm events across the UK in coming decades as well as changes in overall precipitation trends have created the need for initial understanding and eventual prediction of the likely changes to both physical habitats and the organisms residing within them.

Against this background of greater interest, there are great challenges but also great opportunities. Traditional approaches are challenged by interdisciplinary study and the need to account for changing conditions. Current ecological models are static and correlative, making them poor at extrapolating beyond the conditions under which they were calibrated (Urban *et al*., 2016). To reliably model changing conditions, such as the likely changes in sediment supplies and flow regimes as a result of climate or land use change, a shift to process-based modelling is needed (Urban *et al.*, 2016, Zurell *et al*., 2016). Another consideration is that of scale. River managers require insight at sufficient scales (i.e. catchment or greater) but datasets that provide this coverage are typically too expensive or time consuming to collect by field study so novel use of existing datasets or rapid collection techniques are needed (Carbonneau *et al*., 2012). The UK is uniquely positioned to address these challenges due to its extensive biological and chemical monitoring networks, gauging stations and physical habitat classifications (Vaughan and Ormerod 2010).

1.1 Thesis aims

The need for greater understanding of the interactions between freshwater ecology and hydromorphology (i.e. physical habitat) is the key theme that this thesis aims to address. Using national-scale data sets, it evaluates the potential for applying simple, process-based models of sediment transport to predict physical habitat structure and river bed disturbance, and how these link to the ecological traits and community structure of benthic macroinvertebrates. Macroinvertebrates are selected as they are intimately related to the riverbed (Death and Winterbourn, 1995), allied to well- known ecology-habitat requirements (Tachet *et al*., 2002), well sampled in space and time (at least in the UK; Wright, 2000) and have a diverse array of life strategies (Poff, 1997). The focus is alluvial rivers, which make up >95% of river length in the UK (Raven *et al*., 1998). The specific aims of the thesis are to:

1. Review the controls placed on physical habitat, how these link to species distributions, abundance and other ecological characteristics, and how they may change in the future;
2. Develop a simple model of relative riverbed mobility to predict the distribution of bars, a key river habitat feature, across the UK;
3. Assess the effects of bed material and riverbed stability (i.e. disturbance) upon the composition and functional diversity of invertebrate communities;
4. Assess invertebrate community response to riverbed disturbance through time;
5. Appraise the potential to develop simple, process-based models to link fluvial geomorphology and ecology, based on minimal data requirements, that could have applications for river management and restoration.

Chapter 2 reviews the literature on physical habitat controls in rivers and how this links to the distributions of organisms (Aim 1). Topics include the prediction of sediment transport and riverbed disturbance, the potential for using species' ecological traits to understand their interaction with physical habitat, the research opportunities created by nationwide datasets in the UK and the predicted future impacts of climate change on freshwater environments and ecological communities. Gaps in existing knowledge are highlighted to be explored in the subsequent chapters.

Chapter 3 focuses on geomorphic controls of channel form and aims to the infer sediment transport characteristics (e.g. interaction of available energy and sediment calibre) required to create bedforms (Aims 2 & 5). Building on the approach of Vaughan *et al*. (2013), data from 1480 River Habitat Survey (RHS) sites across the UK describing the distribution of bars, a key physical feature in alluvial river channels, are used to test the predictive power of a simple network scale model of stream power and sediment size.

Chapter 4 explores the interactive effects of bed material and riverbed stability upon invertebrate communities (Aims 3 & 5) using data from the river invertebrate prediction and classification system (RIVPACS). Data from 714 sites is used to assess the distribution of communities across substrate and disturbance gradients in terms of traditional community metrics and functional measures such as individual trait distributions and functional diversity.

Chapter 5 investigates the potential role of river bed disturbance in limiting invertebrate community composition using 20-year time series from across England and Wales (Aims 4 & 5). The study period coincided with large improvements in water quality, and so this chapter also tests whether improving water quality increases the resistance or resilience of the benthic community to disturbance. The chapter uses large scale Environment Agency datasets including the gauging station network, routine biological and chemical sampling sites and RHS locations.

Chapter 6 distils the findings of the experimental chapters, explores their limitations and implications and proposes potential areas where future research efforts should be dedicated, before drawing general conclusions (Aim 5).

2 Literature Review: challenges and opportunities for linking physical habitat and organisms in rivers

2.1 Introduction

Physical habitat is one of the major drivers of riverine biodiversity (Benda *et al*., 2004), yet our understanding of the limits placed by physical habitat on patterns of biodiversity is lacking. This is despite there being a large body of studies correlating different riverine organisms against simple observations of physical habitat (Hastie *et al*., 2003; Vaughan *et al*., 2007; Demars *et al*., 2012; Senay *et al*., 2015) and advances in this area are vital if efforts to restore and maintain freshwater ecosystems are to be successful. Improvements in water quality and legislative drivers (e.g. The Water Framework Directive) have, in recent decades, promoted interest in physical habitat and habitat modification to the fore of river management in the UK and Europe (Vaughan *et al*., 2009; Wilby *et al*., 2010). At present, measures to protect or improve freshwater habitat are guided by a conceptual understanding of 'good' habitat, with evidence confined to observational studies of the local habitat requirements of organisms (e.g. Riley, 1921; Percival and Whitehead, 1929), or to large scale conceptual studies of river system function (Vannote *et al*., 1980; Townsend and Hildrew, 1994). As pressures specific to hydromophology (e.g. fine sediment deposition or modifications for flood defence; Kemp *et al*., 2011; Downs and Gregory, 2014) and wider pressures (e.g. land use change or climate change; Wilby *et al*., 1997; Murphy *et al.*, 2009) are predicted to continue to increase into the future, the interaction between physical habitat and biodiversity in rivers will continue to be of importance.

In the current literature review, I survey some of the important developments in linking fluvial geomorphology and ecology and the challenges and opportunities for progress. An exhaustive review of evidence for links between organisms and their habitats is beyond the scope of the current chapter, with the review primarily focussing on freshwater macroinvertebrate interactions with physical processes. Instead, the review will broadly cover the main topics in the thesis aims, beginning with a brief review of the existing literature on the controls placed on physical habitat, before developing a conceptual model of these controls and the pressures they exert on freshwater organisms to underpin the later chapters in the thesis. The review continues by looking at some of the key developments in linking geomorphology to organisms, the role of ecological traits, methods for quantifying sediment transport, the need for better predictive ability in light of future changes and the unique position of the UK in having a network of long-term monitoring locations.

2.2 Controls on physical habitat

Rivers are very diverse landscape features and take different forms principally due to differences in climate, tectonics and pre-existing geology (Figure 2-1; Knighton, 1998). The interactions between these three factors set the relief and sediment sources within a catchment, which are then reworked by flowing water into various forms (Knighton, 1998). Where sediment is lacking, rivers flow over bedrock but alluvial rivers (i.e. those with beds composed of sediment) are much more common in the UK and globally (Raven *et al.*, 1998). In spite of the complexity of these controlling factors, rivers can be broadly grouped into a handful of classes (e.g. meandering, braided, anastomosing, straight; Schumm, 1985) and described by relatively few key features (e.g. dominant substrate, presence of bedforms, width/depth ratio; Seager *et al.*, 2012). Despite its small size, the UK has very diverse geology which can be broadly described as a gradient from hard, impermeable igneous and metamorphic rocks in the north and west through to aquifer bearing sedimentary rocks in the south and east (Raven *et al.*, 2000). This geological gradient determines the baseflow component of flow regimes, with permeable rocks (e.g. chalk) in the south and east having a high baseflow, which buffers any response to rainfall events and temperature changes (Bloomfield *et al.*, 2009). In the north and west, where impermeable rocks are most common, hydrographs have a flashy response to rainfall events and are more prone to changes in temperature or pH (Bloomfield *et al.*, 2009). The lack of significant tectonic activity in the UK excludes it as a major control (Lewin, 1981). Instead, the recent glacial history has created a topographic signature across the majority of the country, which fluvial systems have to adapt to and modify (Figure 2-1; Lewin, 1981). This glacial landscape imposes oversized valleys and varying gradients upon the river network, resulting in lower sediment supplies than in landscapes derived principally by fluvial action (Phillips *et al.*, 2013).

Climate plays a central role in the formation of physical habitat, acting both within the channel and at catchment-wide scales and above (Figure 2-1). Precipitation drives physical habitat creation and renewal as it creates the floods which shape river channels (Benda *et al.*, 2004). The intensity, frequency and total amount of precipitation over a catchment are all important in determining discharge regimes at a point in the fluvial network (Nash and Sutcliffe, 1970). These factors determine how flood events are initiated across a catchment and also how sediment is delivered to the network via sheet runoff or landslides and moved through the network, building and renewing habitat (Benda and Dunne, 1997a). In addition, periods of high discharge may represent disturbance events that shape riverine communities, through mechanisms such as removal of individuals and food resources (Bond and Downes, 2000; Death, 2002), and selection for disturbance tolerant species (Townsend *et al*., 1997). Other events within a catchment can also act to modify the frequency and magnitude of disturbance. Land use, geology/soil type and wildfire can all act to alter the quantity and speed at which water and/or sediment is transferred to the fluvial network during a storm event (Figure 1; Benda and Dunne, 1997a). These factors alter the sediment supply and transport within the channel, affecting the river's ability to create particular types of bedforms that are common at different sediment supply-transport ratios (Montgomery and Buffington, 1997).

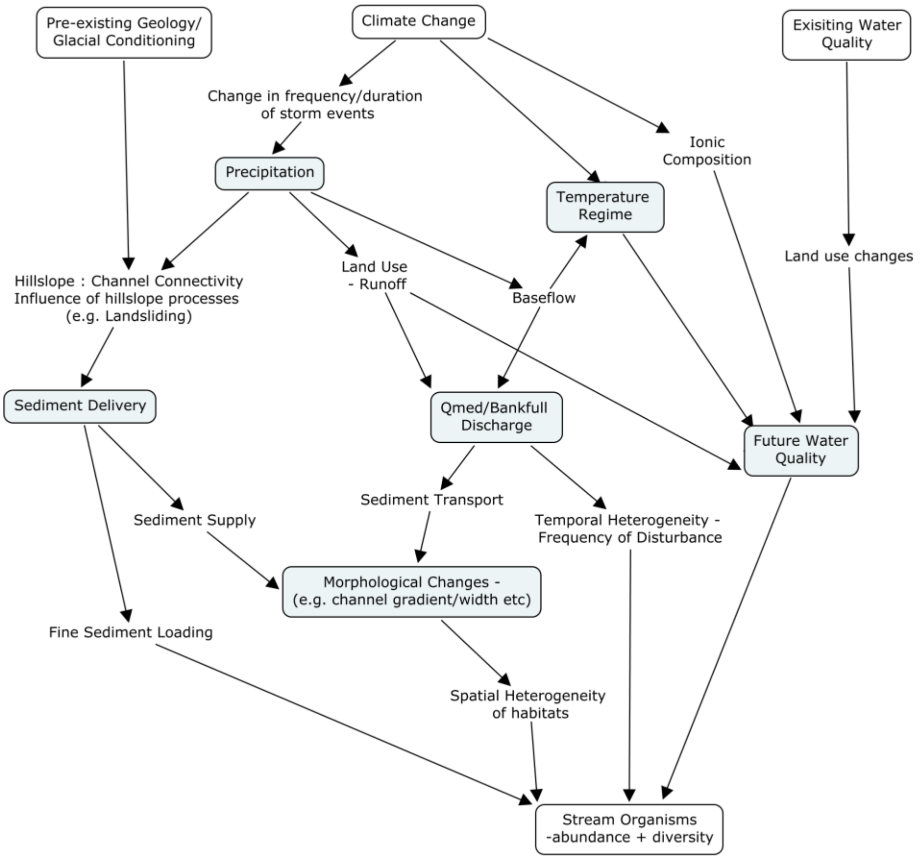


Figure 2-1: Conceptual diagram showing the key controls placed on the abundance and diversity of stream organisms and how those controls interact.

At the broadest scales, temperature plays a role in controlling the distribution of vegetation, potentially altering flood hydrographs (Beven *et al*., 1984) and runoff erosion rates (Douglas, 1967), and in limiting the rate of weathering and therefore sediment supply to the stream network (Walker *et al*., 1981). Water temperature has a limited effect on physical habitat but it is closely linked with air temperature in almost all streams (Webb *et al.*, 2003), with only those supplied solely from groundwater sources having weaker relationships to ambient air temperatures. It is also controlled by the amount of channel shading by vegetation, which again is ultimately a result of climate controlled vegetation patterns (Stott and Marks, 2000).

Humans have an ever increasing impact on physical habitat, with densely populated, developed nations, such as the UK, particularly affected. Channels are directly impacted by extensive modifications (e.g. >40% by length directly modified in the UK; Seager *et al*. 2010), largely for flood control or impoundment, whilst changes in catchment land use (e.g. urbanisation, deforestation or intensive agriculture) alter the runoff of water, sediment and pollutants (Coe *et al*., 2009).

Geomorphological classifications of physical habitat first began to make the link between processes and observed habitat types, with the seminal study of Montgomery and Buffington (1997) creating a classification of mountain stream morphologies based on reductions in slope and a change from supply to transport limited morphologies. Montgomery *et al.* (1999) linked these channel classifications to the distribution and abundance of salmonid spawning, hypothesising that channel type, based on bed slope, limits available spawning area. This early work was further supplemented by Benda *et al.* (2004) who showed that the interaction between river networks and catchment disturbances imposes a spatial and temporal pattern on river habitat distribution, namely via tributary effects whereby large volumes of sediment, delivered by hillslope-connected tributary channels, create changes in channel slope and morphology at junctions with high order trunk channels. Their work also showed that drainage density plays an important role in the routing of sediment through a channel network. Higher drainage densities create a greater proportion of high order channels that are likely to be uncoupled from hillslope processes and are typically transport limited, similar to many catchments in the UK. Wohl (2005) explored the relationship between reach scale morphology and physical controls across a large dataset finding that channel slope, width and sediment size are the key controls placed on reach scale morphology at large spatial scales. Wohl and Merritt (2008) again used a large dataset of mountain streams to understand the differences between the channel types first proposed by Montgomery and Buffington (1997). The patterns between step-pool, pool-riffle and plane-bed channels indicated that physical form is adjusted to maximise flow resistance and reduce downstream variability in flow resistance. These classifications form the basis for linking organisms and habitats.

2.3 Different approaches for linking physical habitat and species' distributions

Researchers from both stream ecology and fluvial geomorphology have investigated the relationships between organisms and physical habitat, yet few have incorporated the other's discipline into their work, leading to limited success. There is a long history of attempts to quantify the habitat preferences of organisms residing in the channel bed, with some of the earliest being by Percival and Whitehead (1929) who quantified organism richness in different channel beds in Yorkshire. Hundreds of subsequent studies have looked at the local influence of substrate composition, channel gradient or flow velocity on stream organisms (e.g. Riley, 1921; Brusven and Prather, 1974; Reice, 1980; Hawkins *et al.*, 1982; Lammert and Allan, 1999). Some of these have described physical habitat in great detail, such as Beauger *et al.* (2006) who studied the relationship between velocity, depth, substrate and macroinvertebrate community structure and Lancaster and Hildrew (1993) who investigated the micro-distribution of benthic macroinvertebrates in relation to flow refugia.

In contrast to detailed studies of individual taxon habitat requirements, Vannote *et al* (1980) took a larger scale view of these relationships by proposing the river continuum concept (RCC) which speculated that the distribution and abundance of stream organisms changed downstream in an orderly sequence based upon increasing discharge and subsequent morphological changes. This was one of the first attempts to produce a general, conceptual model linking physical process, habitat and organisms, and produced testable predictions. The RCC also stimulated several subsequent models. Frissell *et al.* (1986) proposed that river habitats were organised in a hierarchy based on the spatial and temporal arrangement of physical network features and the pool of species available. Montgomery (1999) proposed the notion of process domains, regions within river networks where similar geomorphic processes produced similar physical habitat, rather than the simple trends in habitat envisaged by the RCC. These have been joined by others (e.g. Benda *et al*., 2004;

Thorp *et al*., 2006): what unites them is an attempt to develop a conceptual framework in which mechanistic links between geomorphology and ecology can be made.

Many of the conceptual models that have been developed highlight the important role played by disturbance in determining riverine biodiversity. Disturbance regimes (e.g. floods, landslides, fires) are seen as being important in delivering sediment and woody debris to low order channels, which in turn help to form the physical habitats used by organisms (Benda *et al*., 1997a; 1997b). There is a general consensus that the dynamic interplay between sediment calibre, supply and transport, which controls the distribution of bedforms and the disturbance regime, is the key driver of spatial and temporal physical habitat patches (Poff and Ward, 1990; Townsend and Hildrew, 1994; Wu and Loucks, 1995). Disturbance in an ecological sense refers to events that remove organisms and free up resources such as space, and have long been considered an important factor structuring communities (e.g. Connell, 1978; Townsend and Hildrew, 1994; Miller *et al*., 2010). From the perspective of physical habitat, a disturbance is an event which mobilises sediment within the channel, leading to the building and renewal of bedforms, such as bars, riffles or pools (Poff and Ward, 1990; Benda and Dunne, 1997b). The two definitions may have different thresholds at which an event is termed a disturbance but both require the detachment and movement of either organisms or sediment from the channel bed, a requirement that can be assumed to occur at given shear stress thresholds of incipient motion of the channel bed (Schwendel *et al*., 2010a).

Alongside disturbance, a second common theme is the importance of scale in understanding organism-habitat relationships (Vannote *et al*., 1980; Frissell *et al*., 1986; Poff *et al*., 1997) and this includes combining measurements of physical features and stream organisms in a channel. Interactions range from a single particle or organism in the riverbed to distributions across multiple catchments (Frissell *et al*., 1986). Selecting the relevant scale when studying the relationship between physical features and biota is dependent on the intended use of such a study and the features in question (Wiens, 1989). When looking at the preferred habitat of benthic organisms it is likely that physical features at a patch scale and smaller would be most relevant to the study, whereas the study of community level distributions or organisms with a higher mobility (e.g. fish) is more likely to be conducted at a reach scale or greater in order to capture enough morphological variability. As most restoration and management efforts seek to improve the diversity of physical habitat at a reach scale (>100m) a wider appreciation of community level interaction with physical habitat is required if valid predictions of improvements to the biodiversity of a reach are also to be made.

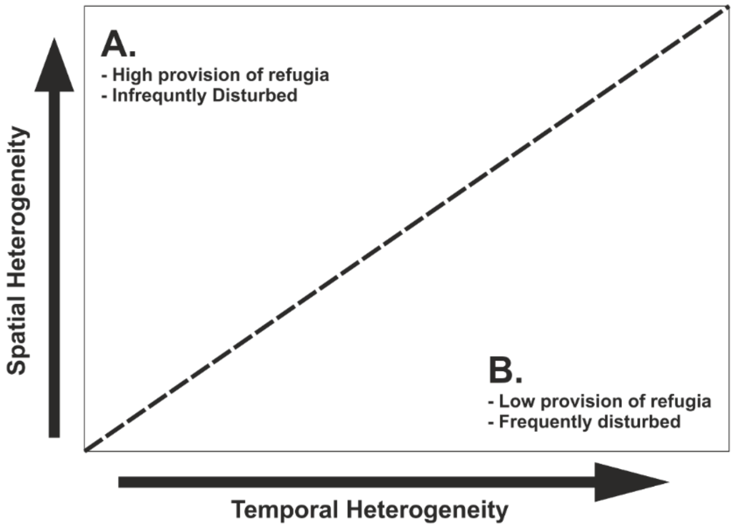
Many studies linking organisms such as macroinvertebrates or fish to physical habitat focus on the ‘patch’ scale. Padmore (1998) introduced the term ‘physical biotopes’ to describe reaches with a given flow type, as derived from substrate and hydraulic parameters, thereby providing an explicit link between physical process and habitat at an ecologically relevant scale. Kemp *et al.* (2000) furthered this idea by linking flow biotopes (hydraulically defined) and ‘functional habitats’ (biologically defined) using the Froude number. Velocity and depth, the main components of the Froude number, were proven to be the main differentiators between biotopes with a clear division between fine and coarse bedded streams and their associated macrophytes. Newson and Newson (2000) discussed the link between physical biotopes and macroinvertebrates using flow type and how both ecologists and geomorphologists work at similar scales within hierarchical systems that are not yet linked. Subsequent work has shown that distinct assemblages of organisms are found in different biotopes (e.g. Armitage and Cannan, 2000; Dallas, 2007; Demars *et al.* 2012). Biotopes provide a better definition than patch or reach as they have a better conceptual underpinning when linking process and habitat.

Ecologists have also been considering habitat-organism interactions at scales similar to biotopes. Statzner *et al.* (1988) speculated that by understanding the conditions near the river bed, given by measures such as Froude number, Reynolds number and shear velocity, which reflect the initiation of sediment transport that renew and build physical habitat, it should be possible to predict the macroinvertebrates that are likely to be present. Subsequent small-scale observational studies have provided evidence to support this by linking trait categories to local flow hydraulics (Lamouroux *et al.*, 2004; Tomanova and Usseglio-Polatera, 2007). Demars *et al.* (2012) found that Froude numbers correlated well with expected trait assemblages in several UK rivers and biotope type explained 40% of the variability seen in trait distributions. Experimental evidence has also supported this, such as McCabe and Gotelli (2000) who discovered that species abundance was lower but richness was higher in an experimentally disturbed stream, whilst Effenberger *et al*. (2008) demonstrated different local macroinvertebrate community compositions between disturbed and undisturbed areas. These studies show the potential for understanding how the habitat preferences of organisms relate to sediment transport and supply and is clearly key to developing knowledge of how macroinvertebrate communities interact with their physical environment and its disturbance regime. Pedersen and Friberg (2007) found substantial variations in invertebrate abundance between riffles judged to be of the same unit, as further investigation revealed physical differences in riffle consolidation and substratum heterogeneity. These findings question whether a morphological unit, for example a pool-riffle sequence, provides a valid scale when assessing invertebrate communities as significant local scale variation exists. Nevertheless, this shift towards more general models of habitat structure/formation, which minimise the reliance on simplified classifications of habitat units and which are based in well-understood process-based theory are likely to provide a better understanding of the links between geomorphology and ecology, and one that should be more reliable to predicting the effects of environment change (Vaughan *et al*., 2009; Urban *et al*., 2016).

2.4 The role of species traits

An important development in deciphering the links between physical habitat and macroinvertebrate communities has been the widespread adoption of species' ecological traits alongside traditional, taxonomic descriptors of communities such as species richness or abundance (Townsend *et al*., 1997; Lamouroux *et al*., 2004; Bonada *et al*. 2007). The use of traits, such as reproduction method, lifespan, size, mobility and dispersal, make ecological links more explicit and also allow an evolutionary perspective. Southwood (1977, 1988) was the first to introduce the idea that physical processes acting at a large spatial scale create a template of habitat patches within which organisms evolve life history strategies. Further studies developed this idea in rivers by adding scales of spatial and temporal variability driven by habitat heterogeneity (Townsend, 1989; Poff and Ward, 1990) and frequency of disturbance (Townsend and Hildrew, 1994). Townsend and Hildrew (1994) provided a conceptual model of how species traits may relate to physical habitat by plotting the distribution of traits on axes of: i) habitat heterogeneity, indicating the provision of refugia from disturbance, for which biotope diversity can be used as a proxy, and ii) disturbance frequency (Figure 2-2). It was proposed that low habitat heterogeneity and frequent disturbance would select for species displaying traits required to survive in disturbed system and the resultant physical habitat itself (e.g. short lifespans, fast reproductive cycles; Figure 2-2). Field validation of these predictions has been provided by a range of studies. Bonada *et al.* (2007) found evidence for species with particular traits existing in intermittent and ephemeral (frequently disturbed)

Mediterranean streams, whilst species traits became less closely coupled to physical habitat features in less frequently disturbed systems with a greater provision of refugia. Townsend *et al*. (1997) found that riverbeds disturbed more frequently by high flows contained a higher percentage of taxa with traits indicative of resistance across a dataset of 54 streams in New Zealand, whilst Lamouroux *et al*. (2004) found that invertebrate traits including size and body form were correlated with hydraulics in 38 river reaches in France.



Species Trait	Area A	Area B
Minimum age at reproduction	Old-young	Young
Descendants per reproductive cycle	Few-many	Many
Reproductive cycles per year	<1-several	Several
Potential Life Span	Long-short	Short
Potential size	Large-small	Small
Total reproductive cycles per individual	Many-one	Few-one
Parental Care	Present-absent	Absent
Reproductive technique	Diverse	Single individual produces offspring
Annual P/B ratio	Low-high	High
Attachment	None-firm	Firm
Body flexibility	Inflexible-flexible	Flexible
Body form	Diverse	Streamlined-flattened
Inundation tolerance	Absent-present	Present
Desiccation tolerance	Absent-present	Present
Mobility	Immobile-mobile	Mobile
Relatively invulnerable life stages	Absent-present	Present
Potential for Regeneration	Absent-present	Present

Figure 2-2: Reproduced from Townsend and Hildrew (1994). Conceptual diagram of the relationship between species traits and spatial heterogeneity, the provision of refugia and temporal heterogeneity, the disturbance frequency. The table shows the expected range of traits present at either Area A or B.

The relationship between species traits and environmental conditions has been shown to be complex as species possess multiple traits that can be impacted in different ways by disturbance, making species relations to single environmental gradients often appear decoupled when in reality there is a relation (Poff *et al.*, 2006). They also showed that many traits are readily adaptable to deal with disturbance (e.g. size at maturity), further complicating their application (Poff *et al*., 2006). A need for a framework that considers multiple traits along with multiple environmental gradients has been discussed by both Poff *et al.* (2006) and Verberk *et al.* (2013) but progress has been slow due to the complexity of trait-environment interactions. For example, Lamouroux *et al.* (2004) found that macroinvertebrate traits including body size, attachment mechanism, feeding habits, lifespan and reproduction/dissemination strategy all significantly correlated with physical habitat variables in two catchments in France. Similarly, anthropogenic modification of the river environment can affect many traits simultaneously (e.g. through impacts of fine sediments; Larsen and Ormerod, 2010). Mouillot *et al.* (2013) developed a generic framework for relating traits to disturbance, by proposing an approach that identifies both winner and loser species due to disturbance. Trait approaches have shown large potential, are clearly linked to biological processes and are benefitting from recent conceptual developments (e.g. Mouillot *et al*., 2013) but there is still more that can be explored.

2.5 Methods for predicting bedform distribution and bed disturbance

Traditional ecological models are static and correlative, making them poor at extrapolating beyond the conditions under which they were calibrated (Urban *et al*., 2016). As changing conditions (e.g. climate, land use) are a key component of current and future interactions between physical habitat and ecological function, process-based models that capture these changes are needed (Vaughan *et al*., 2009). To address the specific aims of this thesis, a process-based approach that captures the key controls on sediment transport and physical habitat distribution in alluvial rivers is required. These controls, primarily the flow conditions of the river and the nature (i.e. size and shape) of the river sediment (Shields, 1936; Andrews, 1983; Parker, 1990), are captured by various approaches that are capable of determining the onset of sediment transport (Figure 2-3). An approach is needed that can be applied at a national scale and is compatible with existing datasets, which are typically limited in their information of channel morphology, sediment and flow (Figure 2-3). In the absence of reliable measurements of the processes governing bedform distribution and disturbance, a simple means of estimating sediment transport is needed.

Sediment transport equations provide a well-understood, detailed method for studying the onset of riverbed disturbance but require detailed information on flow velocities and/or sediment composition and as such, can only be applied at scales where the data can be obtained within time and cost constraints: this typically limits them to reach scales or less (Ackers and White, 1973; Yang, 1976; Mueller *et al*., 2005). Although these mechanistic approaches could provide new insights into geomorphology-ecology interactions, they are far too complex to be applied generally at a national scale.

Stream power has been widely used at catchment or regional scales to predict zones of erosion and deposition (e.g. Newson *et al*., 1998a; Knighton, 1999; Parker *et al.*, 2011; Bizzi and Lerner, 2012) and channel features (e.g. Gurnell *et al*, 2010; Vaughan *et al*., 2013). It has modest data requirements and provides a simple means of estimating the energy available to do work in the channel, based on channel slope, discharge and, when calculated per unit area (termed specific stream power), channel width (Bagnold, 1977). It has grown in popularity as the spatial scale of studies has increased with the advent and now wide use of Digital Terrain Models (DTM's) for catchment studies (Knighton, 1999; Bizzi and Lerner, 2012; Phillips and Desloges, 2013). Whilst stream power provides a rapid, simple means of estimating sediment transport capacity it does not include any measurement of the sediment being transported through a reach and as such cannot reliably predict sediment transport rates. Parker (2011) attempted to improve the physical basis for using stream power by calculating dimensionless critical stream power, based on Einstein's (1950) dimensionless sediment transport equation, finding that it corresponded well with sediment transport rates measured in laboratory flumes and empirical evidence that predicted critical unit stream power to be proportional to $D_i^{1.5}$ (D_i = size of mobilised particles in mm; Petit *et al.*, 2005). The inclusion of a measure of bed grain size in the dimensionless critical stream power equation provides a simple means of estimating whether the material making up the channel bed is in motion at the given stream power, essential in predicting sediment transport.

Another potential method of assessing the sediment transport capacity of a river reach is by using the Shields Regime Diagram (Shields, 1936). The diagram estimates the mode of sediment transport experienced by a channel bed based on flume studies of particle motion and suspension. Two axes are combined to provide this information. The first axis is the particle Reynolds number, which is effectively a measure of the mean sediment size of the riverbed. The second axis is dimensionless shear stress, a measure of the propensity for movement of sediment on the riverbed, which is calculated using flow depth, channel gradient and mean sediment size (Shields, 1936). Together, these axes differentiate between different geomorphic processes occurring at each location, chiefly bed-load and suspended-load transport, and the range of substrate sizes present in the riverbed, which in combination have been shown to control alluvial bedforms (van Rijn, 1984; Buffington and Montgomery, 1997).

The Rouse number, the ratio of settling and shear velocities, provides an alternative means of finding the mode of bed material transport at a site. Dade and Friend (1998) introduced the terms competence and capacity to show that channels exhibit different sediment transport modes based on sediment supply-transport ratios. Competence is a measure of the largest grain size the can be mobilised by a flow, whilst capacity is a measure of the sediment capacity of a stream that is not limited by sediment supply. They showed that abrupt changes in the downstream fining of bed substrate represented the point at which channels switched transport modes, based on the Rouse number. The Rouse number is not used in the thesis as it has many similarities to the thresholds of bed and suspended load transport used in the Shields diagram, the chosen method for quantifying the mode of transport and disturbance in Chapter 4.

These different approaches are used at varying times in the following chapters largely depending on their data requirements in relation to the available datasets. Chapter 3 uses specific stream power to predict the distribution of bedforms across the UK. Specific stream power was chosen due to its low data requirements and previous performance in predicting channel features (Vaughan *et al*., 2013). Chapter 4 uses the Shields regime diagram to link invertebrate community diversity and function to the distribution of physical habitats and disturbance. The Shields diagram was selected due to its well-defined association with physical process (i.e. bed load and suspended load transport) and its relative simplicity in comparison to more rigorous methods for estimating sediment transport. Chapter 5 uses critical specific stream power to estimate when disturbance occurs across time-series flow data from gauging stations. It was selected again due to its low data requirements and its proven relationship to gravel-bed rivers, which are common across the UK. Chapter 6 compares the use of these methods in the previous chapters and discusses their potential applications in river management.

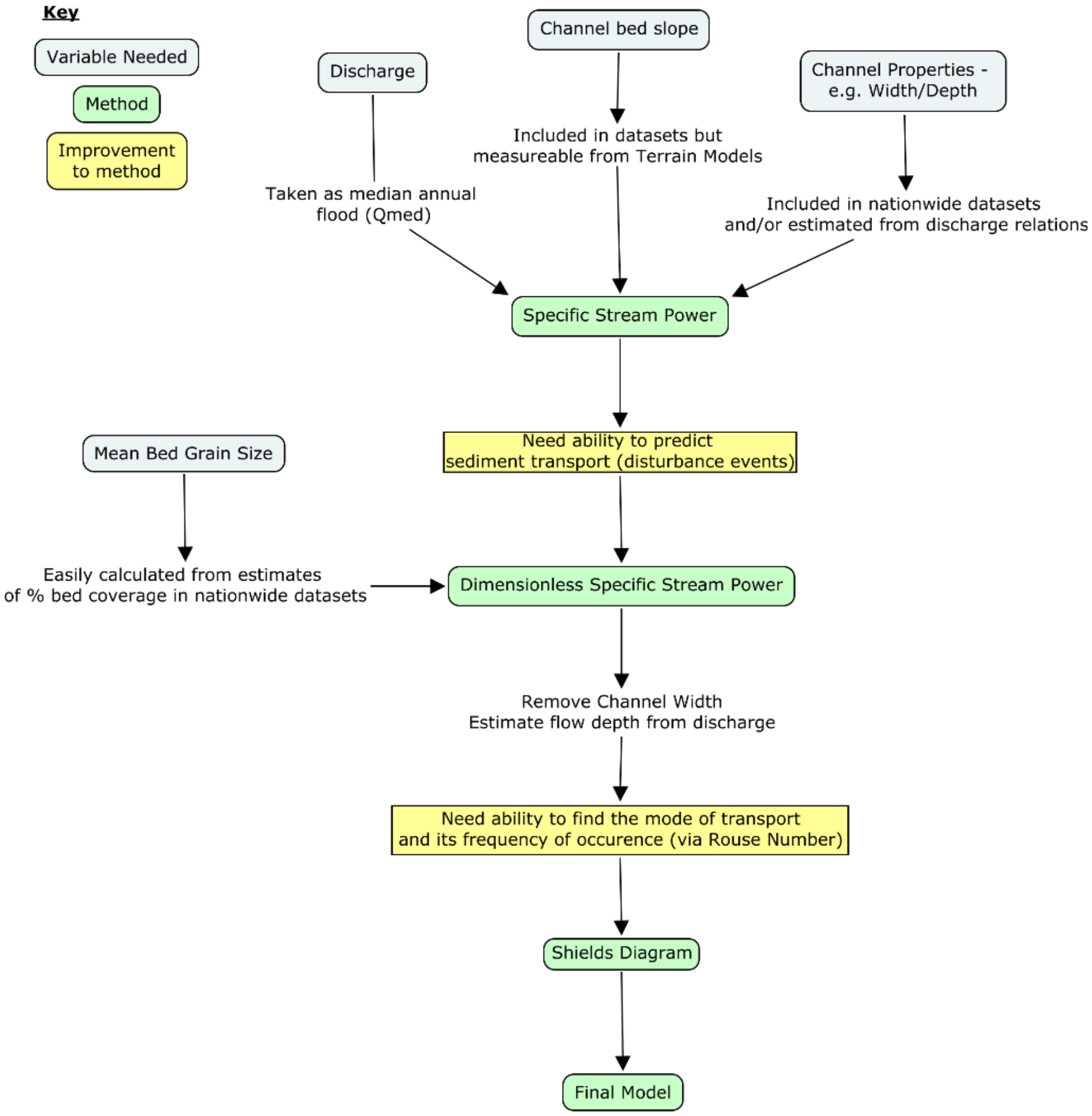


Figure 2-3: A conceptual diagram of the progression of development of a simple method for predicting the frequency of disturbance at a location. Explanatory power, in terms of process, is increased with the addition of the mode of sediment transport. The simple variables required for each method are included.

2.6 Climate change and the need for better prediction

The evidence for future climate change is now unequivocal and much of the debate around the river environment is centred on whether we are already beginning to be impacted by climatic changes and what future predictions can be made (Coulthard *et* *al*., 2012; Kendon *et al*., 2014; Markovic *et al*., 2014). Predictions of climate change impacts on the UK have been refined over the past two decades and now provide detailed information about the total amount, frequency and intensity of precipitation events (e.g. Murphy *et al.*, 2009), which in turn will affect the hydrological cycle, sediment transport and disturbance regimes in the fluvial network. Despite these advances, there is still uncertainty about the impacts on the flow regime. In many temperate regions of the world, there has been a general assumption that flood frequency and magnitude will increase, but current evidence suggests that only flood frequency and timing are changing, whilst magnitude remains the same (Mallakpour and Villarini, 2015; Bloschl *et al*., 2017; Wasko and Sharma, 2017).

Across the catchment and over longer timescales, the delivery of sediment to the channel is likely to increase as more frequent and severe storms are predicted to trigger more landslides and increase sheet runoff (Wilby *et al.*, 1997), a principal delivery mechanism of fine sediment to the channel. Land cover changes, which in turn may be a response to changing climate, could act to exacerbate this increase (Coulthard *et al*., 2012). Much of this relates to intensive farming practices, which increase soil compaction and remove natural vegetation that can store water and retain fine sediment (i.e. topsoil), thereby increasing sheet runoff (Evans *et al*., 2016). A continued growth of urban areas, with extensive impermeable surfaces, would also accelerate runoff. The increasing delivery of fine sediments is recognised as a major stressor on riverine communities (e.g. Wood and Armitage, 1997; Larsen and Ormerod, 2010; Kemp *et al*., 2011; Jones *et al*, 2014).

These changes in streamflow and sediment supply are likely to lead to morphological changes in channels over coming decades. Both short and long term changes are likely as the shape, gradient and sediment composition of channels respond to new environmental conditions. A better understanding of the relationship between these hydromorphological changes and community composition and function is key to making future predictions of climate impacts on freshwater communities. Critically, the novel conditions generated by climate and land use changes are likely to challenge traditional approaches to predictive modelling, especially when the impacts of different stressors may interact (Piggott *et al*., 2015). Despite these challenges, prediction will be as least as, if not more, important than it has been in the past. To address the shortfall of traditional predictive models, reliable, accurate, process-based models of river channels and organism distributions and function are needed (Urban *et al*., 2016; subsequent chapters of this thesis).

2.7 Nationwide datasets and the emergence of river restoration in the UK

The greater availability of remotely sensed imagery and increased computing power has driven the collection of physical variables across larger spatial scales over the last decade (Carbonneau *et al*., 2012). This move to a catchment scale approach to environmental management across Europe has largely been driven by the Water Framework Directive (2000/60/EC). The Directive places emphasis not just on improving the ecological and water quality of freshwater systems but also on achieving ‘good hydromorphological status’. Improvements in water quality over recent decades have highlighted the impact of physical modification on the hydromorphology of freshwater systems (Vaughan *et al.*, 2009). A slew of new restoration techniques have followed, focussing on restoring river reaches to a ‘natural’ state often by techniques such as meander reintroduction, installation of large woody debris (LWD) or by flow barrier removal (Newson and Large, 2006). To fully assess whether these new approaches are appropriate for a river reach there is an urgent requirement for tools that place a reach within its larger catchment setting with regards to habitat type and sediment supply and transport (Everard, 2004). This effort has led to a number of papers attempting to classify channel and habitat types based mostly on rapid GIS-derived variables and then linking the classification with ecological impacts. For example, May and Lisle (2012) used a digital elevation model to assess the availability of salmonid habitat, based on channel slope classifications, across multiple catchments in the Pacific Northwest. Richards *et al*. (1997) found that GIS-derived reach scale variables (e.g. cross-sectional area, percentage of fines) were strongly correlated with invertebrate life-history traits, whilst catchment scale variables (e.g. geology) were less well correlated, whilst Bizzi *et al*. (2016) used various remote sensing techniques to characterise the hydromorphological properties of river across Europe.

The development of catchment scale tools requires large, often nationwide, datasets to understand the range of channel types and physical habitats that are present. Many studies focus on local scale classifications and often overlook their context within a catchment system (Everard, 2004), especially when considering their role in sediment supply and transport. The UK may be unique in having a collection of large scale databases of river attributes that has been ongoing since the 1990s (Vaughan and Ormerod, 2010). In addition to routine water quality and biological (primarily macroinvertebrate) sampling, the Environment Agency's River Habitat Survey (RHS) database has assembled >24,000 sites spanning a period since 1994. RHS is a simple tool to quickly characterise the physical structure of rivers as a series of 500m survey reaches, with information recorded for the dominant bed/bank materials, flow types, instream and riparian vegetation and simple morphological attributes such as presence/absence of bedform features, bank profiles and any artificial features or modifications to the channel (Raven *et al*., 1997; Environment Agency, 2003). Many studies have utilised the RHS database since its creation (e.g. Jeffers, 1998; Hastie *et al*, 2003; Orr *et al*., 2008; Bizzi and Lerner, 2012) and the UK-wide coverage of its two national baseline surveys (1994–6 and 2006–8; Seager *et al*., 2010) have greatly increased its potential usefulness when used alongside GIS-derived variables.

RHS has supported efforts in the UK, and other parts of Europe, to improve the understanding of the links between physical channel processes and biotopes (Newson *et al*., 1998b). Jeffers (1998) ordinated the first RHS baseline based on the map-derived variables of altitude, slope, distance from source and height from source, finding that physical habitat features could be predicted using only these variables. Vaughan *et al.* (2013) built on this approach, adding a number of GIS-derived variables to the method, improving the predictive capability of the ordination. It was found that a combination of specific stream power and catchment area were robust predictors of the physical attributes of channels. Another approach is to look at species specific distributions across Britain in relation to physical habitat features from the RHS database, as has been completed for organisms including bats (Langton *et al.*, 2010), river birds (Vaughan *et al.*, 2007) and macro-invertebrates (Naura and Robinson, 1998; Hastie *et al.*, 2003; Vaughan and Ormerod, 2012). Other studies have taken parts of the RHS database in an attempt to either classify channels based on flow biotopes (Harvey *et al.*, 2008a), stream order (Orr *et al.*, 2008), stream power (Bizzi and Lerner, 2012; Vaughan *et al.*, 2013) or sediment transport regimes (Parker *et al.*, 2012). RHS has also been used to study the links between physical channel attributes and rock type (Harvey *et al.*, 2008b), pool-riffle spacing (Emery *et al.*, 2007) and aquatic plant morphotypes (Gurnell *et al.*, 2010). Bizzi and Lerner (2012) utilised GIS-derived controls such as channel slope, specific stream power and floodplain extent along with data describing the physical habitat types, from the RHS database, to identify typologies of channel along the River Lune in north England. This wide range of studies demonstrates the value of large scale hydromorphological datasets, such as RHS, particularly for planning targeted efforts at a catchment or national scale.

2.8 Conclusions

Habitat-organism interactions in rivers are governed at the largest scales by climate, geology and, increasingly, human actions. These broad controls are imparted on rivers via trends in water chemistry, flow regime and sediment supply/transport, which in turn determine the conditions that are tolerated by organisms which specific suites of traits. Studies of the habitat preferences of freshwater organisms have a long history (Percival and Whitehead, 1929) but have remained restricted to either to small scales (i.e. several organisms within a river reach) or to conceptual studies of larger scale trends (Vannote *et al*., 1980; Townsend and Hildrew, 1994), largely due to data collection constraints. The advent of open datasets and rapid data collection methods (e.g. LiDAR) now provides greater opportunities for the large scale collection of geomorphic data (Carbonneau *et al*., 2012). Traditional ecological studies of habitat-organism interactions use static, correlative models that are considered to be poor at extrapolating to environmental change (e.g. in climate or land use). As robust predictions of these changes continue to gain importance, models grounded in process-based theory, which minimise the reliance of simplified classification of habitat units may offer a better approach (Urban *et al*., 2016).

In recent years, widespread efforts have taken place across freshwater sciences to promote studies with a multidisciplinary, holistic approach (Vaughan *et al*., 2009). A push from legislation (e.g. the WFD) has seen river management, particularly across the UK and continental Europe, transition to a catchment based approach (delivered via River Basin Management Plans). Despite this, the understanding and tools required by river managers to robustly plan interventions at this scale are lacking and efforts to combine the traditionally separate disciplines of hydrology, geomorphology and ecology are urgently needed (Vaughan *et al*., 2009). This thesis aims to be part of those efforts by contributing to our understanding of geomorphology-ecology interactions, with particular focus given to the role of bedform distribution and disturbance in structuring ecological communities.

The UK is uniquely positioned to address these research gaps as it has possibly the densest, longest-term record of flow, chemistry and biology monitoring in the world. These often undervalued datasets enable studies of geomorphological-ecological interactions across large spatial scales and relatively long timespans (>10 years). Here, I make use of different collections of five of these datasets as the basis of each analytical chapter.

3 Controls on the spatial distribution of bars within the alluvial rivers of Great Britain

3.1 Abstract

Bars function as important in-river sediment stores that can significantly alter channel form as well as acting as unique transitional habitats that alternate between terrestrial and fluvial realms. Despite considerable effort to explain the controls on bar formation at local reach scales, our understanding of such controls at network and regional scales has been limited until recently by the paucity of catchment-scale observations. Such lack of understanding could limit the effectiveness of river restoration strategies that are increasingly being implemented in catchments across Europe. This chapter utilized 1480 River Habitat Survey sites across Great Britain to model the spatial distribution of bars, using specific stream power at bankfull discharge (ω), coupled with mean riverbed grain size, to reflect the balance between river energy and relative riverbed mobility. Bars were most commonly found in gravel-bed rivers where $\omega > 30$ W m^{-2} at bankfull discharge, conditions typical of upland rivers found in northern and western Britain. Bar prevalence was overestimated in channelized rivers, likely due to increased flow velocities inhibiting the development of depositional bedforms or the removal of coarse material for flood control/navigation, and in chalk geologies, likely due to their uniquely dampened flow regimes. Prevalence was underestimated in small, lowland rivers with cohesive riverbeds and abundant channel vegetation. My data helps to identify key elements in river and catchment management that must be addressed if bars are to be restored and maintained in British rivers.

3.2 Introduction

Bars are a basic morphological unit of alluvial channels, forming part of the ubiquitous riffle-bar-pool sequence that provides regularity to the channel planform, most obviously in rivers with alternating bars, meander bends or braids (Leopold and Wolman, 1957; Kleinhans, 2010). They are key in-channel sediment storage features (Benda and Dunne, 1997), play an important role in channel dynamics by dictating the pattern of bank erosion and channel planform evolution (Kleinhans, 2010), and also create unique habitats for a range of organisms including birds, invertebrates and macrophytes (Eyre *et al*., 2001; Madsen *et al*., 2001). Our current understanding of the controls on the spatial distribution of bars is largely split between theoretical knowledge of the processes that build and sustain bars (e.g. river planform, sediment transport and supply) and applied knowledge of where human-induced changes in flow and sediment regimes (e.g. via channelization) has led to the demise of bar forms. Here, we aim to discover the major controls on the spatial distribution of bars, at a scale relevant to river management, by comparing predictions of bar occurrence from a statistical model based on river process with real-world observations of bar occurrence in often heavily-managed river systems.

Bars are commonly classified into point, alternate and mid-channel according to differences in their mechanisms of formation and position within the channel. They can be split into ‘free’ and ‘forced’ depending on their ability to migrate downstream (Seminara and Tubino, 1989; Kleinhans, 2010). Free bars form in a straight channel due to the instability of turbulent flow creating perturbations (bars) in the erodible channel bed (Tubino *et al*., 1999). Both alternate and mid-channel bars can form in this way when a threshold width-to-depth ratio is exceeded (Kleinhans, 2010), although the latter also requires a high relative sediment supply (Hooke, 1986; Kleinhans and van den Berg, 2011). Mid-channel bars often form where abrupt increases in channel width and sediment supply occur, such as at confluences or where rivers exit mountain ranges (Leopold and Wolman, 1957; Ashmore, 1982, 1991; Ashworth, 1996). High flow events can also rapidly increase channel width in portions of the river network, promoting bed-material deposition and mid-channel bar building (Hooke, 1986; Carson and Griffiths, 1987; Friedman *et al*., 1996; Madej and Ozaki, 1996). Forced (or fixed) bars are formed by either (1) variations in local channel width, such as around fixed obstructions (*e.g*., a large boulder/fallen tree) or at confluences (Kleinhans, 2010) or (2) in meander bends where channel curvature forces the flow to deposit material on the inside of the bend. Point bars, which are formed when secondary flow currents stack bed-material up on the inside of a meander (Nanson, 1980; Dietrich and Smith, 1983), are the most common example of forced bars.

The mechanism of transition from a channel with free alternate bars to forced point bars is widely debated. Bar theory suggests that free bars promote bank erosion, increasing channel curvature until the bars become fixed, whilst bend theory suggests that fixed bars are induced by channel curvature (Blondeaux and Seminara, 1985; Tubino and Seminara, 1990; Tubino *et al*., 1999). Seminara and Tubino (1989) showed that in a straight river, alternate bars migrate fast enough to uniformly erode the banks, widening the channel and eventually forming mid-channel bars, which suggests that another factor, such as bank erodibility, controls a change from a straight to meandering channel. Vegetation or cohesive sediment may act to decrease bank erodibility, with straight channels that have stronger banks typically becoming narrower and deeper (Hey and Thorne, 1986; Soar and Thorne, 2001), potentially promoting localized bank erosion that leads to meandering. Channels with weaker banks become wider and shallower, developing a braided planform (Parker, 1976; Xu, 2002).

Advances in our understanding of the controls on bed-material routing through the river network and of the processes underlying bar formation have been made through field (Lewin, 1976; Nanson, 1980; Hooke, 1986; Church and Rice, 2009), numerical modelling (Lisle *et al*., 2000) and laboratory–based (Ashmore, 1991; Lisle *et al*., 1991) studies. Despite these advances, relatively little attention has been given to bar distribution at the network-scale with most studies instead focusing at the reach scale, largely due to data constraints as network-scale analysis is too large for any field campaign and beyond current remote sensing capability (Legleiter *et al*., 2004; Carbonneau *et al*., 2012). However, river management in much of Europe is now planned at the catchment scale and an understanding of the distribution of bars at a similar scale is needed by river managers in order to: (1) target restoration efforts at river reaches where bar restoration would be sustainable; (2) monitor parts of the network where significant accretions of sediment are expected, as these may increase flood risk (Lane *et al*., 2007); and (3) mitigate and plan for future changes in river morphology (e.g. due to climate or land use change) that may reduce bar habitat, impacting upon freshwater organisms and the key ecosystem services they provide (Macklin and Lewin, 2003; Coulthard *et al*., 2012).

In this study, we aim to quantify the conditions under which point, alternate, and mid-channel bars develop in rivers across Great Britain to gain insight of the controls on bedform habitat features at the scales at which river management is now planned. The presence of different bar types was obtained from 1480 semi-natural and modified rivers with River Habitat Survey (RHS), the standard method for recording river physical habitat in England and Wales (Seager *et al*., 2012). We developed a statistical model that couples specific stream power, a measure of a river's capacity to perform work on its bed and banks (or modify the channel form through sediment transport), with mean riverbed grain size to reflect the balance between this energy and the relative riverbed mobility. Specific stream power has been used widely in sediment transport studies (Bagnold, 1977; 1980) to assess channel patterns (Chang, 1979; Nanson and Croke, 1992; Van Den Berg, 1995) and to predict channel features, (Bizzi and Lerner, 2012; Vaughan *et al*., 2013). We offer an explanation for the apparent threshold value of specific stream power required for bar occurrence and assess shortfalls in the model, accounting for the influence of catchment geology, channelization and emergent vegetation upon bar formation.

3.3 Methods

3.3.1 RHS

The RHS was developed in 1994 to characterize the physical character and quality of river habitats across the UK (Raven *et al*., 1998). It has since been used at over 25,000 sites in the UK and elsewhere across Europe. An individual RHS involves a survey of a 500-m length of channel with ten *spot-checks* that record features at 50-m intervals and a *sweep-up* section that records the presence, absence, or extensiveness (≥33% of channel length) of features within the reach (Raven *et al*., 1998). Features include the type and extent of channel vegetation, any modifications to the channel and the dominant substrate type. Channel dimensions are also measured on a straight, uniform section, preferably across a riffle, at each survey site (Raven *et al*., 1998). Finally, each RHS location has an accompanying estimate of channel slope, measured from 1:50,000 scale maps over a 1-km length centred on the mid-point of the study reach (Raven *et al*., 1998). Map-derived channel slope corresponds well with field measurements (Montgomery *et al*., 1998) and is often more accurate than slope derived from digital elevation models due to errors in channel length estimation as a result of pixel size (Clarke *et al*., 2008; Fisher *et al*., 2013).

Point, alternate (side) and mid-channel bars were identified and recorded separately in the RHS, with point bars located on the inside of distinct meanders, alternate bars attached to the bank but not located on the inside of distinct meanders, and mid-channel bars detached from both riverbanks with elevations below bankfull depth to distinguish them from mature islands (Raven *et al*., 1998). Each bar type was further sub-divided as ‘vegetated’ (>50% cover) or ‘un-vegetated’ (<50% cover). The presence or absence of six bar types (i.e., three types, each sub-divided between vegetated and un-vegetated) within each 500-m reach was recorded using the sweep-up component of RHS. The spot-check component was not used as bars occurring between each 50-m check would be missed.

This study utilized the most recently available baseline RHS data for Great Britain: the 2007-08 baseline survey of England and Wales (consisting of 4849 reaches) and the 1995-96 baseline survey of Scotland (consisting of 769 reaches) (Seager *et al*., 2012). Baseline surveys were chosen because they provided systematic coverage by randomly selecting watercourse reaches in every 10-km grid square, with three reaches selected per 10-km^2 in England and Wales and one reach selected per 10-km^2 in Scotland. The initial sample size was reduced to 1480 survey reaches by filtering out (1) non-alluvial channels (<80% survey reach composed of alluvial bed material); (2) sites without measurements of average bed slope or bankfull width and (3) sites where reliable discharge estimates could not be extracted, typically topographically flat areas with multiple channels and artificial drainage networks (e.g. in parts of Eastern England) (Figure 3-1A). Whilst this approach is limited by the geomorphic information recorded by RHS (Newson, 2002), it is offset by the ability to carry out large scale assessments of river morphology (e.g. Newson *et al*., 1998a; Emery *et al*., 2004; Harvey *et al*., 2008).

3.3.2 Discharge Estimation

Previous studies have shown that bankfull discharge, the flow that fills the channel to the bank-tops, is the most influential discharge on channel form (Pickup and Warner, 1976; Williams, 1978; Andrews, 1980; Phillips and Jerolmack, 2016). Yet its infrequent nature and the natural variation in channel capacity along a river reach make it difficult to estimate (Ferguson, 1981). Andrews (1980) estimated bankfull discharge to have a recurrence interval of 1.18 to 3.26 years whilst Carling (1988) estimated it as 0.9 years. In the absence of a nearby gauging station, the median annual flood, or the 2-yr recurrence flow, is typically used instead of bankfull discharge (Wharton, 1995; Gurnell *et al.*, 2010; Bizzi and Lerner, 2012). A disadvantage of this approach is that channel-forming (or bankfull) discharge may not be represented well by median annual flood where the river channel has been enlarged for flood conveyance (Wharton, 1995). This study used estimates of median annual flood, originally calculated as part of the Flood Estimation Handbook (Kjeldsen *et al.*, 2008), which were extracted from the Peak River Flows dataset provided by the Centre for Ecology and Hydrology (CEH).

3.3.3 Substrate Size

Using a similar method to Gurnell *et al*. (2010), median substrate size (D_{50}) was estimated by converting the ten spot measures of substrate type, taken every 50-m in each 500-m RHS reach, into an average phi score based on approximate values for median particle size of each size class:

$$D_{50} = \frac{(-8 * BO - 7 * CO - 3.5 * GP + 1.5 * SA + 6 * SI + 9 * CL)}{(BO + CO + GP + SA + SI + CL)}$$

Where BO = boulder, CO = cobble, GP = gravel-pebble, SA = sand, SI = silt and CL = clay.

3.3.4 Specific Stream Power

As a measure of the ability of river flows to perform work on the boundaries of a channel (*i.e.*, banks and channel bed), the specific stream power (ω; W m^{-2}) provides a relatively straightforward approach to measuring the propensity for sediment transport, and is defined as:

$$\omega = \frac{\rho g Q S}{w}$$

where ρ is equal to the density of water (1000 kg m^{-3}), g is the gravitational constant (9.81 m s^{-1}), S is equal to average bed slope (m m^{-1}), as included in RHS, and w is equal to channel width (m), taken as the bankfull width measured at each RHS site.

3.3.5 Statistical Methods

All statistical analyses were performed in R (v 3.3.0; R Development Core Team, 2016). Generalised Additive Models (GAMs) with a logit link and binomial errors were used to predict the probabilities of occurrence of the different bar types, based on the presence or absence of each type within the 500m RHS length, using ω and D_{50} as predictor variables. Vegetated and un-vegetated versions of each bar type were modelled separately (six models) and in combination (three models), along with one global model for the presence of any bar type. GAMs were chosen over other modelling techniques because they are more flexible and are able to capture non-linear trends without adding large complexity in most instances. The two predictor variables in each case were modelled using tensor products of thin-plate regression splines, with the degree of smoothing determined by generalized cross validation (Wood, 2006). This approach accommodates non-linear interactions between predictors, whilst minimizing the risks of overfitting the data by fitting too complex a relationship (Wood, 2006; Vaughan *et al*., 2013). Thin plate regression splines are appropriate smoothers for large datasets and can be selected and diagnosed in the same way as other modelling techniques (Wood, 2006).

The accuracy of the predictions was assessed in terms of both discrimination (i.e., the ability of the model to distinguish reaches differing in their likelihood of bar formation) and calibration (i.e., the accuracy of the predicted probabilities). Discriminatory ability was assessed by the concordance index (c-index), which represents the probability that if two sites are selected at random, one with and one without the feature of interest, the model assigns a higher likelihood of occurrence to the site that has the feature present (Harrell, 2001). Therefore, a c-index of 0.5 is equivalent to chance, showing no discriminatory ability, and a c-index score of 1 shows perfect discrimination. Steyerberg (2009) defined c-index scores of > 0.7 as demonstrating ‘modest’ or ‘acceptable’ discrimination, c-index scores > 0.8 as ‘good’ and c-index scores > 0.9 as ‘excellent.’ To test calibration, residuals were calculated from the fitted models to indicate where bar occurrence was over (residual < -0.5) or under (residual > 0.5) estimated. The residuals were investigated to identify potential reasons for these poor estimations, finding potential differences in the models’ predictive ability due to changes in underlying geology, channel vegetation or substrate type. The observed prevalence (proportion of each group with bars present) was compared to the mean predicted probability of bars within each group to identify where the model poorly estimated bar presence or absence. The underlying bedrock geology (e.g. limestone, sandstone, chalk) was extracted from the British Geological Survey 1:625k map. The model development did not include testing against an independent data set or a subset of the RHS baseline data.

3.4 Results & Discussion

Rivers were included from across Britain with very few gaps in their geographic distribution, with an absence of sites limited to low-lying regions of Eastern England and the Somerset Levels (Figure 3-1A). RHS reaches ranged in catchment area from five to 4984 km^2, with median annual discharges from 0.1 to 963.5 m^3 s^{-1} and estimated specific stream powers of between one and 1116 W m^{-2}. The dominance of coarse gravel-bed rivers in Britain was evident with mean bed material ranging from silt and clay (9% of sites), through sand (16%), gravel-pebble (46%), and cobble-boulder (29%) (Figure 3-1B).

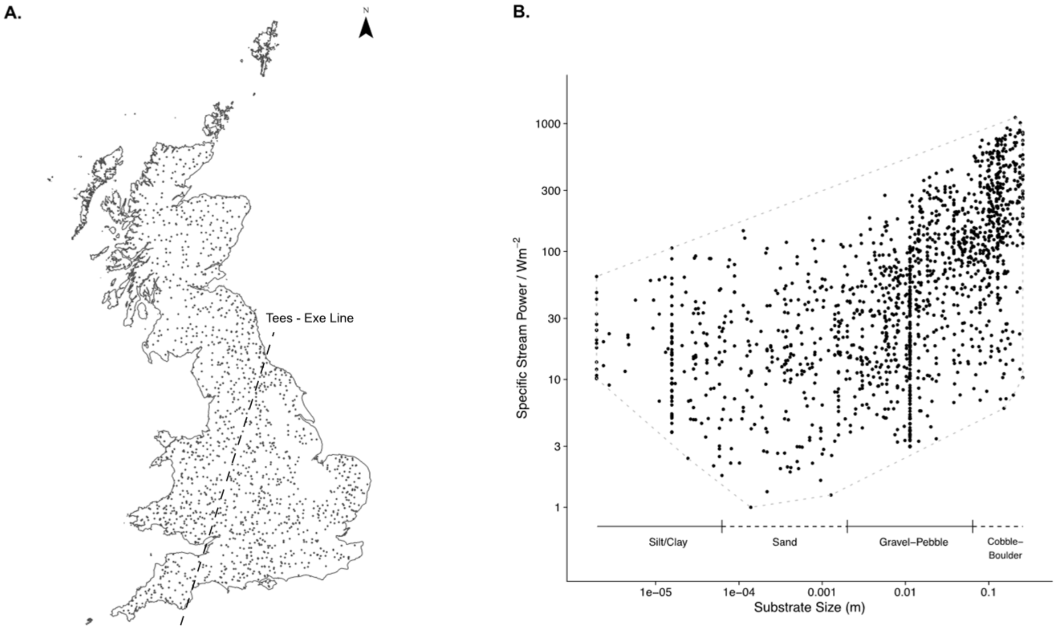


Figure 3-1: Distribution of the 1480 RHS sites used in the study on (A) a map of Britain and (B) the D_{50}-ω axes. The grey, dashed line is a convex hull that incorporates all RHS sites.

3.4.1 National controls on bar distribution

Point, alternate and mid-channel bars were all most commonly observed in gravel-bedded rivers with $\omega > 30$ W m^{-2} that drained areas of northern and western Britain, including much of Scotland, Wales and north-west and south-west England (Figure 3-2A; Figure 3-3A; Figure 3-4). This change in river type across Britain is often described as the divide between upland and lowland Britain and is sometimes denoted as a line between the rivers Tees and Exe (Ferguson, 1981; Figure 3-1A). The variation in overall bar occurrence was largely driven by alternate bars, the most common bar type, present at 67% of the RHS sites, whilst point and mid-channel bars were present at 43% and 40% of sites respectively (Table 3-1). Alternate bars were also the most predictable using the D_{50}-ω model, with greater discrimination (C = 0.78) than for point (C = 0.72) and mid-channel bars (C = 0.71) (Table 3-1). Overall, the generalised additive model displayed good discriminatory ability (C = 0.80) between sites with and without bars and predictors in all models were significant at $p < 0.001$.

Table 3-1: C Index (predictive ability) scores for the models used in the study. Initially models were split into bar types and whether vegetation was present or absent. The frequency of results for each category along with the percentage of the dataset that they represent is also shown.

C - Index		**D_{50}-ω**	**Frequency**
Point Bars	*Unvegetated*	*0.73*	*564 (38%)*
	Vegetated	*0.66*	*230 (16%)*
	Combined	0.72	643 (43%)
Alternate Bars	*Unvegetated*	*0.79*	*879 (59%)*
	Vegetated	*0.64*	*449 (30%)*
	Combined	0.78	993 (67%)
Mid-Channel Bars	*Unvegetated*	*0.71*	*429 (29%)*
	Vegetated	*0.67*	*302 (20%)*
	Combined	0.71	589 (40%)
All Bars		0.80	1090 (74%)
Total Number of Sites			1480

Alternate bars were common across a wider range of conditions that the other bar types, with point and mid-channel bars present under closely defined conditions. Point bars were most frequent (up to 73% of RHS reaches) in gravel-bed rivers within a 30-500 W m^{-2} range of ω (Figure 3-2B). In contrast, the region of highest alternate bar occurrence spanned the entire range of ω values in cobble-boulder bed rivers, peaking (up to 92% of reaches) in boulder-bed rivers with ω ~ 10 W m^{-2}, and was only confined to ω > 30 W m^{-2} in gravel-pebble bed rivers (Figure 3-2C). Mid-channel bars, the rarest of the three bar types, were most common (up to 57% of reaches) in rivers with beds of gravel or coarser material with ω of 30-300 W m^{-2} (Figure 3-2D).

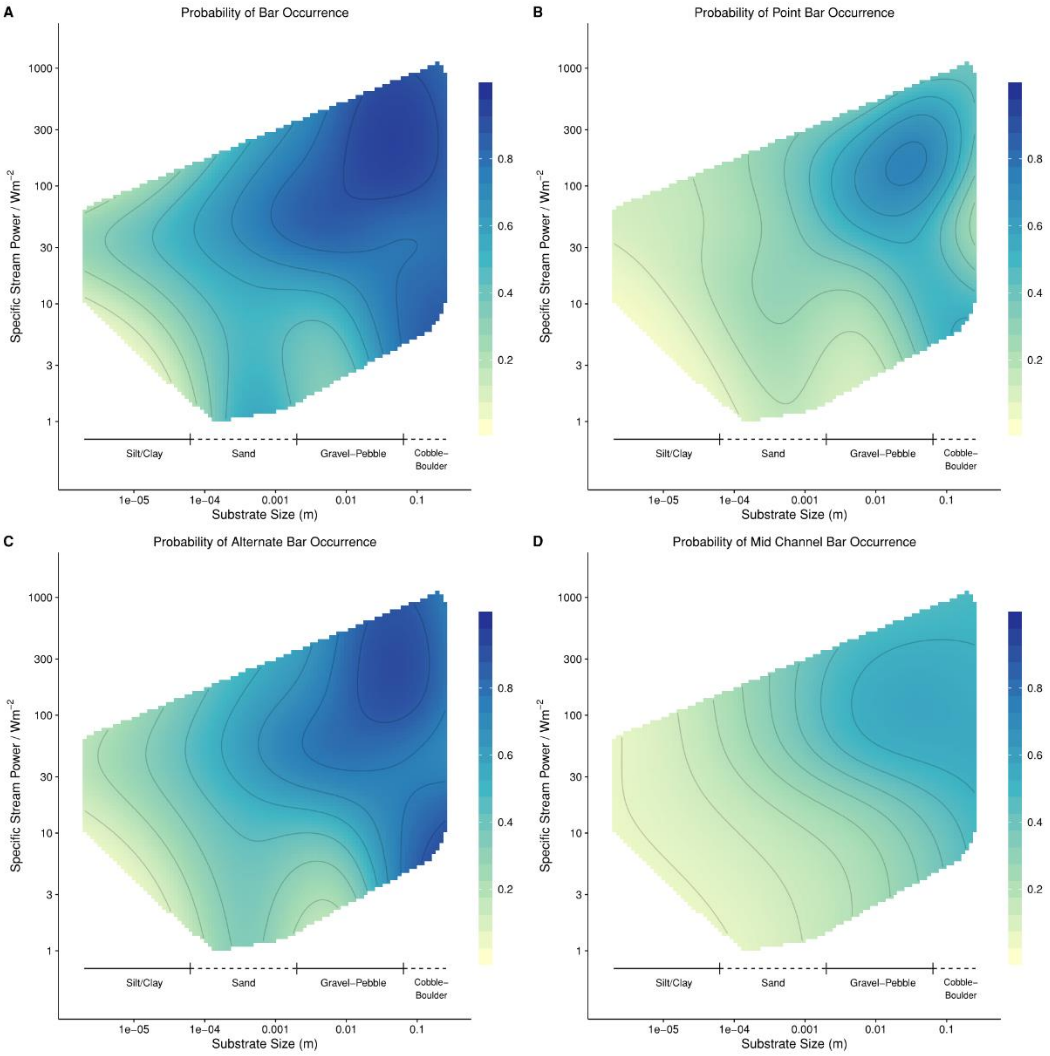


Figure 3-2: The probability of occurrence of (A) all bar types, (B) point bars, (C) alternate bars and (D) mid-channel bars are modelled using general additive models on the D50-ω axes. The colour-bars indicate areas of low-high probability of bar occurrence.

The spatial distributions of the different bars across Britain were similar, differing mostly in their overall frequency in the dataset and in the regions of peak occurrence probability for point and alternate bars (Figure 3-3B; 3-3C, 3-3D). Point bar occurrence peaked in unmodified rivers draining >50 km^2 of upland areas of England and Wales with sedimentary geology, such as the Usk, South Tyne, Cothi and Dulas (Figure 3-3B). Point bar occurrence was notably lower in upland regions with hard, igneous geology, such as much of Scotland and the Lake District whilst alternate bars were prevalent across a much larger area, including all of Wales and upland areas of Scotland and England, seemingly regardless of changes in underlying geology (Figure 3-3C). Mid-channel bars had the same spatial distribution as alternate bars, except their probability of occurrence was lower, reflecting that they were less commonly found (Figure 3-3D).

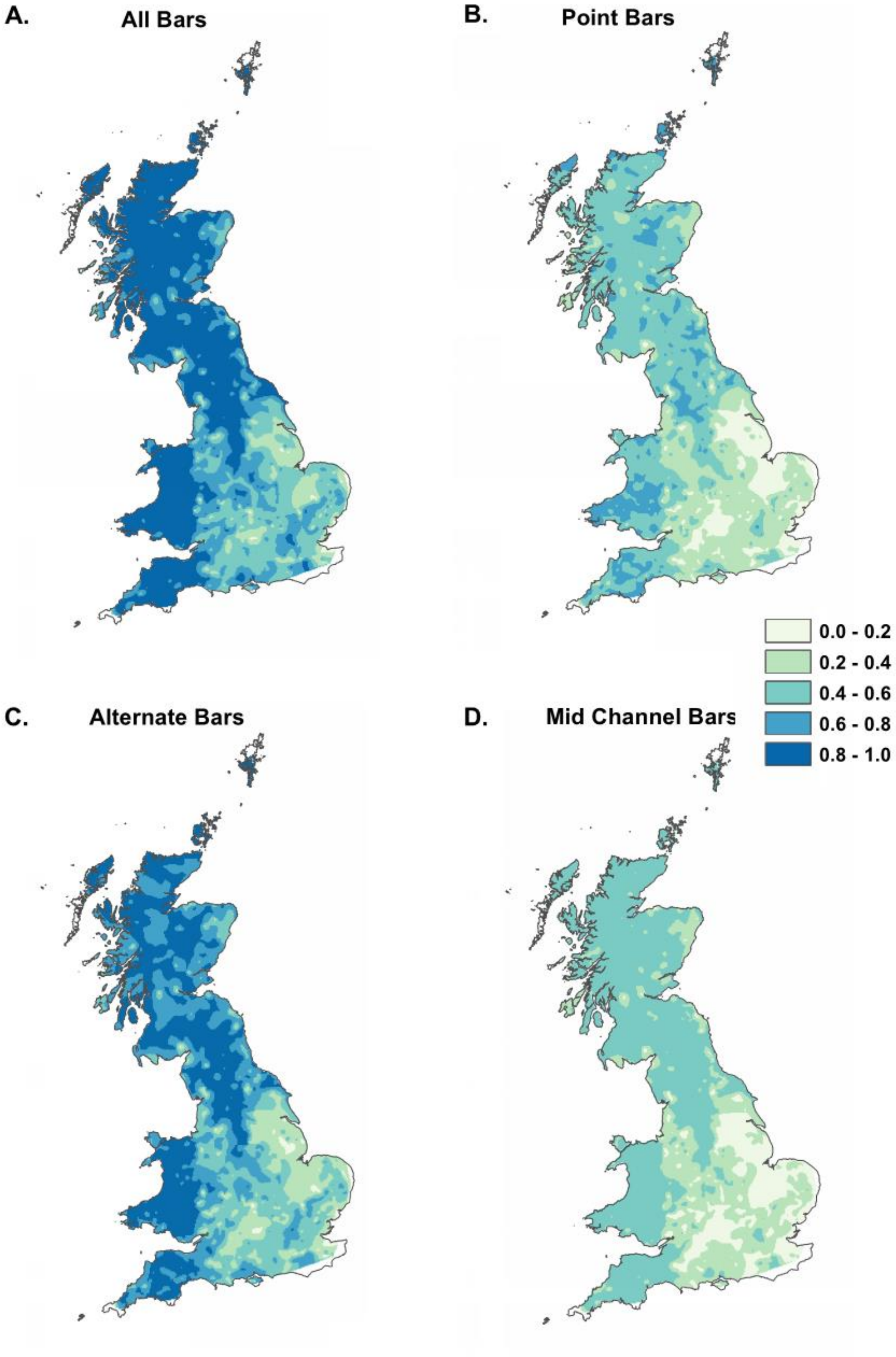


Figure 3-3: Interpolated maps of the probability of bar occurrence, as modelled on the D50-ω axes, for (A) all bar types, (B) point bars, (C) alternate bars and (D) mid-channel bars. The colours indicate areas of low-high probability of bar occurrence.

At large spatial scales, the type and amount of sediment available to a river, controlled by geology, climate and human activity, along with a river's ability to transport that sediment, controlled primarily by gradient, discharge and width, dictates the planform of alluvial river channels (Mackin, 1948; Schumm, 1985). River planform is closely related to the type and abundance of bar forms present within the channel. For example, point bars are a feature indicative of meandering rivers, whilst mid-channel bars are common in braided rivers. Crosato and Mosselman (2009) successfully modelled bar occurrence in a cross-section based on width to depth ratio, bed roughness, channel gradient and sediment characteristics, all similar components to the D_{50}-ω model used here.

The relatively modest data requirements to estimate specific stream power have seen it applied to studies of channel pattern and bar occurrence in rivers globally. Nanson and Croke (1992) and Ferguson (1981; 1987) reported ranges of ω for meandering rivers of 10-60 W m^{-2} and 5-350 W m^{-2} in Australia and the UK respectively, corresponding closely to the range of ω with the highest probability of point bar occurrence in this study (Figure 3-2B). Braided rivers, of which mid-channel bars are a key feature, are relatively uncommon in Britain but wandering, gravel-bed rivers are commonly found across upland areas and are likely to accommodate alternate and occasional mid-channel bars (Newson *et al*., 1998a; Orr *et al*., 2008). Nanson and Croke (1992) reported a ω range of 300-600 W m^{-2} for wandering, gravel-bed rivers in Australia, which corresponds with the highest probability of alternate bar occurrence found here (Figure 3-2C). Mid-channel bar formation has been shown to be closely related to over-widening of the channel (Knighton, 1972; Hooke, 1986, Luchi *et al*., 2010a), although there is still uncertainty about whether bar formation precedes or follows channel widening (Luchi *et al*., 2010b). External factors that induce local over-widening, such as channel modification for flood defence schemes (Brookes *et al*., 1983) or tributary input (Benda *et al*., 2004), allows mid-channel bars to form in a range of river types (e.g. meandering, braided, wandering). This may explain the less defined region of highest occurrence for mid-channel bars in comparison to point bars which are restricted to rivers with a meandering planform (Figure 3-2B; 3-2D).

3.4.2 Critical Specific Stream Power

All three bar types were more prevalent at stream powers greater than ca. 30 W m^{-2}, but especially point bars (Figure 3-6). Brookes (1987) reported a threshold for erosion of 25 W m^{-2} in British rivers downstream of channelization works, whilst Orr *et al*. (2008) identified the boundary between deposition and erosion dominance in the River Eden as 30 W m^{-2}. A number of studies have derived equations for the specific stream power required to initiate the movement of bed material of a given size, termed the critical specific stream power (ω_c). Bagnold (1980) proposed an equation based on specific stream power to predict bedload transport, which was subsequently revised by Ferguson (2005) to account for differences between the grain size of the material in transport and the dominant bed material and to allow for hiding and protrusion effects. Petit *et al*. (2005) used field studies of Belgian rivers with catchment areas from 40-500 km^2 to produce a relationship between the size of mobilised particles (D_i) and the critical specific stream power (ω_c). Finally, Parker *et al*. (2011) modified Einstein's (1942) bed-load transport equation to produce an equation for ω_c based on a dimensionless critical stream power values derived from flume studies. These three approaches for estimating ω_c predict that pebble-sized material (26-44 mm), will be transported when ω is equal to 30 W m^{-2} (Table 3-2).

This may explain the increases in bar prevalence above 30 W m^{-2} indicated here, as the majority of rivers in Britain have gravel-beds (74% of our RHS sites had beds composed of gravels, pebbles or cobbles) and bars will only be formed where sediment can be transported ($\omega > \omega_c$) into and out of a river reach (Hooke and Yorke, 2011). This interaction between sediment supply and transport determines the amount of sediment available to be stored (as bedforms – e.g. bars) within a river reach. For a river reach to contain mobile bedforms, sediment supply needs to be in excess of or in long-term equilibrium with sediment transport.

Alternate bars were still abundant below 30 W m^{-2}, where sediment transport ($\omega > \omega_c$) occurs less often (e.g. 1 in 10-year flow required). The presence of alternate bars in this portion of the model is speculated to be due to the occurrence of relict, inactive bedforms in static riverbeds. These static forms would have been created when upstream sediment supply was reduced (e.g. due to impoundments) or where local channel conditions were modified to increase flow conveyance, resulting in an increase in transport capacity. In both of these scenarios the amount of sediment exiting a river reach would be in excess of that entering the reach, resulting in a gradual coarsening of the riverbed sediment (armouring), creating static bedforms that were disconnected from the flow regime (Kleinhans and Van den Berg, 2011; Mao *et al*., 2011).

Table 3-2: Equations for critical specific stream power as produced in Petit *et al*. (2005), Ferguson (2005) and Parker *et al*. (2012) and the predicted grain size of material entrained by a flow with a specific stream power of 30 W m^{-2}. The values for D_i and D_b in Ferguson's (2005) equation were taken as equal, despite there being a difference between the size of material in transport and the dominant bed material in alluvial rivers with mixed beds.

Approach	**Critical Specific Stream Power ω_c (W m^{-2})**	**D_i at 30 W m^{-2} (mm)**
Petit *et al*. (2005)	$\omega_c = 0.130{D_i}^{1.438}$	44
Ferguson (2005)	$\omega_c = 0.104\,\frac{{D_b}^{1.5}}{S^{0.17}}\left(\frac{D_i}{D_b}\right)^{0.67}$	26
Parker *et al*. (2012)	$\omega_c = \omega_{c*}\,g\,(\rho_s - \rho_w)\sqrt{\frac{\rho_s - \rho_w}{\rho_w}\,g\left(\frac{D_i}{1000}\right)^3}$	28
Constants	g = gravitational constant (9.81 m s^{-1}), ρ_s = density of sediment (2650 kg m^{-3}), ρ_w = density of water (1000 kg m^{-3}), D_i = grain size entrained by the flow (mm), D_b = grain size for the dominant bed material (mm), ω_{c*} = dimensionless critical stream power (0.1, Parker *et al*. 2012)	

3.4.3 Regional controls on bar distribution

The analysis of the residuals from the D_{50}-ω model indicated where bar occurrence was over-or under-estimated (Figure 3-4A) and suggested that channel modification, catchment geology, in-channel vegetation and cohesive bed material (i.e. silt/clay) were important controls on bar occurrence. Seager *et al*. (2012) reported that up to 43% of total riverbank length in England and Wales has been directly modified in some way with the indirect impacts of land use change even more widespread. Rivers in lowland areas, such as much of eastern England and north-east Scotland, and in regions that once supported heavy industries (e.g. coal mining), such as the Midlands, South Yorkshire and the South Wales valleys, were highly modified with 60-100% of the riverbanks at each RHS site modified (e.g. re-profiled or reinforced) in some way (Figure 3-4B). Bar occurrence was typically over-estimated in these regions (Figure 3-4A), likely due to a combination of channelization creating reaches where sediment is rapidly flushed through the system (Hooke, 2003), upstream impoundments create barriers to sediment transport (Petts, 1980) and where past dredging of the channel, to increase channel capacity for flood control or navigation, has removed the coarse sediment required to build bar forms (Sear *et al*., 1995). To assess the impact of this extensive channel modification on bar distribution, the D_{50}-ω models for each bar type were re-run including a term indicating the proportion of the 500m RHS reach that was modified and then the predictions for sites with 0% and 100% modification were compared. The extent of modification term was significant at $p < 0.001$ in all models. Point bar prevalence was 20% higher (0.5 vs 0.3) in fully modified sand-bed rivers versus unmodified counterparts (Figure S2). Point bars were also up to 15% more common in fully modified, cobble-bed rivers with $\omega < 30$ W m^{-2} (Figure 3-7). Alternate bars were up to 10% more common in modified sand-bed rivers than at unmodified sites, whilst mid-channel bars showed no change in occurrence between unmodified and modified sites (Figure 3-7). Sand-bed rivers are typified by dune-ripple sequences, although channel curvature still allows forced bar forms (e.g. point bars) to arise (Blondeaux and Seminara, 1985); this may explain why point bars are more common in highly modified, sand-bed rivers as overall channel curvature is less likely to be modified by human activity than smaller bank protection or in-channel changes. Future advancements of this study should seek to test the model against an independent data set or a subset of the RHS baseline data used to increase the robustness of the results.

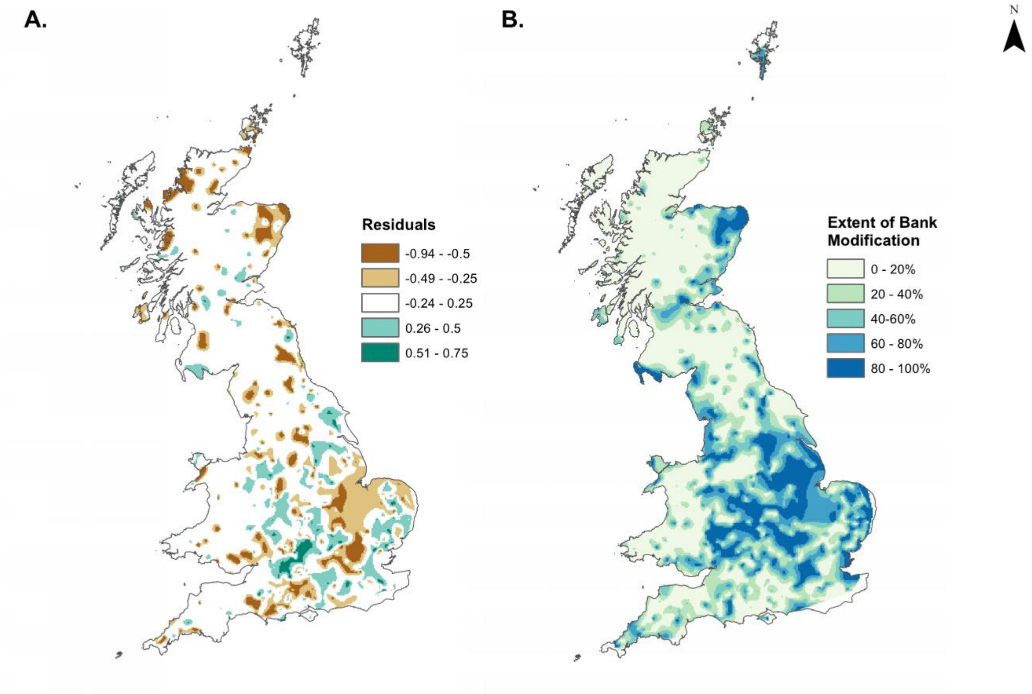


Figure 3-4: (A) Interpolated map of model residuals scores denoting the success of the D50-ω model of all three bar types. A score near to zero indicates good agreement between predicted probabilities and bar presence/absence, whereas scores closer to -1 or 1 indicate over- or under-estimates of bar prevalence respectively. (B) Interpolated map of the extent of bank modification. The colours indicate the percentage of bank length within each RHS site that has been noticeably modified.

The D_{50}-ω model overestimated the prevalence of bars in chalk streams (52% expected vs 41% observed), particularly when compared to predictions in other major geology types (Figure 3-5A). Chalk streams in Britain are confined to a small region in southern England and are characterised by a very stable, groundwater-fed flow regime, a gravel bed and often an abundance of in-channel vegetation (Berrie, 1992; Harvey *et al*., 2008). A hypothesis for the lack of bars in these unique streams is that the lack of fluctuations in stage does not allow transitional features, such as bars, to form as they do in rivers with lower baseflow components.

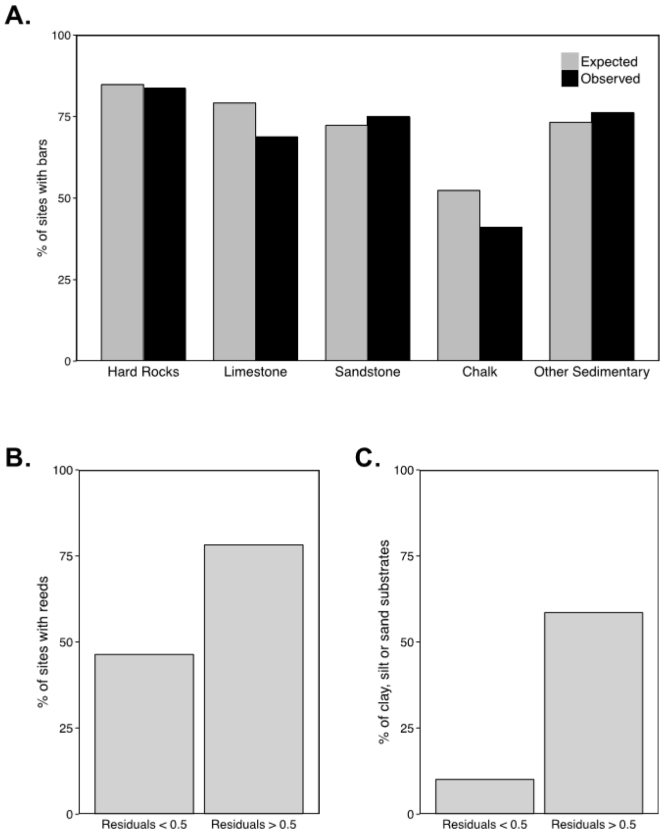


Figure 3-5: (A) Percentage of RHS sites characterized by rock type based on the mean predicted probability of the D_{50}-ω model (expected) compared to the mean probability of the actual values (observed). RHS sites with bars present that were poorly predicted by the model (residual >0.5) are split from RHS sites with bars that were well-predicted (residuals <0.5) to highlight that poorly predicted sites are more likely to have (B) emergent marginal macrophytes present and (C) a substrate composed of clay, silt or sand.

Lastly, bar occurrence was underestimated in rivers that were typically < 5m wide and found across lowland England (Figure 3-4A). Approximately 78% of these rivers (with Residuals > 0.5) had emergent marginal macrophytes present, compared with only 46% of the rest of the dataset (Figure 3-5B). The presence of in-channel vegetation helps to stabilise bar surfaces and promote deposition, acting as a positive feedback for bar growth (Hickin, 1984; Corenbilt *et al.*, 2007). Also, 59% of these rivers had beds made up of sand, silt or clay, compared with 10% of the rest of the dataset (Figure 3-5C). An assessment of the photographs included with each RHS survey indicated that these fine-grained bars were either (1) point bars formed by the flow forcing effect of channel curvature (Blondeaux and Seminara, 1985) or (2) bars formed as a result of a channel obstruction, typically large woody debris, that acts to reduce flow velocity and promote deposition (Piegay and Gurnell, 1997).

3.5 Conclusion

This study has used a nationwide dataset of river forms to demonstrate that alternate, point and mid-channel bars, which are closely linked to channel pattern, are most commonly found in gravel-bed rivers with specific stream powers (ω) in excess of 30 W m^{-2} at bankfull discharge. These conditions are most common in upland rivers found to the north and west of the Tees-Exe line. Using equations for critical specific stream power (ω_c) derived in previous studies, it is estimated that at 30 W m^{-2} material sized between 26-44 mm, corresponding to pebble-sized particles, is mobilised. The dominance of gravel-bed rivers in Britain can explain the ω threshold as bars will only be present where the bed material is readily transported and organised ($\omega > \omega_c$) by the effective (bankfull) discharge. Point bars were found to most commonly occur in channels with ω of 30-500 W m^{-2}, which corresponds to published ω ranges for active meandering channels and in upland regions of Britain with a sedimentary geology. Alternate and mid-channel bars were most common when ω equalled 250 W m^{-2} and 280 W m^{-2}, corresponding with published ranges for wandering, gravel-bed rivers that are abundant across Britain, regardless of geology type. Bar prevalence was overestimated in severely channelized rivers, likely due to increased flow velocities inhibiting the development of depositional bedforms or the removal of coarse material for flood control/navigation, and in chalk geologies, likely due to their uniquely dampened flow regimes, whilst it was underestimated in small, lowland rivers with cohesive riverbeds where bar forms are sustained by the presence of channel vegetation or large woody debris. The model used here suggests that in rivers with an adequate sediment supply, active bars will be present where rivers are capable of initiating sediment transport at bankfull discharge. However, the presence of any channel modifications is likely to increase the transport capacity of the river such that sediment is flushed through the reach, thereby preventing bar formation. Any bars that exist under these conditions will likely represent relict, inactive features. If bars are to be restored and maintained in British rivers the practice of channelization, typically for flood control, needs to be reversed.

3.6 Appendix

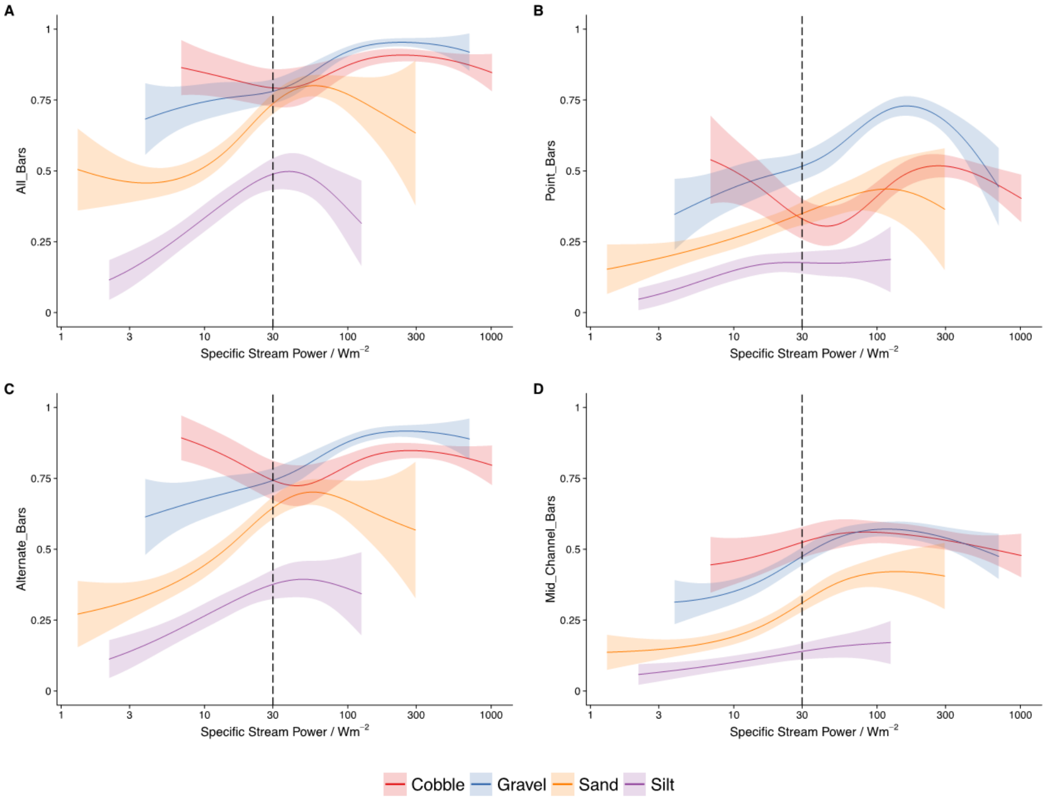


Figure 3-6: The probability of occurrence of (A) all bar types, (B) point bars, (C) alternate bars and (D) mid-channel bars for the range of specific stream power values at the mid-point of each substrate type along with the standard error of each prediction. The dashed black line indicates the identified threshold ω of 30 W m^{-2}.

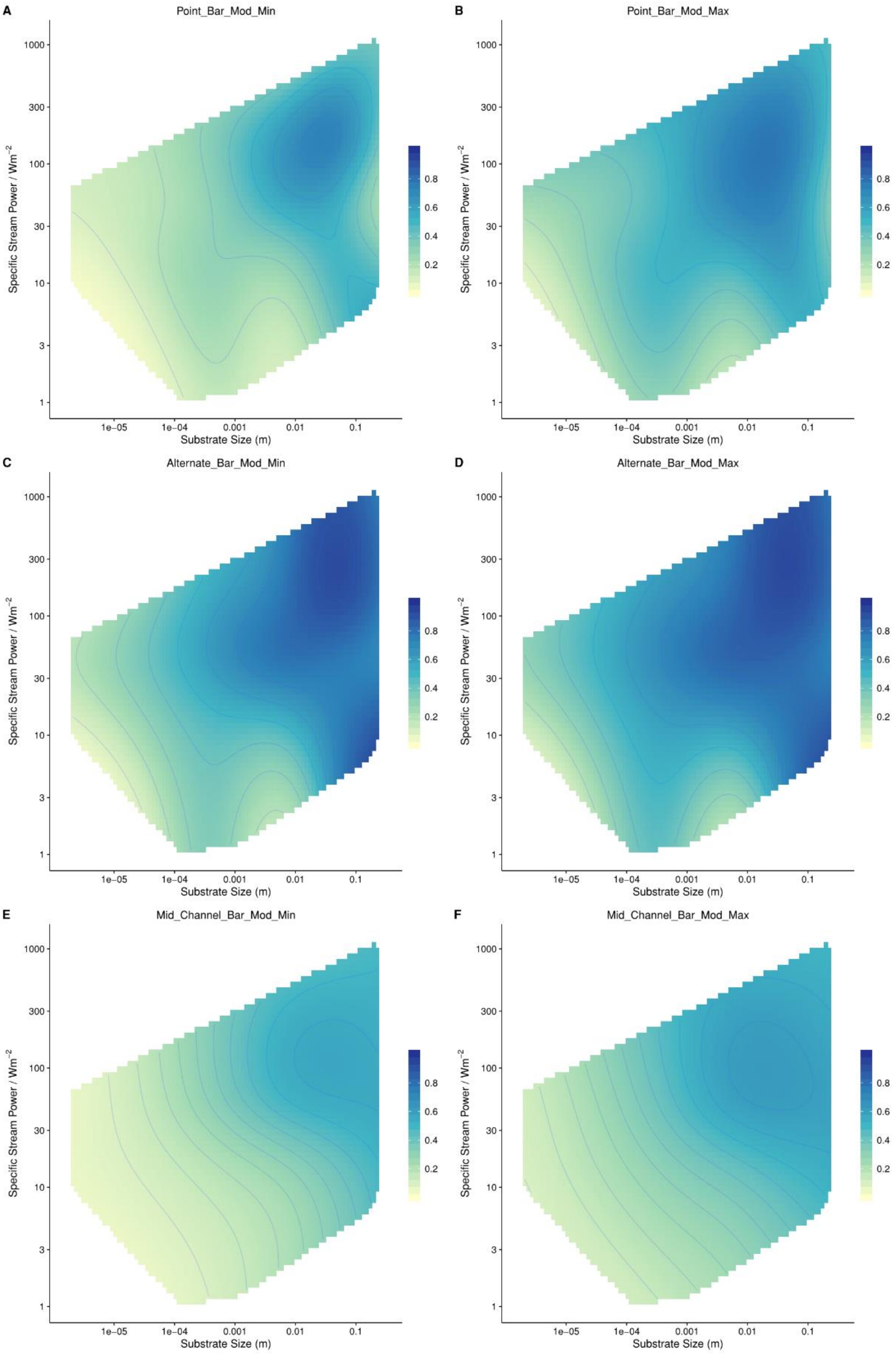


Figure 3-7: The predicted probability of occurrence of (A & B) point bars, (C & D) alternate bars and (E & F) mid-channel bars at minimum (A, C, E) and maximum (B, D, F) channel modification.

4 Effects of bed composition and stability on river invertebrates

4.1 Abstract

Despite conceptual or descriptive studies for over a century, the interaction between river ecology and geomorphology is still poorly understood. The role of sediment transport in renewing habitat and acting as a disturbance to ecological communities could be particularly important, but has never been adequately quantified. Here, I used a unique dataset describing invertebrate communities, water quality and hydraulic character from 714 sites across Britain to examine how physical habitat distribution and disturbance controls invertebrate community composition. Specifically, the Shields Regime Diagram, a simple, mechanistic model of particle entrainment, was used to examine variations in invertebrate community composition, function, and trait character in relation to changing estimates of substrate and sediment transport. Invertebrate community response to disturbance varied between rivers with gravel/cobble and silt/sand substrates. An increase in the propensity for disturbance was found to reduce invertebrate community richness, abundance and functional diversity in gravel/cobble substrates, with traits indicative of greater resistance or resilience, such as short lifespans, aerial dispersal and smaller aquatic stages also becoming more prevalent. In silt/sand substrates, patterns were more complex as communities with highly-abundant taxa became dominant with increasing transport ability, perhaps indicating that there are fundamental differences in what constitutes disturbance (cf. gravel/cobble). These results are consistent with other studies of disturbance, within rivers and in wider ecosystems, and provide further evidence of a common response to habitat variability across ecosystems.

4.2 Introduction

Rivers are among the most complex and diverse environments, and as a consequence support some of the most diverse ecological communities on Earth (Strayer and Dudgeon, 2010). Understanding the interaction between these communities and their habitat is a major goal in river ecology, as part of wider efforts to reveal the drivers of biodiversity patterns in a range of ecosystems (Sala *et al*., 2000). This has assumed greater importance as rivers face intensifying pressures such as urbanisation, deforestation, hydropower development and climate change (Dudgeon *et al*., 2006; Johnson *et al*., 2009; Vorosmarty *et al*., 2010; Markovic *et al*., 2014; Henriuqes *et al.,* 2015). An improved understanding of the interface between fluvial geomorphology and river ecology will be key if freshwater communities are to be managed for resilience in the face of these multiple pressures, yet most studies are restricted to one of the separate disciplines (Newson and Newson, 2000; Vaughan *et al*., 2009, Vaughan and Ormerod, 2010; Rice *et al*., 2010). Here, I use a novel multidisciplinary approach, combining nationwide ecological sampling and a basic model of geomorphic processes, to examine the role of the disturbance of bed sediments on the structure and function of benthic invertebrate communities.

Interactions between geomorphology and ecology in fluvial environments are arguably more dynamic and tightly coupled than in terrestrial environments (Fisher *et al*., 2007; Corenbilt *et al*., 2011). This is particularly true in alluvial rivers, which are much more common than their non-alluvial (bedrock) counterparts, with unconsolidated sediments forming benthic habitats that are frequently redistributed by river flow. Sediment is sorted and stacked by flow to create repeatable features in the river channel, such as riffles, pools and bars, which support different communities of organisms or their different life stages (Vannote *et al*., 1980; Poff, 1997; Benda *et al*., 2004). Riffles and pools are typically found in sequence, with pools forming narrower, deeper sections of river channel that are maintained by scouring at high flows, and riffles forming wider, shallower sections where the largest sediment transported by the river accumulates. Bars are the principal form of in-channel sediment storage and themselves have a diverse range of forms, being found in meandering and braided rivers (Chapter 3). They are responsible for much of the habitat heterogeneity found in these systems and can support both freshwater and terrestrial organisms (Eyre *et al*., 2001; Madsen *et al*., 2001). Together, these and other morphological features form a dynamic ‘template’ upon which riverine organisms have evolved (Townsend and Hildrew, 1994), being continually reshaped and renewed by sediment transport initiated during high flow events.

There is a long history of descriptive studies linking river organisms to their preferred habitats (Riley, 1921; Percival and Whitehead, 1929), yet research quantifying these relationships is typically confined to the microhabitat scale (Jowett *et al*., 1991; Statzner *et al*., 2000) or to single rivers (Rempel *et al*., 2001; Jowett, 2003). Studies looking at larger spatial scales, producing generic theories about the geomorphology – ecology interface, such as Vannote *et al*.'s (1980) River Continuum Concept or Frissell *et al*.'s (1986) hierarchical view of river systems, remain conceptual and largely qualitative. More importantly, the descriptive nature of most studies – correlating the observed community to a static view of habitat features – provides limited insight into the underlying mechanisms, and are likely to generalise poorly in a changing environment: rectifying this limitation is a research priority in many environments (Urban *et al*., 2016). From the geomorphic perspective, models linking to the ecology would benefit from capturing the key controls on sediment transport in alluvial rivers. These are primarily the flow conditions of the river and the nature (i.e. size and shape) of the river sediment itself, which together control the morphology of physical habitat and drive the rate at which physical habitat forms are created and renewed in both space and time (Shields, 1936; Andrews, 1983; Parker, 1990). This relationship between flow and sediment will determine how often the riverbed is mobilised and transported, which directly impacts on channel form, in-channel and riparian vegetation and presumably also on river organisms that may be inhabiting the riverbed, through the extent of different habitats and the disturbance regime. Concomitantly, from the biological perspective, the ability to include fundamental processes that shape communities, such as evolution, dispersal and inter-specific interactions, should lead to a deeper understanding and greater predictive ability (Urban *et al*., 2016).

Efforts to provide a more mechanistic link between biology and the physical environment using first principles were initiated by Southwood (1977; 1988) who proposed that our understanding of organism-habitat relationships should focus on the strategies employed by organisms to persist and thrive in their environments. He argued that these strategies had a spatial and temporal component, principally related to resource availability and stability. In river systems, Townsend and Hildrew (1994) developed this idea into the Habitat Template Theory, which described habitats on two conceptual axes, with a spatial axis represented by environmental heterogeneity and the refugia from disturbance that such heterogeneity creates, and a temporal axis represented by the regularity of disturbance events. These axes then provide the template into which organisms have evolved, developing ecological traits adapted to those conditions (Townsend and Hildrew, 1994). Poff (1997) added an explicit scale component to the idea of a habitat template, drawing on the hierarchical view of rivers proposed by Frissell *et al*. (1986), describing it as a series of filters running from basin to microhabitat scales that organisms with specific traits have to pass through in order to persist in an environment. In essence, many of these conceptual models recognise the importance of riverbed sediment mobility in controlling species distributions and community structure, yet the links are often qualitative and implicit within a larger disturbance and heterogeneity framework.

Several previous studies have tried to directly link measures of river hydraulics or bed mobility to the zonation of river organisms, in particular for freshwater invertebrates. Statzner and Higler (1986) were the first to assess benthic invertebrate zonation in relation to measures of stream hydraulics and found that in fourteen streams across the world, changes in species assemblages were linked to changes in the hydraulics. Death and Winterbourn (1995) and Death (1995) found, using a dataset of 11 freshwater habitats in New Zealand, that river reaches with more mobile beds were colonised by communities with lower diversity, consisting of taxa with ecological traits that confer resistance to, and facilitate re-colonisation after, flood events. Selecting a measure of riverbed stability that is analogous to a disturbance episode for freshwater invertebrates has proved tricky, with a number of different approaches proposed including an all-encompassing sediment stability index (Schwendel *et al*., 2012), the Pfankuch Index (Schwendel *et al*., 2010a), a measure based on the direct measurement of tracer stone movement, and the physically based measure of shear stress (Schwendel *et al*., 2010b). Many of these methods also involve labour-intensive fieldwork, limiting the geographical scope of studies and therefore their generality. An additional complication of linking riverbed movement and invertebrate community composition lies in defining whether riverbed movements act directly to remove invertebrates themselves, or indirectly, by removing their food sources such as biofilms (Bond and Downes, 2000; Death, 2002). In part due to these challenges, general, process-based models linking river bed dynamics and ecological community structure are lacking, despite the empirical and conceptual developments of recent years.

In ecology, the use of ecological traits (cf. taxonomy), promoted by the habitat template theory, has driven a fruitful field of research into community structure (Poff, 1997; McGill *et al*., 2006; Verberk *et al*., 2013) that can provide greater insight into the links between organisms and the physical environment. This trait-based approach has the advantages of not only linking to the habitat template, but also providing a notion of community function (e.g. by looking at feeding guilds; Poff, 1997; Lamouroux *et al*., 2004) and being able to distinguish between patterns of community structure driven by niche, as opposed to neutral mechanisms (Mouillot *et al*., 2013). Several studies have looked at how traits are linked to bed composition (i.e. habitat) and transport. For example, Demars *et al*. (2012) showed that river biotopes (distinct areas of riverbed between 1-100 m^2) were better predictors of macroinvertebrate trait profiles (*variance explained* = 40%) than genus-level composition (variance explained = 26%). Where riverbeds are more frequently mobilised, communities have been found to possess traits indicative of disturbance, such as high mobility, a streamlined body form and aerial dispersal (Townsend *et al*., 1997; Lobera *et al*., 2017). Moving beyond the prevalence of individual traits, multivariate trait assessments have provided new insights into communities and the assembly rules that shape them by considering community-level functional diversity (Mouillot *et al*. 2013). This includes properties such as functional richness – the full set of functional roles performed by a community – and functional dispersion – how functionally distinct individual taxa in a community are and to what extent they overlap with potential competitors (Mouchet *et al*., 2010). Importantly, these new techniques make it possible to look at the relative contributions of habitat filtering and inter-specific competition to community structure (Mason *et al*., 2005) and lead to testable predictions. For example, highly disturbed environments should restrict functional diversity, favouring a subset of traits that engender resilience, whereas in more benign environments, the inter-specific competition and limiting similarity principle may produce more functionally dispersed communities (Mouchet *et al*., 2010; Mouillot *et al*., 2013). This approach provides new scope for a community-level assessment of how the habitat template shapes riverine communities.

This chapter aims to link the processes shaping organisms and communities (e.g. evolution) with the physical processes shaping alluvial habitats (e.g. sediment type, transport mode and frequency), based on the conceptual understanding that the physical processes set the template upon which evolution occurs. Building on the habitat template approach of Townsend and Hildrew (1994), this relationship is examined at the individual taxon level, using a trait-based approach, and at the community level, using both standard taxonomic metrics (e.g. richness) and functional diversity measures of ecological communities, with a focus on traits expected to respond to bed mobility and disturbance. Invertebrate data were obtained from the river invertebrate prediction and classification system (RIVPACS) reference data set, including >700 samples from rivers from across Great Britain (Davy-Bowker *et al*., 2007). The invertebrate data are linked to the two axes that form the Shields regime diagram, a simple, static model of particle entrainment based on mechanistic first principles, which is a well-established tool in fluvial geomorphology (Parker *et al*., 2003; Parker *et al*., 2007; Wilkerson and Parker, 2010). The first axis is the particle Reynolds number, which describes the size of the sediment that makes up the riverbed. whilst the second is the is the dimensionless shear stress, which describes the propensity for riverbed movement. Together, these axes differentiate between different geomorphic processes occurring at each location, chiefly bed-load and suspended-load transport, and the range of substrate sizes present in the riverbed, which in combination have been shown to control alluvial bedforms (van Rijn, 1984; Buffington and Montgomery, 1997). I focus on the trends within substrate types (e.g. silt, sand, gravel, cobble) as these are expected to be most reflective of where geomorphic processes, such as bed-load transport, become active and influence on invertebrate community composition.

Three main hypotheses are tested, predicting that invertebrate communities which reside in more readily-disturbed riverbeds will have:

1. Lower taxonomic richness and evenness, as expected in high-disturbance environments (Odum, 1985);
2. Lower functional richness and dissimilarity among taxa, consistent with a strong selection pressure for traits to resist disturbance (Mason *et al*., 2005);
3. A greater prevalence of resistance traits, such as short lifespans, fast reproductive cycles and aerial dispersal (Odum, 1985; Bonada *et al*., 2007; Doledec *et al*., 2011).

Additionally, the extent to which the Shields Diagram can explain differences in two sets of traits not explicitly linked to disturbance (feeding guilds and locomotion) will be examined. The predicted trends in these traits are a change from traits indicative of soft sediments (e.g. burrowing, absorbers) to hard sediments (e.g. crawling, scrapers) as sediment calibre increases (Quinn and Hickey, 1994; Jowett, 2003).

4.3 Methods

4.3.1 RIVPACS dataset

The RIVPACS data set was collected between 1978 and 2002 at 725 ‘reference’ sites deemed as being as near-natural as is possible in Britain, and contains information on water quality, invertebrate community composition and river form (Wright *et al*., 1998; 2000; Davy-Bowker *et al*., 2007). The dataset is particularly valuable due to its high taxonomic resolution, standard sampling protocol and restriction to watercourses less likely to be impacted by poor water quality and physical or catchment modification (Murray-Bligh *et al*. 1997). For this study, the seasonal invertebrate sampling data was summed into an annual dataset. The data were used at species-level for analyses based on taxonomic metrics (e.g. richness), whilst species were combined into genera for trait-based analyses, as this was the finest resolution at which trait data were available (see below). Six chemical and physical variables were retained to provide contextual information for each sampling site (Table 4-1). Eleven sites with missing chemical and/or physical data were removed, leaving a total of 714 sites across England, Wales and Scotland (Figure 4-2A).

Table 4-1: Chemical and physical variables from the RIVPACS dataset used to describe each sampling location. Details of the measurement methods taken from UKTAG (2008).

Variables	Description
Alkalinity	Mean annual total alkalinity (mg L^{-1} CaCO3). Values in Scotland were based on environmental data collected over the year prior to sampling and those in England and Wales were based on environmental data collected in 1995 (or the first year that the site was sampled).
Distance from source	Measured as the distance along the watercourse (to the nearest 0.1 km) between the site and its furthest source, regardless of whether that source was on a tributary known by a different name. The source was considered to be the beginning of the line marking the watercourse on the Ordnance Survey 1:50,000 scale map.
Substrate type	Estimated as percentage coverage of four classes across the entire river width: Boulders & Cobbles (>64 mm), Pebbles & Gravels (2-64 mm), Sand (0.06-2 mm), Silt & Clay (<0.06 mm). There were no records of bedrock channels and therefore all sites can be considered to be alluvial channels.
Channel slope	Measured from Ordnance Survey 1:50,000 scale maps and recorded to the nearest 0.1 metre km^{-1}.
Watercourse width	The width of the water surface (not the stream channel), measured at right angles to the channel to the nearest metre. Measurements taken concurrent with spring, summer and autumn invertebrate sampling to create a mean value.
Channel depth	Depth was averaged from measurements at quarter, half and three-quarter distances across the water surface width in the sampling area. Measurements taken concurrent with spring, summer and autumn invertebrate sampling to create a mean value.

4.3.2 Invertebrate Traits

Eight candidate ecological traits were selected from the invertebrate trait database of Tachet *et al*. (2002) to describe resistance and resilience strategies (Table 4-2). These captured traits such as lifespan, reproductive method and number of reproductive cycles per annum, which are widely used to indicate relative resistance and resilience (Bonada *et al*., 2007; Larsen and Ormerod, 2010; Doledec *et al*., 2011; Gutiérrez-Cánovas *et al*., 2015). Although not indicative of resistance or resilience strategies, the traits of locomotion method and feeding guild were also selected (Table 4-2), to further assess the power of combining traits and simple geomorphic models akin to a habitat template (Quinn and Hickey, 1994; Jowett, 2003). In the Tachet database, each genus is assigned a fuzzy-coded score from zero to three indicating its affinity to each individual category within each trait group (e.g. individual scores for each reproduction method; Tachet *et al*., 2002). These were converted to percentage affinity to each trait category to standardise for potential differences in the fuzzy-coded scores (Gutierrez-Canovas *et al*., 2015). Individual categories for each trait group summed to 100%.

Table 4-2: Eight candidate ecological traits (37 individual categories) for resistance/resilience to bed disturbance and two additional traits (16 categories) for invertebrate locomotion and feeding methods. Trait data from Tachet et al. (2002).

Trait Group	**Trait Categories**
Resistance / Resilience traits	
Body size	<0.25 cm, 0.25 – 0.5 cm, 0.5 – 1 cm, 1 – 2 cm, 2 – 4 cm, 4 – 8 cm, >8 cm
Respiration method	Gill, plastron, spiracle, tegument
Lifespan	<1 year, >1 year
Aquatic Stage	Adult, egg, lava, nymph
Reproductive Cycles per year	<1, =1, >1
Dispersal method	Aerial active, aerial passive, aquatic active, aquatic passive
Reproduction method	Asexual, clutches cemented or fixed, clutches free, clutches in vegetation, clutches terrestrial, isolated egg cemented, isolated egg free, ovoviviparity
Resistance form	Cocoons, diapause or dormancy, eggs, housing, none
Additional traits	
Locomotion Method	Crawler, burrower, flier, surface swimmer, full water swimmer, interstitial, permanently attached, temporarily attached.
Feeding Guild	Absorber, deposit feeder, filter feeder, parasite, piercer, predator, scraper, shredder.

4.3.3 Geomorphic Template

In alluvial rivers, riverbed sediment is transported in two main ways; as bed load, where material rolls along the riverbed typically for relatively short distances (e.g. riffle to riffle), or as suspended load, where material is lifted off the bed surface into the river flow and transported over greater distances (Bagnold, 1956; Engelund and Hansen, 1967). The dominance of each process is controlled by the depth and velocity of flow and the calibre (principally the size) of sediment within the river channel (Dade and Friend, 1998). For example, larger material (e.g. cobbles/pebbles) is typically transported as bedload, whilst smaller material (e.g. sand/silt) is carried as suspended load (Dade and Friend, 1998). As such, riverbeds composed of differing amounts of these materials can behave very differently under flood flow conditions (Wilcock *et al*., 2001; Curran and Wilcock, 2005).

To capture the two main transport mechanisms (bed load vs suspended load), along with a measure of the propensity for riverbed movement (i.e. disturbance), the Shields regime diagram was chosen (Shields, 1936; Figure 4-2B). In simple terms, the model captures variation in physical habitat (through changing substrate size; x-axis of Figure 4-2B) and disturbance regime (through changing propensity for riverbed movement; y-axis of Figure 4-2B), whilst also providing a clear link to geomorphic process via the laboratory defined thresholds for bed load and suspended load transport (Andrews, 1994). Previous studies linking river hydraulics and physical habitat have used the same or closely related measures of substrate size (e.g. D_{50}, Reynolds number) and flow energy (e.g. shear stress, specific stream power, Froude number) in a similar approach (Clifford *et al*., 2006; Bizzi and Lerner, 2012; Vaughan *et al*., 2013; Chapter 3)

4.3.3.1 Shields Regime Diagram

The Shields' (1936) regime diagram comprises the dimensionless Shields' number (τ^*) and the particle Reynolds number (Re_p) which were defined by Parker *et al*. (2003) as:

$$\tau^* = \frac{dS}{RD_{50}}$$

$$Re_p = \frac{D_{50}\sqrt{RgD_{50}}}{\upsilon}$$

where d is flow depth in metres, S is the energy slope in m/m, approximated as the downstream channel bed slope, R represents sediment submerged specific gravity (equal to 1.65), g is the gravitational constant (9.81 m s^{-2}), D_{50} is mean substrate size in metres, v is the kinematic viscosity of water (equal to 1×10^{-6} m^2 s^{-1}). The variable τ^* indicates the likelihood that bed material of a particular size will be mobilized at a particular flow depth, whilst Re_p is a measure of the resistance of the bed material to movement.

Movement of the bed material, as either bed-load or suspended-load, is defined by laboratory defined thresholds and it is this basis in process-based theory that has seen the Shields diagram used in previous studies (Parker *et al*., 2003; Parker *et al*., 2007; Wilkerson and Parker, 2010). Yet these thresholds continue to be contested in scientific literature (Bunte *et al*., 2013), with evidence of wide variations even within a single riverbed (Turowski *et al*., 2011). Here, the equation for the threshold of bed-load motion was calculated from Shields's (1936) flume experiments by Brownlie (1981) and was amended by Parker *et al*. (2003) to the following:

$$\tau^*_{motion} = 0.5\left[0.22{Re_p}^{-0.6} + 0.06\left(10^{-7.7{Re_p}^{-0.6}}\right)\right]$$

Dietrich (1982) defined the equation for the threshold of suspension as the following:

$$\tau^*_{suspension} = e^{\left\{b_1 + b_2 * \ln(Re_p) - b_3 * [\ln(Re_p)]^2 - b_4 * [\ln(Re_p)]^3 + b_5 * [\ln(Re_p)]^4\right\}}$$

where the variables $b_{1\text{-}5}$ are dimensionless coefficients.

4.3.3.2 Flow Depth Estimation

The Shields Regime Diagram requires a representative flow depth to predict the mode of sediment transport present at a point in a channel. Here I chose the flow depth at bankfull discharge, the flow that fills the channel to the bank-tops, as it has been shown to be the most influential discharge on channel form (Pickup and Warner, 1976; Williams, 1978; Andrews, 1980; Phillips and Jerolmack, 2016). However, its infrequent nature and the natural variation in channel capacity along a river reach make bankfull discharge difficult to estimate (Ferguson, 1981). Andrews (1980) estimated bankfull discharge to have a recurrence interval of 1.18 to 3.26 years whilst Carling (1988) estimated it as 0.9 years. In the absence of nearby gauging stations, the median annual flood, or the 2-yr recurrence flow, is typically used instead of bankfull discharge (Wharton, 1995; Gurnell *et al*., 2010; Bizzi and Lerner, 2012). A disadvantage of this approach is that channel-forming (or bankfull) discharge may not be represented well by median annual flood where the river channel has been modified. This was not a problem with the RIVPACS data as sites are selected for their lack of modification (Wright *et al*., 1998).

The 2-yr recurrence flow at each site was extracted from the peak river flows grid product, produced by the Centre for Ecology and Hydrology (CEH) using the Flood Estimation Handbook statistical procedure (Robson and Reed, 1999; Morris, 2003). The flow depth was then estimated using the depth-discharge relation of Thayer (2017). Numerous depth-discharge relations exist but the relation of Thayer (2017) was deemed most suitable due to its applicability in both sand and gravel bedded rivers and its relative simplicity, only requiring measures of discharge (Q_{bf}), mean substrate size (D_{50}) and channel gradient (S).

For gravel-bed rivers:

$$d = 0.152 * {Q_{bf}}^{0.327} * {D_{50}}^{-0.048} * S^{-0.117} \quad (r^2 = 0.895)$$

For sand-bed rivers:

$$d = 0.076 * {Q_{bf}}^{0.222} * {D_{50}}^{-0.032} * S^{-0.278} \quad (r^2 = 0.923)$$

4.3.3.3 Substrate Size

Mean substrate size (D_{50}) was estimated by converting the four measures of percentage coverage by substrate type into an average ϕ score based on approximate values for median particle size of each size class (Harvey *et al*., 2008):

$$D_{50} = \frac{(-7.75 * BOCO\ - 3.5 * GP + 1.5 * SA + 6 * SICL)}{(BOCO + GP + SA + SICL)}$$

where BOCO = boulder-cobble, GP = gravel-pebble, SA = sand, SICL = silt-clay.

4.3.4 Data analysis

4.3.4.1 Invertebrate metrics

Invertebrate community structure was quantified using both taxonomic and trait-based metrics. Taxon richness, total abundance, rarefied richness and evenness provided a basic overview of community structure. Hurlbert's (1971) formulation was used to rarefy taxon richness and evenness was calculated using Pielou's (1975) method. Both were calculated using R's *vegan* package (Oksanen, 2016).

Ecological traits were used in two ways: i) *individually*, as the percentage of individuals at each site that possessed a given trait, and ii) combined into multivariate functional diversity measures for whole communities. Prior to the analyses, the set of candidate ecological traits for resistance/resilience to disturbance (Table 4-2) was reduced by selecting those trait groups (out of the eight groups) whose mean R^2 values were > 0.2 from models of each trait category's distribution on the Shields regime diagram (37 categories in total, Table 4-2; Gutierrez-Canovas *et al*., 2015). This was required to: i) ensure that the functional patterns could be clearly identified (Villéger *et al*., 2008; Gutierrez-Canovas *et al*., 2015) and ii) greatly reduce overall computational times for the null model analysis (see below), which were very long due to the number of sites. Five trait groups, containing a total of 21 individual categories, met this condition: the number of reproductive cycles per year, lifespan, dispersal method, reproduction method and aquatic stage (Table 4-3). For the analysis of individual ecological traits, the 21 categories were further reduced by only retaining those that had an $R^2 > 0.2$. Highly disturbed communities were expected to have a greater proportion of individuals possessing traits indicative of resistance and/or resilience: faster reproductive cycles, shorter lifespans, aerial dispersal, larval aquatic stage and cemented or fixed eggs. By dispersing aerially, species are able to reduce their time spent in the channel (therefore avoiding a potential high flow event) and cover greater distances, particularly upstream, speeding up recolonization of a river reach after a disturbance event (Schmidt *et al*., 1995; Hughes, 2007). Eggs held in place by cementation resist high shear stresses exerted in fast flows but typically require a hard substrate to be fixed to (Diaz *et al*., 2008).

Table 4-3: Individual and groups of traits, as described in Tachet et al. (2002), shown with R^2 values for fitted models of each trait or mean values for each trait grouping (in brackets). R^2 values in bold indicate the traits with the strongest affinities (>0.2) to the geomorphic template used in the model whose trends are described in Section 4.4.3.

Trait Name		**R^2**	**Trait Name**		**R^2**
Resistance / Resilience traits					
Reproduction Method (0.21)	Asexual	0.18	*Aquatic Stage (0.20)*	Adult	**0.43**
	Clutches cemented or fixed	**0.33**		Egg	0.07
	Clutches free	0.02		Lava	**0.28**
	Clutches in vegetation	0.07		Nymph	0.03
	Clutches terrestrial	0.04	*Lifespan (0.28)*	<1 year	**0.28**
	Isolated egg cemented	0.41		>1 year	**0.28**
	Isolated egg free	0.19	*Dispersal Method (0.26)*	Aerial Active	**0.47**
	Ovoviviparity	**0.38**		Aerial Passive	0.03
Reproductive Cycles per year (0.37)	<1	**0.43**		Aquatic Active	0.15
	=1	**0.31**		Aquatic Passive	**0.42**
	>1	**0.37**			
Additional Traits					
Locomotion Method (0.12)	Burrower	**0.30**	Feeding Guild (0.16)	Absorber	**0.21**
	Crawler	0.18		Deposit feeder	0.14
	Flier	0.08		Filter feeder	0.10
	Surface swimmer	0.08		Parasite	0.01
	Full water swimmer	0.08		Predator	0.10
	Interstitial	0.07		Piercer	0.06
	Permanently attached	0.05		Scraper	**0.36**
	Temporarily attached	0.11		Shredder	**0.23**

Functional diversity, the variability in a set of ecological traits at the community level, can be summarised in a multidimensional space, known as ‘functional space’ (Villéger *et al*., 2008; Mouillot *et al*., 2013). The functional space was created using principal coordinates analysis (PCoA) of the ecological traits of the 242 invertebrate taxa based on Euclidean distances (Legendre and Legendre, 1998; Villeger *et al*., 2008). The number of PCoA axes retained represents the number of dimensions in which functional space is defined (Villéger *et al*., 2008). A broken stick model was used to find optimum number of PCoA axes to use to balance simplicity against the explanatory power of the PCoA (Gutierrez-Canovas *et al*., 2015). Six axes, explaining 80% of the variance in the trait data, were selected for inclusion in the calculation of functional metrics.

Three functional metrics that recognise complementary facets of functional diversity were calculated using the FD package in R (Villéger *et al*., 2008; Laliberté and Legendre 2010); (1) functional richness (FRic), a measure of the volume of functional (trait) space occupied, (2) functional evenness (FEve), a measure of the evenness of the distribution in macroinvertebrate abundance across the functional space and (3) functional dispersion (FDis), the extent to which taxon abundance is spread towards the extremes of functional space (Figure 4-1). FRic and FDis in particular are valuable for assessing the potential assembly rules for communities (Mason *et al*., 2013). Strong environmental filtering results in lower functional diversity, with reduced FRic and lower FDis (Figure 4-1), as fitness of a taxon is maximised by being close to some optimum (e.g. possession of a particular set of traits for withstanding bed disturbance). With more benign conditions (e.g. less bed disturbance), fitness is maximised by minimising potential niche overlap – hence competition – among taxa (consistent with the limiting similarity principle; Abrams, 1983), so greater dispersion in functional space would be expected (Mason *et al*., 2013; Figure 4-1).

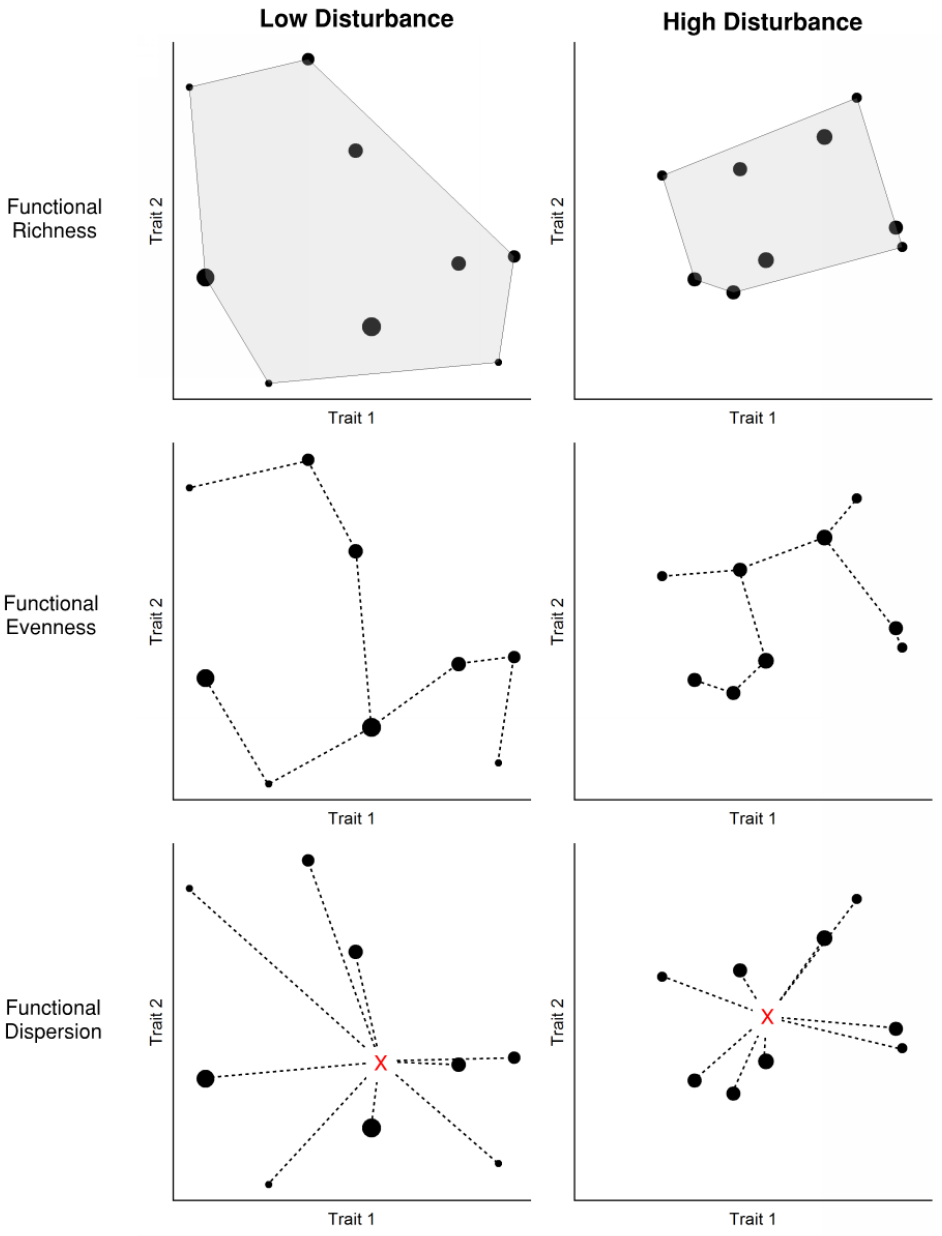


Figure 4-1: Predicted effects of increased riverbed disturbance on functional diversity indices in multidimensional functional space (two dimensions are shown here for simplicity). Each point represents one taxon, plotted according to its trait values, with point diameter proportional to taxon abundance. Functional richness (FRic) is calculated as the size of the convex hull that encapsulates all of the points in space, and is independent of abundance. Functional evenness (FEve) uses the minimum spanning tree (dashed line) to measure the regularity between point spacing and size (i.e. abundance) along the tree. Functional dispersion (FDis) measures the overall distance of all taxa from the centroid of the community and is weighted by abundance. Increased disturbance is expected to result in lower FRic (i.e. a smaller convex hull), higher FEve (i.e. more regular spacing and size along the minimum spanning tree) and lower FDis (i.e. a lower mean distance to the centroid) (Legendre and Legendre, 1998; Villeger et al., 2008).

4.3.4.2 Null models

Variations in taxonomic richness, which may be sensitive to differences in abundance among samples, can generate spurious relationships between environmental and functional variables (Villéger *et al*., 2008; 2011). Null models provide a basis for overcoming this problem, simulating the expected changes in functional diversity that would result from varying richness, against which the observed patterns of functional diversity can be compared. This null modelling process was used to correct FRic and FDis for potential sampling effects: the formula for FEve makes it independent of taxonomic richness (Villéger *et al*., 2008). The independent-swap method was used to create 999 artificial site vs genera matrices from the original dataset (Gotelli, 2000; Mason *et al*., 2013). Functional richness and functional dispersion were then re-calculated for the artificial matrices at each of the 714 sites. The mean expected values and standard deviations (from the null modelling) and the observed trends were then used to calculate the standard effect size for the two functional metrics:

$$SES = \frac{(I_{obs} - I_{sim})}{\sigma_{sim}}$$

where I_{obs} = observed value of the index (FRic or FDis), I_{sim} = the mean value of the index from the iterations of the null model and σ_{sim} = the standard deviation of the index from the model iterations (Gotelli and McCabe, 2002). The trend in standardised effect size can be interpreted in the same way as measures such as species richness, whilst standard effect sizes greater than +/- 2 are deemed to exceed the approximate 95% significance level, indicating that the observed values are significantly different to a random expectation (Mason *et al*., 2013). The null model adjusted values of FRic and FDis are denoted ses.FRic and ses.FDis respectively.

4.3.4.3 Regression modelling

Community metrics, functional metrics and individual traits were modelled as a function of τ^* and Re_p, the two axes of the Shield's diagram, using generalised additive models (GAMs) with identity links and Gaussian errors. Alkalinity, to control for variation in water chemistry, and distance from source, to control for river size, were also included as covariates, as these can have large effects upon the invertebrate community (Wright *et al*., 1998). τ^* and Re_p were modelled using a tensor product of thin-plate regression splines, whilst the other variables were modelled using standard regression splines, with the degree of smoothing determined by generalized cross validation (Wood, 2006). This approach accommodated interactions between τ^* and Re_p, whilst minimizing the risks of overfitting the data by fitting too complex a relationship (Wood, 2006; Vaughan *et al*., 2013). As a non-linear method, GAM is able to detect sudden changes, such as those expected to occur at the thresholds of bed load and suspended load transport, or a unimodal response consistent with the intermediate disturbance hypothesis (Connell, 1978). The fit of each model was checked by examining plots of the residuals.

To assist with interpretation of the models, predictions were generated along four slices through the Shield's diagram. Fixed values of Re_p were used, corresponding to rivers with substrates of cobble, gravel, sand and silt. This method allowed for comparison between riverbeds composed of different sediment calibres, particularly fine and coarse substrates, which are known to function in distinct ways. Riverbeds composed of sand derive their stability principally through bedform resistance (Smith, 1970), whilst coarse riverbeds (i.e. gravel and cobble) are more reliant upon the resistance of individual particles (Andrews, 1983). The wider gradient from coarse to fine riverbeds is most representative of catchment position and was deemed to be less useful for the study of the hypotheses considered here. This process which drives this gradient is termed downstream fining, whereby particle size decreases with distance downstream, largely due to particle abrasion and selective transport (Hoey and Ferguson, 1994).

These slices were then plotted alongside one another to show the variation in predicted values of the biological metrics for the different substrate types as the propensity for disturbance increased and the transport process changed from no bed movement towards bed load dominant to suspended load dominant. This method simplified identification of potential nonlinear changes in community composition at the predicted threshold values for bed and suspended load transport.

4.4 Results

The RIVPACS sites were distributed across Britain (Figure 4-2A), with some bias towards upland rivers as a result of their lower likelihood of modification and generally higher water quality. Lowland sites were largely restricted to high baseflow chalk streams in south east England. The sampling density was higher in coarse bed rivers (gravel/cobble) than finer substrates (Figure 4-2B). This is to be expected as these rivers are much more common in Britain, in addition to the greater representation of upland rivers in the data set. Despite this, the sites spanned a broad range of sediment transport modes and propensities, ranging from boulder channels that are unlikely to experience bed load transport at bankfull discharge, through to rivers with silt beds that are constantly being redistributed by suspended load transport (Figure 4-2B).

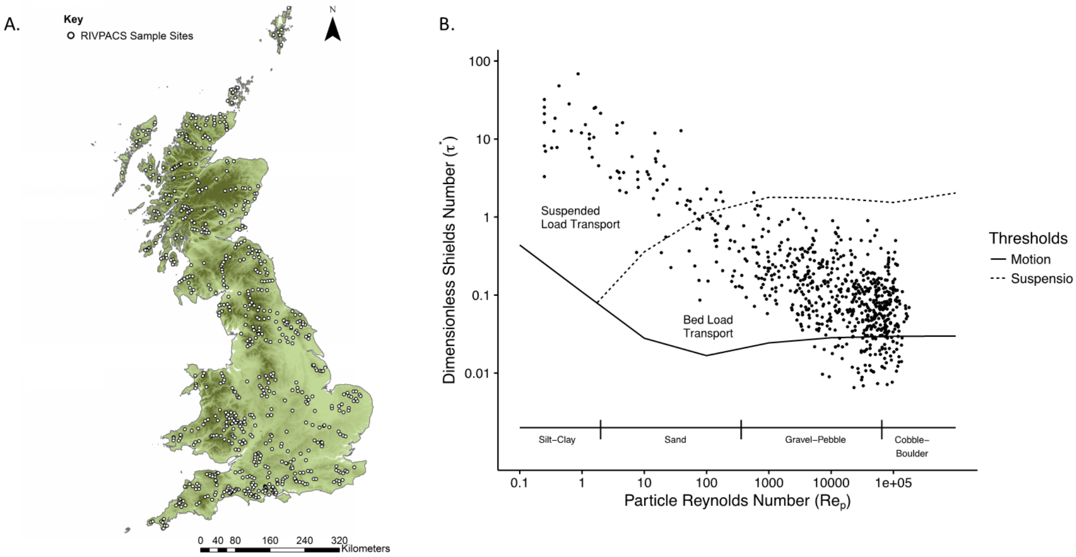


Figure 4-2: (A) A map showing the location of the 714 RIVPACS sites used in the study. The bias towards upland rivers, due to the requirement for relatively pristine watercourses, is evident. (B) The same 714 RIVPACS sites plotted on the Shields Regime Diagram. The black line denotes a laboratory defined threshold for the initiation of bed load motion of sediment (Parker et al., 2003), whilst the dotted black line represents the threshold for suspended-load transport (Dietrich, 1982).

The tensor smooths of τ^* and Re_p were statistically significant at $p < 0.001$ in every GAM for community and functional metrics, other than evenness and functional evenness, which both had non-significant p values (>0.18) i.e. there was no systematic variation in taxonomic or functional evenness across the Shields' diagram (

Table 4-4). The additional predictors of alkalinity and distance from source were significant at $p < 0.01$ in all models except for FDis (alkalinity $p = 0.83$, distance from source $p = 0.028$), ses.FRic (distance from source $p = 0.40$) and ses.FDis (both variables $p > 0.10$;

Table 4-4) but were retained in the models to simplify the interpretation of results.

4.4.1 Community metrics

The GAMs for the community metrics varied widely in their explanatory ability, from rarefied richness ($R^2 = 0.10$), through richness (0.35), to abundance (0.46). Overall, increasing disturbance propensity (τ^*) resulted in decreased species richness across all substrate types, and a decrease in abundance in cobble, gravel and sand substrates (Figure 4-3B & 4-3D). Rarefied richness showed a contrasting response to disturbance propensity between coarse (gravel and cobble) and fine (sand and silt) substrates, with a steep decrease with disturbance in sand and silt substrates, and little to no change with disturbance in gravel and cobble substrates (Figure 4-3F).

In gravel to boulder substrates, species richness ranged from 66-88 yet in finer substrates (clay to sand) a higher range of 81-96 was observed, with no evidence for nonlinearity over the motion/suspension thresholds (Figure 4-3B). Abundance declined with increasing disturbance propensity from 6500 to 2250 individuals per sample in cobble substrates, with the steepest decline around the threshold of bed load motion, and it also declined from 6600 to 4000 in gravel substrates, mirroring the trends in species richness (Figure 4-3D). In sand substrates, no significant change with increasing propensity for disturbance was observed and in silt substrates abundance increased from 4800 to 7600 (Figure 4-3D). This increase in abundance in silt-clay substrates was driven by a small number of taxa, including *Potamopyrgus*, *Gammarus*, dipterans and oligochaetes. Species richness and abundance both showed distinct overall minima in cobble-boulder substrates with the highest propensity for disturbance (Figure 4-3A & 4-3C).

Rarefied richness showed little or no change with disturbance propensity in cobble or gravel substrates (Figure 4-3F). This indicates that the observed decline in species richness in gravel and cobble substrates was driven by a reduction in the overall abundance of individuals i.e. a sampling effect (Magurran, 2004). Rarefied richness in sand and silt declined from 46 to 38 taxa, indicating that the decreases in standard species richness with increasing disturbance propensity were independent of overall abundance. As with species richness, the slices through the rarefied richness surface showed no evidence of nonlinearity as they crossed the motion and suspension thresholds (Figure 4-3E).

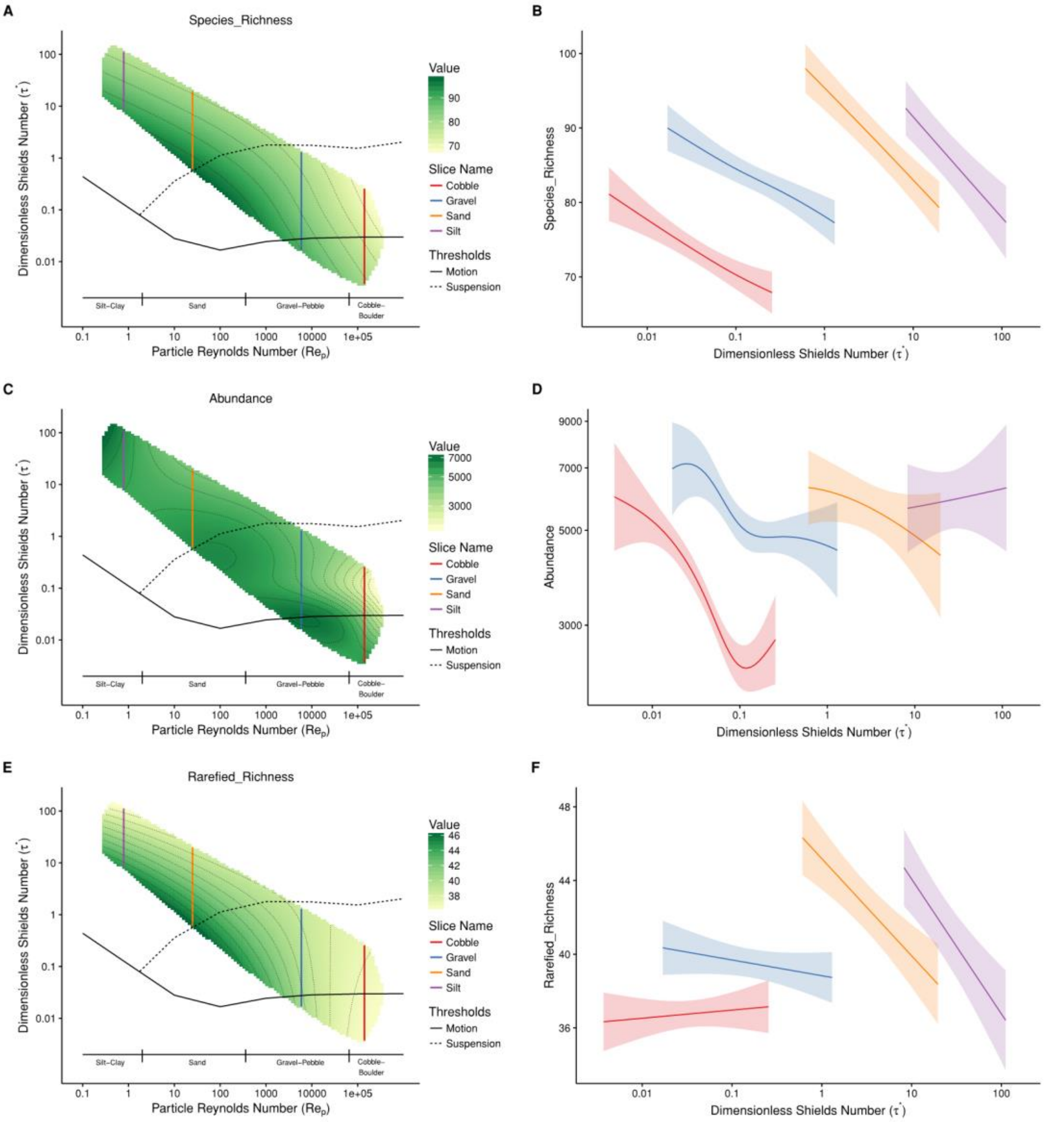


Figure 4-3: The community metrics of species richness (A & B), abundance (C & D) and rarefied richness (E & F) are plotted as Generalised Additive Models on the Shields Regime Diagram (left) with slices through the models plotted against the y-axes of the Shields Regime Diagram (right), which represents the propensity for riverbed disturbance in the form of sediment transport. The coloured lines and error bars denote slices taken through the GAM at cobble (red), gravel (blue), sand (orange) and silt (purple) substrates.

4.4.2 Functional diversity

The GAMs for FRic and FDis had R^2 values of 0.33 and 0.18 respectively, which once corrected for richness and abundance, decreased to 0.14 for ses.FRic and 0.10 for ses.FDis. Functional richness was similar across silt, sand and gravel substrates, with little evidence of an effect of disturbance propensity, whilst FRic declined rapidly with disturbance propensity in cobble substrates (Figure 4-4A; 4-4B). When correcting for taxonomic richness, ses.FRic revealed a strong contrast in the effect of disturbance propensity (τ^*) across the substrate gradient (Figure 4-5A; 4-5B): ses.FRic declined with disturbance propensity in cobbles, increased weakly in gravel, and showed large increases in sand and silt. Although species richness declined with increasing propensity for disturbance in sand and silt substrates (Figure 3B), the communities became more functionally diverse relative to the number of taxa present. For cobble substrates, the trends in FRic and ses.FRic were the same, indicating that the decline in FRic was not an artefact of declining taxonomic richness.

Functional dispersion decreased with increasing substrate size as well as increased propensity for disturbance (Figure 4-4C; 4-4D). When corrected for the variation in richness and abundance between sites, ses.FDis showed a broadly similar pattern, decreasing with disturbance propensity in the coarser substrates (Figure 4-5C; 4-5D). The decrease in average ses.FDis with increasing substrate calibre was smaller than for FDis (Figure 4-5D).

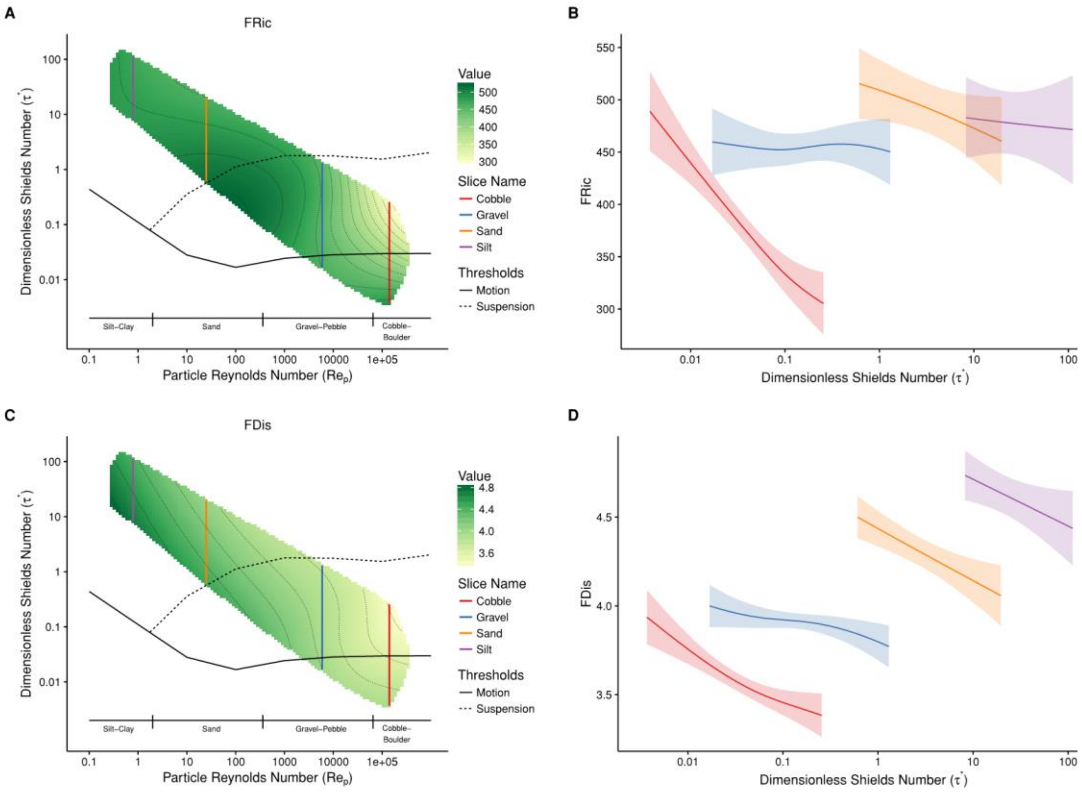


Figure 4-4: The metrics of functional richness (FRic; A & B) and functional dispersion (FDis; C & D) are plotted as Generalised Additive Models on the Shields Regime Diagram (left) with slices through the models plotted against the y-axes of the Shields Regime Diagram (right), which represents the propensity for riverbed disturbance in the form of sediment transport. The coloured lines and error bars denote slices taken through the GAM at cobble (red), gravel (blue), sand (orange) and silt (purple) substrates.

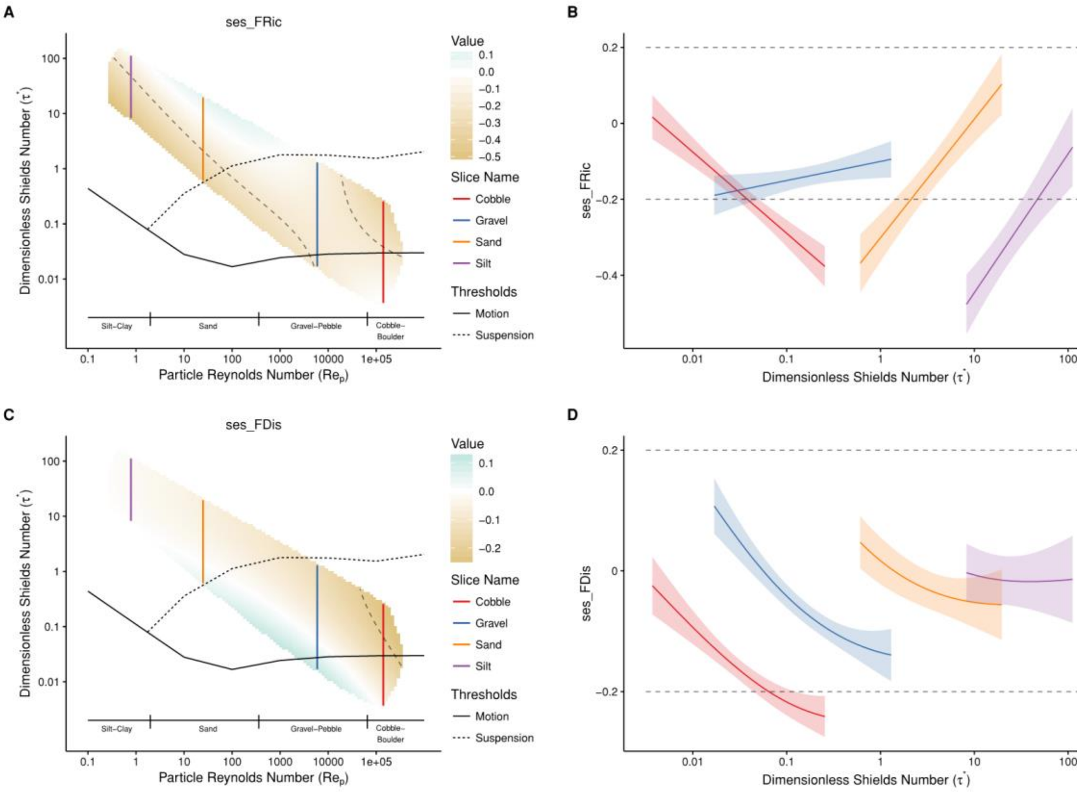


Figure 4-5: Null models of functional richness (A & B; ses.FRic) and functional dispersion (C & D; ses.FDis) are plotted as Generalised Additive Models with a diverging colour gradient on the Shields Regime Diagram (left). The dashed grey lines are thresholds of +/- 0.2 which indicate the approximate 5% significance level and are deemed as significantly different to the random expectation (Mason et al., 2013). Slices through the models are plotted against Dimensionless Shields Number (right) which represents the propensity for riverbed disturbance in the form of sediment transport. The coloured lines and error bars denote slices taken through the GAM at cobble (red), gravel (blue), sand (orange) and silt (purple) substrates.

4.4.3 Individual resistance/resilience traits

The tensor smooths of τ^* and Re_p were statistically significant at $p < 0.001$ in every GAM of the selected individual traits (Table 4-5). Variation in many of the ecological traits was consistent with the hypothesis that communities in rivers with a higher propensity for disturbance would have a greater proportion of resistance traits, although there were some notable exceptions. Consistent with hypothesis 3, invertebrate communities in rivers with increasing bed disturbance propensity had greater proportions of taxa with shorter lifespans (< 1 year), aerial dispersal, larval aquatic stages and clutches of cemented or fixed eggs (Figure 4-6 to Figure 4-9). Short lifespans (<1 year) were generally more common than longer lifespans (>1 year) and made up ever greater proportions of communities with increasing propensity for disturbance in cobble (70-80%), gravel (60-75%) and sand (55-60%) substrates (Figure 4-6A). Silt substrates showed little change with increasing propensity for disturbance and had the highest proportions of lifespans >1 year at approximately 45% (Figure 4-6B).

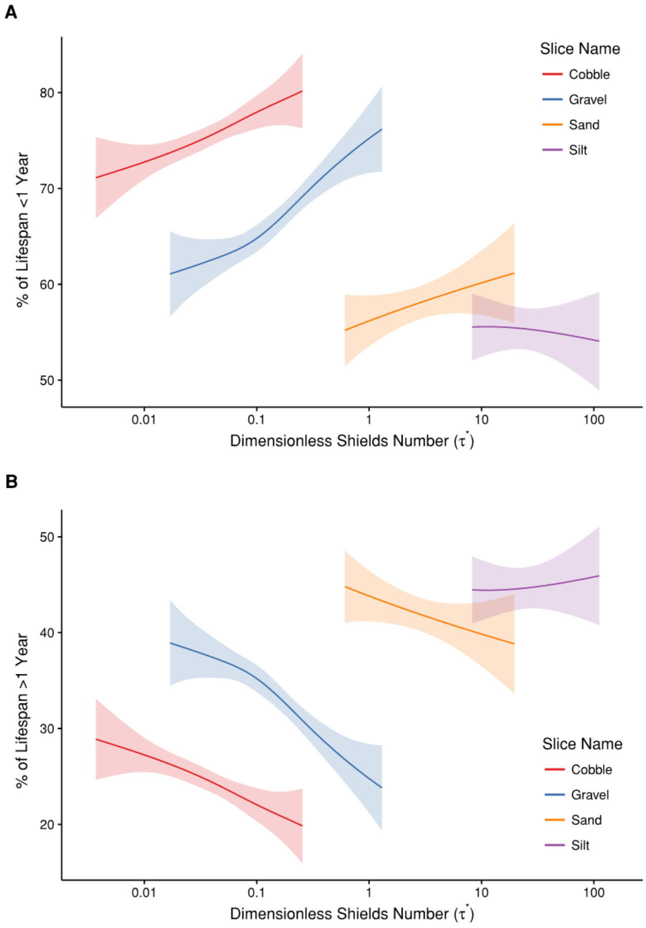


Figure 4-6: The proportion of an invertebrate community with lifespans of (A) <1 year and (B) >1 year, plotted against a measure of propensity for disturbance (Dimensionless Shear Stress - τ^**). The coloured lines and error bars denote slices taken through the GAM at cobble (red), gravel (blue), sand (orange) and silt (purple) substrates.*

The proportion of individuals that passively dispersed in the water column declined with increasing disturbance propensity in all substrates and ranged from 55% of a community in silt substrates to 35% in cobble substrates (Figure 4-7A). Conversely, the proportion of individuals with the aerial active dispersal method increased with increasing propensity for disturbance in all substrates and ranged from 26% of a community in highly-disturbed cobble substrates to <15% in low disturbance silt substrates (Figure 4-7B).

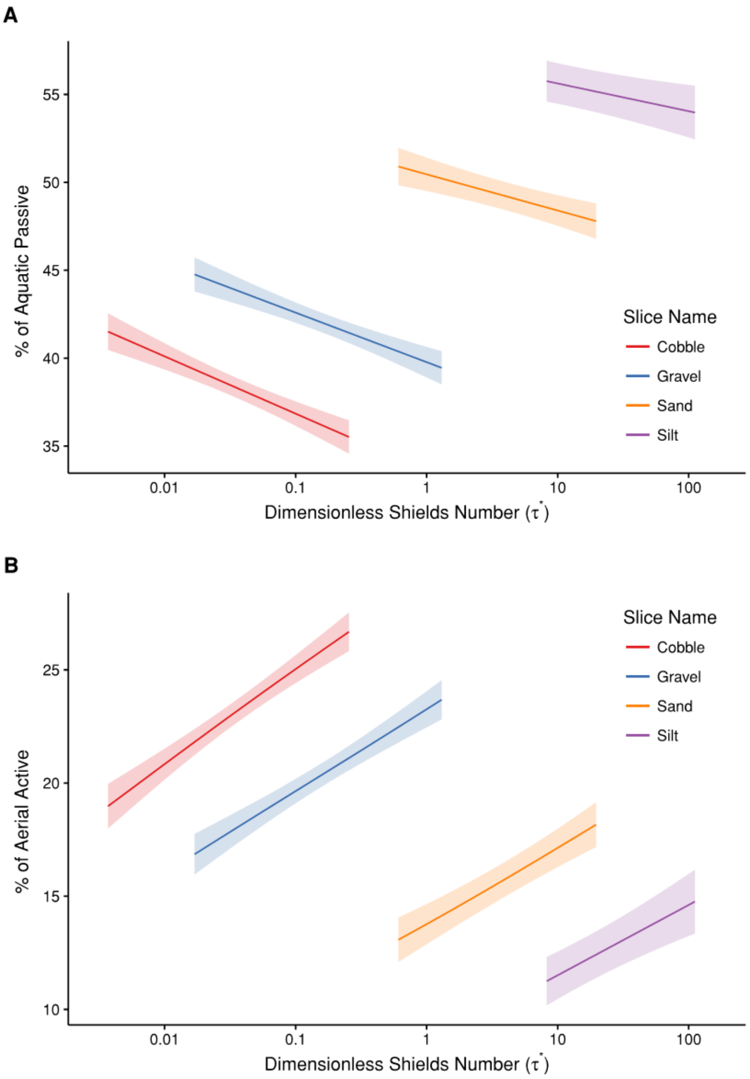


Figure 4-7: The proportion of an invertebrate community with dispersal methods of (A) aquatic passive and (B) aerial active, plotted against a measure of propensity for disturbance (Dimensionless Shear Stress - τ). The coloured lines and error bars denote slices taken through the GAM at cobble (red), gravel (blue), sand (orange) and silt (purple) substrates.*

A larval aquatic stage was common in all environments, ranging from 33 to 44% of a community, becoming more common with increasing propensity for disturbance in gravel and cobble substrates but showing no change in silt and sand substrates (Figure 4-8A). An adult aquatic stage was most common (approx. 20% of individuals) in silt and sand substrates, showing little change with increased propensity for disturbance, and inverse to larval aquatic stage, adult stage declined from 16% to 5% in gravel and cobble substrates (Figure 4-8B).

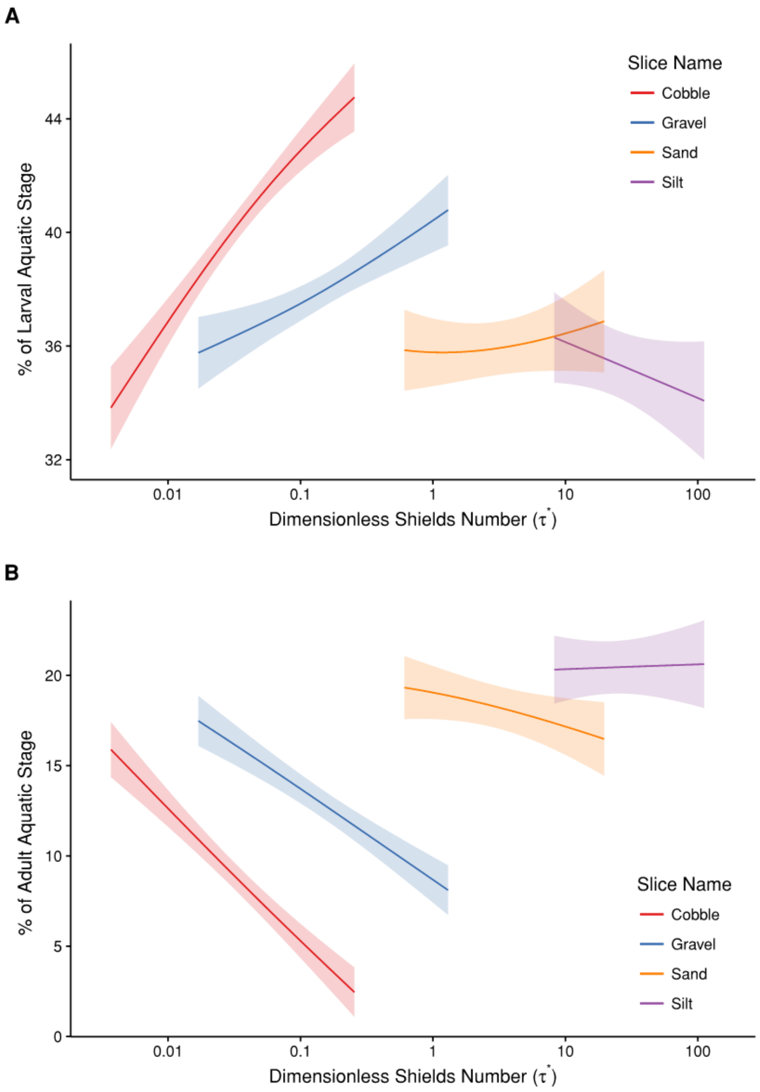


Figure 4-8: The proportion of an invertebrate community with aquatic stages of (A) lava and (B) adult, plotted against a measure of propensity for disturbance (Dimensionless Shear Stress - τ^**). The coloured lines and error bars denote slices taken through the GAM at cobble (red), gravel (blue), sand (orange) and silt (purple) substrates.*

In gravel and cobble substrates, cemented or fixed eggs (isolated or in clutches) became more common with increasing propensity for disturbance, whilst ovoviviparous individuals declined. Conversely, ovoviviparity became more common and cemented isolated eggs became less common with increasing propensity for disturbance in sand and silt substrates, whilst an increase in cemented clutches remained. Between 20 and 30% of each community in sand, silt and low disturbance gravel and cobble substrate was ovoviviparous, decreasing to 0% in highly disturbed cobble substrates (Figure 4-9A). Cemented isolated eggs were most common in highly disturbed cobble and gravel substrates, where they made up 20-25% of each community (Figure 4-9B). Cemented or fixed clutches were common across all areas, making up 30% of communities in low disturbance silt substrates and up to 50% of communities in highly disturbed cobble substrates (Figure 4-9C). Reproduction by eggs was more common in coarse substrates, whilst ovoviviparity was more common in fine substrates.

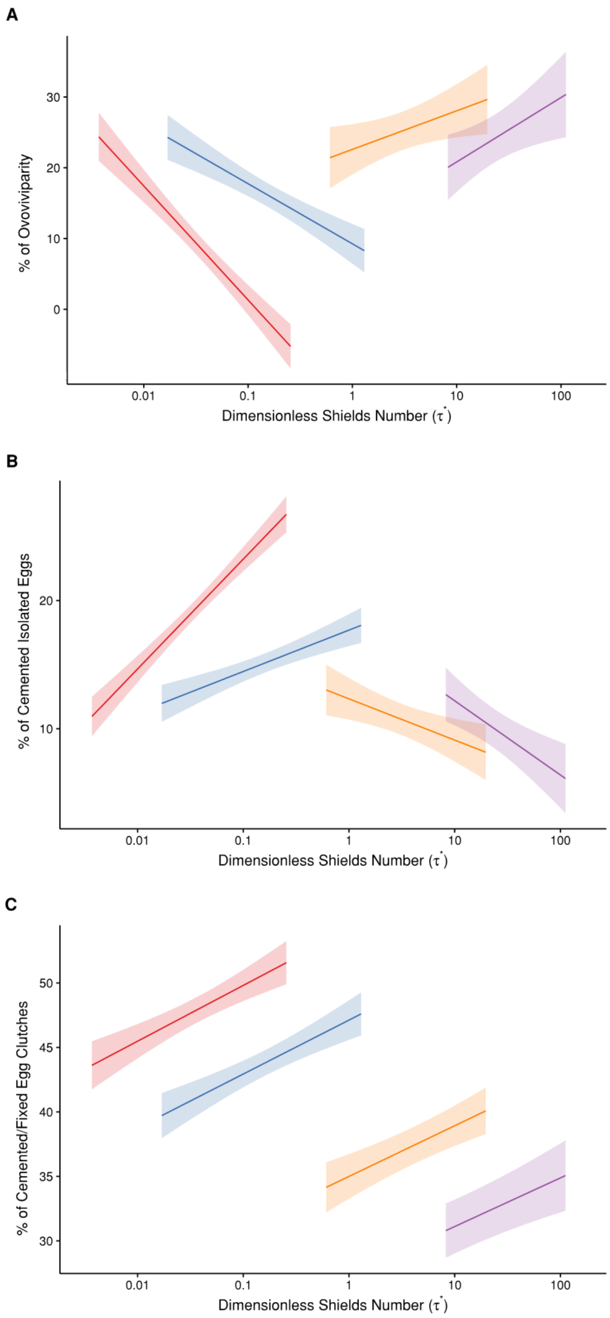


Figure 4-9: The proportion of an invertebrate community with reproduction method of (A) ovoviviparity, (B) isolated cemented eggs and (C) clutches – cemented or fixed, plotted against a measure of propensity for disturbance (Dimensionless Shear Stress - τ^**). The coloured lines and error bars denote slices taken through the GAM at cobble (red), gravel (blue), sand (orange) and silt (purple) substrates.*

Slow reproductive cycles (<1 per annum) were rare (always ≤8% of the community) and had a complex relationship with increasing disturbance propensity. In cobble substrates, the proportion increased from 2 to 8% of the community and peaked at the threshold for bedload transport, whilst gravel substrates showed no clear trend and sand or silt substrates showed a decreasing trend (Figure 4-10A). Thus, the increase in slower reproductive cycles with increasing propensity for disturbance was driven by single (=1) reproductive cycles per annum becoming more common and a corresponding reduction in the proportion of communities with multiple cycles per annum (Figure 4-10B; 4-10C). Despite this, multiple reproductive cycles per annum composed >50% of every community across all substrates and disturbance propensities, other than cobble substrates with a high propensity for disturbance, where one cycle per annum was the most common (Figure 4-10B; 4-10C).

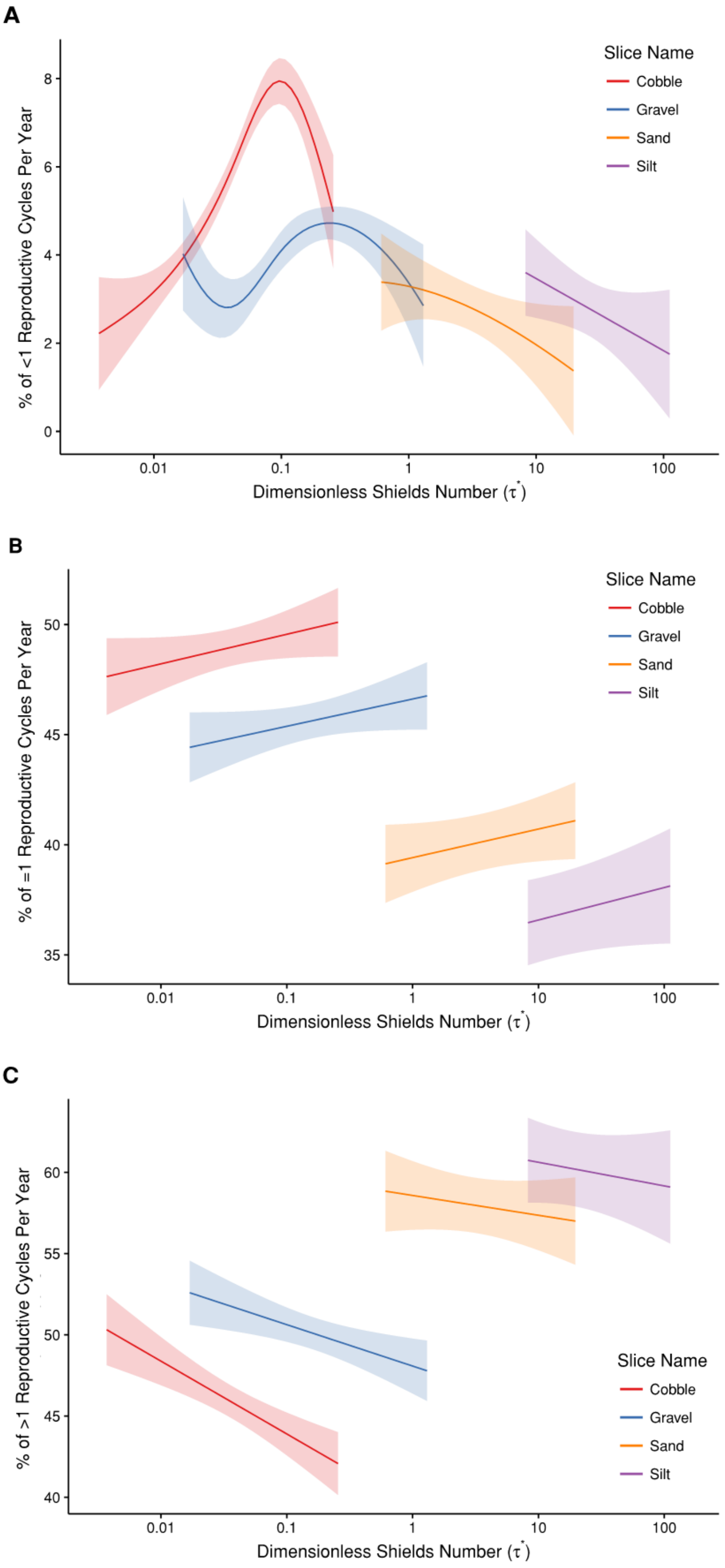


Figure 4-10: The proportion of an invertebrate community with reproductive cycles of (A) <1 cycle p/y, (B) 1 cycle p/y and (C) >1 cycle p/y, plotted against a measure of propensity for disturbance (Dimensionless Shear Stress - τ^*). The coloured lines and error bars denote slices taken through the GAM at cobble (red), gravel (blue), sand (orange) and silt (purple) substrates.

4.4.4 Feeding guilds and locomotory traits

Variation in locomotion and feeding traits matched expectations as substrate type changed from soft (e.g. silt and sand) to hard (e.g. gravel and cobble). Soft substrates had the highest proportion of burrowing organisms (15 to 25% of a community; Figure 4-11B) and as a result of Oligochaetes, the highest proportion of absorbers (3 to 5% of a community; Figure 4-12A). Burrowers typically declined with increasing propensity for disturbance, whilst absorbers showed no change. Crawlers and scrapers became more common with increasing sediment calibre and propensity for disturbance, and were common in all regions, but shredders had a more complex response to both axes (Figure 4-11A; Figure 4-12B; Figure 4-12C). Increasing propensity for disturbance led to an increase in shredders in sand and silt substrates and a decrease in cobble and gravel, with them least commonly found (< 20% of a community) in cobble and gravel substrates with high propensity for disturbance (Figure 4-12B).

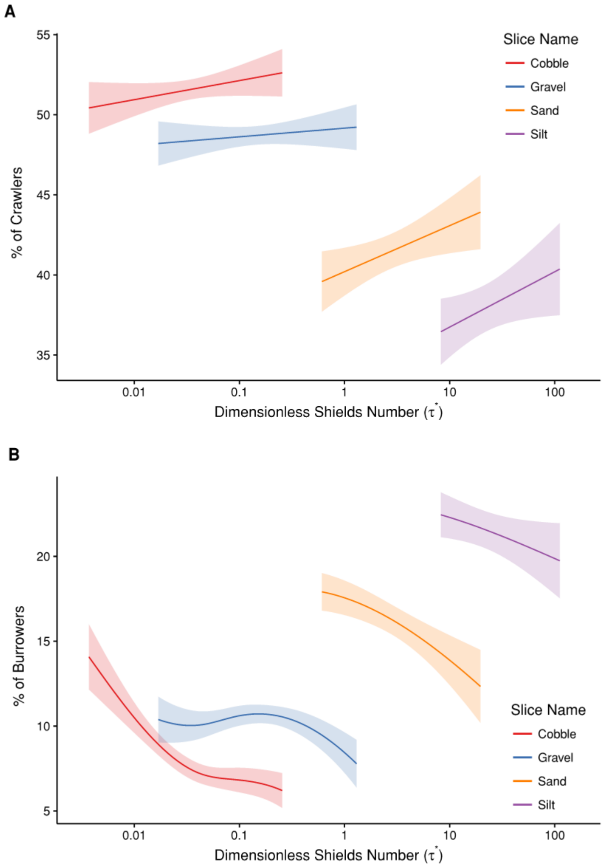


Figure 4-11: The proportion of an invertebrate community with locomotion methods of (A) crawler and (B) burrower, plotted against a measure of propensity for disturbance (Dimensionless Shear Stress - τ^*). The coloured lines and error bars denote slices taken through the GAM at cobble (red), gravel (blue), sand (orange) and silt (purple) substrates.

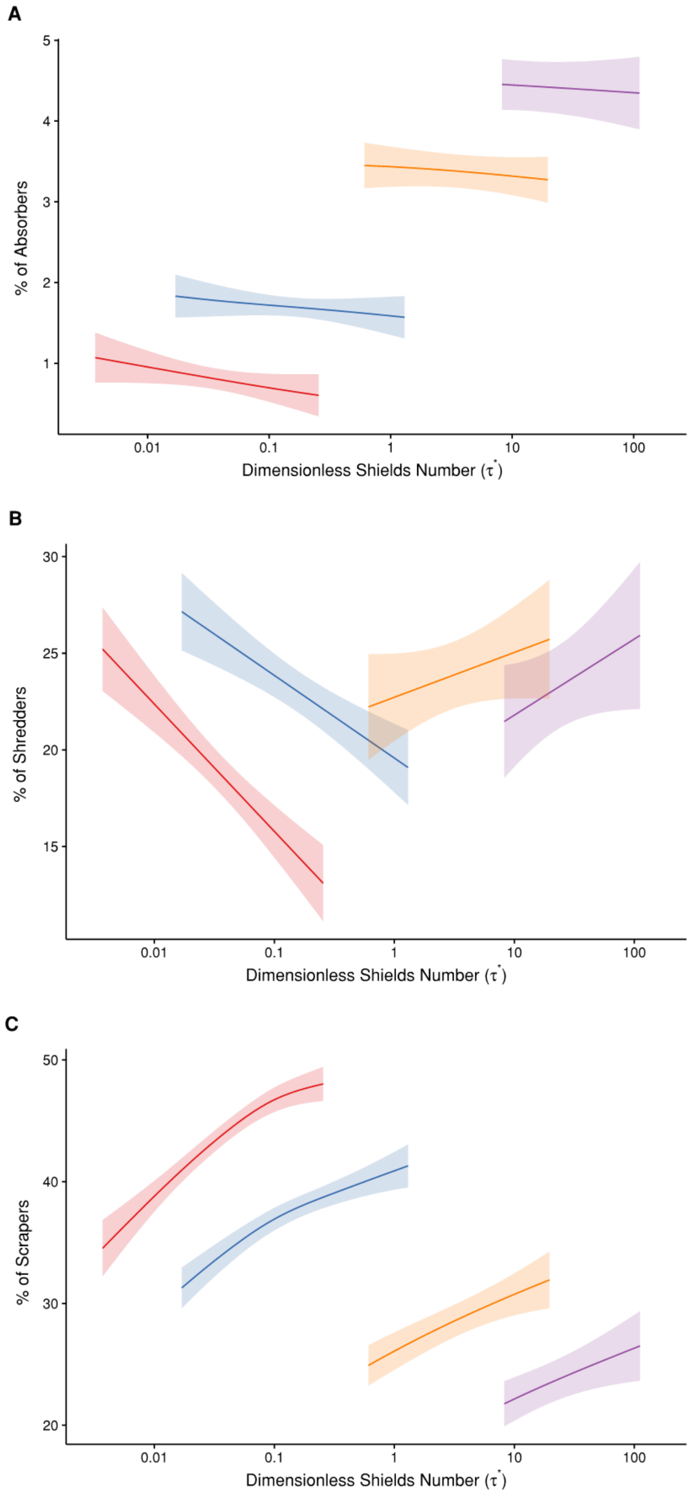


Figure 4-12: The proportion of an invertebrate community with feeding methods of (A) absorber, (B) shredders and (C) scrapers, plotted against a measure of propensity for disturbance (Dimensionless Shear Stress - τ^*). The coloured lines and error bars denote slices taken through the GAM at cobble (red), gravel (blue), sand (orange) and silt (purple) substrates.

4.5 Discussion

Understanding the interactions between physical habitat and biodiversity is important and understanding at sufficient scales to inform river management is vital if mitigations or adaptations to future change are to be successful. At present, due to resource and data limitations, studies have been restricted to small scales or simply correlate observed organisms to simple measures of observed habitat e.g. current bed material composition (e.g. Death and Winterbourn, 1995; Townsend *et al.*, 1997). This study has combined a large, national-scale data set with a simple, static model of particle entrainment based on mechanistic first principles to link physical habitat with benthic community composition in UK rivers. The model was selected due to its low data requirements and solid grounding in past studies and theory (Parker *et al.*, 2003; Parker *et al.*, 2007; Wilkerson and Parker, 2010). Whilst more mechanistic modelling is desirable (Meyer-Peter and Muller, 1948; Wilcock and Crowe, 2003), the requisite data are typically more difficult to obtain, particularly at the national scale considered here. The adoption of the Shields' diagram is a first, pragmatic step towards more mechanistic modelling. Here I discuss key limitations of the study before discussing the results in detail.

4.5.1 Limitations

There were four important limitations to this study, namely the reliance on secondary data and current trait information, the inability to account for outside factors that also control invertebrate communities (e.g. climate, resource availability, competition) and the lack of field verification of dimensionless shear stress.

Firstly, in spite of the strengths of the RIVAPCS data set (e.g. sample size, taxonomic resolution), the use of secondary data has a number of limitations (Vaughan and Ormerod, 2010), which here included (1) the under-representation of lowland watercourses as RIVPACS selects pristine sites it is inherently biased to upland areas (Figure 4-2A), and (2) restrictions on the quality of available data for water quality and channel morphology. The use of the Shields Regime Diagram as a representation of the range of the channel morphologies present in the dataset introduced a reliance on the various components used to calculate τ^* and R_{ep}, which make up the axes of the Shields Regime diagram. The components, namely flow depth, bankfull discharge, channel bed slope and median surface grain size, were all estimates and potential error in each of these has scope to introduce a significant composite error.

The potential sources of error in the components and how these have been considered in this study are discussed below:

1. Flow Depth: This estimation was reliant upon the relations of Thayer (2016), which themselves were reliant upon the estimation of bankfull discharge and slope. Thayer (2016) demonstrated that the depth relations for gravel and sand bed rivers were more accurate than existing relations. In a test of the relations using independent data, they found that the median value of the depth predictions was 1.61% and 2.48% lower than the actual values for gravel and sand bed rivers respectively (see Table 2 from Thayer, 2016).
2. Bankfull Discharge: Taken as the 2-year recurrence flow from the CEH peak river flows grid product which itself is estimated using the Flood Estimation Handbook (FEH) statistical procedure (Kjeldsen *et al*., 2008). This method introduces two types of potential error, the accuracy of the statistical method for deriving peak flows and the applicability of using the 2-year recurrence flow as a proxy for bankfull discharge. The accuracy of the FEH procedure for estimating peak flows was tested by Calver *et al*. (2009) who found that at 2-year recurrence flows, estimations were within +/- 30% of gauged flows. The applicability of using the 2-year recurrence flow is discussed in Section 4.3.3.2.
3. Channel Slope: Included in the RIVPACS dataset and calculated from the contours on a 1:50000 map. The estimation of channel slope from digital elevation model derived contours has been shown to be very sensitive to the elevation data and the calculation of channel length (Jain *et al*., 2006; Neeson *et al*., 2011). Given the relatively large scale of the mapping used to derive channel slope, estimates are likely to be most accurate in larger rivers where the true channel length is best represented. In smaller rivers, the channel length is likely to be under-estimated (leading to an over-estimation of slope) as the complexity of a small meandering channel would be under represented by the ‘blue-line’ shown on the mapping.
4. Median Substrate Size (D50): The estimation of D50 using the four groups of sediment type (silt, sand, gravel-pebble, cobble-boulder) would introduce error as the potential variation in grain size is minimised using this approach. Given that improved data is not available at this scale it is difficult to attribute a proportion of error to the data. The estimation of riverbed substrate size could be improved by using pebble counts or sediment sieving, which would have provided greater accuracy.

Each of these estimated components was assessed visually to ensure that range of values were sensible prior to their use.

The second limitation of the study was the trait database (Tachet *et al*., 2002) used to assign traits to invertebrate taxa, which is limited by (1) the understanding of the life-history of each taxa, as some are better studied and understood than others and (2) where taxa have multiple abilities within a single trait category, often due to them possessing different traits at different life stages. This lack of understanding and/or clarity may mask some trends in the distribution of trait data.

Thirdly, a range of other factors that could influence the macroinvertebrate community (e.g. climate) will vary simultaneously with bed material and disturbance patterns across the country. This is consistent with the low variances explained by the models (all < 50%), common problem with ecological models (Moller and Jennions, 2002). The inclusion of distance from source in all of the models was intended to account for changes in river size (i.e. available habitat) but the geographic distribution in the dataset, ranging from upland, high-energy Scottish rivers, through to lowland, low-energy chalk rivers in South-East England and the subsequent differences in climate and resource availability (e.g. food, nutrients) would not have been accounted for (Ferreira and Chauvet, 2011). Alkalinity was included in the models to broadly account for variations in water quality but a host of other water quality variables (e.g. temperature, phosphate, BOD, fine sediments) are known to also strongly influence community distribution (Quinn *et al*, 1997; Vaughan and Ormerod, 2014). It is therefore difficult to confidently assume that some of the trends along the disturbance gradient are not trends in competition, resource availability, water quality or climate impacts, which are all known to strongly influence community composition. This is particularly true for cobble substrates as the majority of sites with a high propensity for disturbance are high-energy, upland rivers in the most northerly areas of Britain (i.e. Scotland), where resource availability and climatic conditions (e.g. temperature, sunlight) would be at their lowest and harshest respectively. Despite this, functional metrics are known to be more closely aligned to environmental conditions than traditional community metrics and are therefore expected to offer greater insight into ecology-geomorphology interaction (Naeem *et al*., 2012).

Finally, dimensionless shear stress, the measure termed as propensity for disturbance in the model used here, has received little field validation (Whiting and

Dietrich, 1990) with previous studies being limited to empirical models (Parker *et al*., 2003) or laboratory flumes (Petit, 1994). There is therefore some uncertainty of how accurate the modelled thresholds are in natural riverbeds. These considerations would, however, require extensive field testing and were beyond the scope of this study.

4.5.2 Effects of disturbance and substrate type on invertebrate community composition and function

The within-substrate trends shown here have provided qualified support for the original hypotheses that invertebrate communities would respond to increasing propensity for riverbed disturbance by becoming less diverse (taxonomically and functionally; hypotheses one and two) and would show a general homogenisation around traits associated with resistance and/or resilience (hypothesis three). This is in broad agreement with other studies of freshwater invertebrate community response to natural and anthropogenic stressors, including drought, land use, sedimentation and salinity (Bonada *et al*., 2007; Larsen and Ormerod, 2010; Gutiérrez-Cánovas *et al*., 2015), and to previous small-scale studies looking at river bed mobility (Death, 1995; Death and Winterbourn, 1995; Townsend *et al*., 1997). Yet overall trends in species richness (Figure 4-3B) and functional dispersion (Figure 4-4D) do not support these hypotheses, although these gradients are representative of a shift from upland to lowland channels (coarse to fine grained sediments), rather than gradients of varying disturbance. By combining traditional taxonomic metrics and trait-based approaches using single-traits and functional diversity metrics, the results offer stronger support for the role of riverbed stability in structuring invertebrate community composition. This relationship differed by bed material type, with a marked difference in response to increasing disturbance propensity between communities in gravel or cobble substrates and those in sand or silt substrates. The response in gravel and cobble substrates broadly supported all three hypotheses, whilst sand and silt substrates often contradicted this response, with limited support for hypothesis one (lower taxonomic richness), and little support for hypotheses two and three.

With increasing disturbance in sand and silt substrates, richness decreased whilst overall abundance decreased in sand but increased in silt as taxa including *Potamopyrgus, Gammarus,* dipterans and various oligochaetes came to dominate. Conversely, trait composition became more diverse (increasing ses.FRic), with many traits indicative of resistance/resilience (short lifespan, multiple reproductive cycles) showing little change across the disturbance gradient, whilst others (active aerial dispersal) increased. A potential explanation for this trend in functional richness in sand and silt substrates is the role of inter-specific competition, as predicted by the Habitat Template Theory (Townsend and Hildrew, 1994). If applying the theory, communities in this habitat would place high on the temporal disturbance axis but low on the spatial heterogeneity axis, resulting in disturbance having a greater role in controlling community composition than resource competition between species. In less disturbed areas, high competition for resources would limit the functional richness of a community as species with less suitable traits would be excluded by species with more suitable traits (Menge and Sutherland, 1987; Power *et al*., 1988). Another possible explanation is the role of mass effects, where high dispersal between local communities can alter apparent responses to local habitat (i.e. disturbance). In this scenario, poorly-adapted species immigrate into an area from less-disturbed habitats (e.g. channel margins, riparian zones, nearby tributaries), which would add a small number of species at low abundance to highly disturbed silt/sand substrates. Although only at low abundance, these additional species would increase ses.FRic, which ignores abundance, and have little effect on ses.FDis, which incorporates abundance. The increase in active aerial dispersal across the disturbance gradient in silt/sand substrates offers support that mass effects are most active in this portion of the model.

In gravel and cobble substrates rarefied richness showed no change with increasing disturbance, highlighting that the decline in species richness was an artefact of decreasing abundance. Trait diversity declined in cobble substrates, whilst ses.FRic showed little change in gravel substrates, and traits such as short lifespans, larval aquatic stage, active aerial dispersal and cemented eggs became more prevalent with disturbance in both substrates. Ses.FDis declined with increasing disturbance in cobble and gravel, consistent with an increasing role for environmental filtering over interspecific competition, in support of hypothesis 2 and previous studies (Mason *et al*., 2005, Mouchet *et al*., 2010; Mouillot *et al*., 2013). This was a much larger effect than in silt or sand, where inter-specific competition appears to increase in importance relative to environmental filtering. These trends in community and trait diversity are in close agreement with the results of previous studies of invertebrate response to riverbed disturbance (Reice, 1985; Death and Winterbourn, 1995; Death and Zimmermann, 2005), which have all focussed on coarse-bedded rivers (i.e. riverbeds made up principally of gravels and/or cobbles).

Disturbance is a multidimensional concept including frequency, intensity and period, and theoretical work indicates that different combinations of disturbance frequency and intensity can produce qualitatively different responses (Miller *et al*., 2010). Here, this concept is consistent with the difference in response between communities in sand/silt substrates and gravel/cobble substrates, which can, at least partly, be attributed to differences in frequency and mode of sediment transport in these systems. In rivers with silt and sand substrates, material is regularly transported in suspension by flows at or below bankfull, whereas in coarse substrates, there is a much greater range in transport frequency across the spectrum of sediment calibre, with some substrates very rarely experiencing bed load transport and others frequently being reworked by flow that approximates bankfull discharge (Turowski *et al*., 2010). The regularity of bed disturbance and sediment transport in sand and silt systems may be such that it forms the baseline condition and therefore does not act as a disturbance to a community in the same manner as it does in rivers with gravel or cobble substrates. In essence, the taxa adapted to this environment are capable of thriving, particularly with a reduction in potential inter-specific competition, whereas in high-energy gravel or cobble bed rivers communities can only persist (rather than thrive) due to other resource constraints (Vannote *et al*., 1980). An example of such taxa is *Potamopyrgus antipodarum*, an invasive species in the UK, which occurs in very high densities and uses its high tolerance of siltation as a competitive advantage (Alonso and Castro-Diez, 2008).

In most instances there was no evidence that the invertebrate community varied non-linearly with bed disturbance, showing neither a unimodal response for richness – consistent with the intermediate disturbance hypothesis (Connell, 1978) – nor a sharp change in slope around the threshold between bed and suspended load: the relationship selected by generalised cross validation when fitting the GAMs indicated linear relationships. The latter may have been confounded by the estimated locations of the transport threshold. Only the slices taken through cobble substrates captured the threshold of bed load transport, which provided limited evidence of a threshold effect for total abundance and the number of reproductive cycles per year. In silt/sand substrates values always plotted above the suspension threshold at bankfull discharge, ruling out any non-linear trend around the threshold.

4.5.3 Trophic relationships

As predicted, the variations in substrate and flow energy across the Shields regime diagram were able to distinguish variations in the prevalence of different feeding guilds and locomotion methods in stream communities. For locomotion, crawlers and burrowers were the most strongly related to the two axes of the diagram, and varied based primarily with substrate size, and secondarily with disturbance propensity: crawlers favoured stony and less stable substrates, and burrowers soft substrates (e.g. silt/sand) with lower disturbance propensity. The habitat preferences of organisms with these traits is well-understood (e.g. Quinn and Hickey, 1994; Jowett, 2003), and these results provide further support for the use of the Shields regime diagram, and process-based models in general, in assessing ecology-geomorphology interactions.

The response of feeding guilds was more complex and not only related to substrate size but also to how river geomorphology dictates food availability. Scrapers rely on algae or biofilms that themselves require stony substrates in fast-flowing, shallow watercourses (Cummins and Klug, 1979) and were therefore most prevalent in high-energy cobble substrates and became more common with increasing flow energy in all substrate types. Shredders feed on coarse organic matter (organic matter >1mm in size; Bird and Kaushik, 1981) which in the UK is principally composed of deciduous terrestrial leaf litter (Abelho and Graca, 1996). Geomorphology also has a key role in the distribution of coarse organic matter within a river reach, with deposits concentrated in low-energy areas such as pools and backwaters, which are subsequently flushed out when riverbed transport is invoked by high flows (Cummins *et al*., 2005). These geomorphic features do not occur in all rivers and therefore also act to limit the spatial distribution of shredders (Quinn and Hickey, 1994). The proportion of absorbers was strongly correlated with decreasing substrate size. Further investigation revealed that oligochaetes were the only absorbers in the dataset and resultantly this distribution is likely controlled by their prevalence for burrowing, rather than their feeding guild.

4.6 Conclusion

The study set out to understand how a simple mechanistic model of particle entrainment could be used to identify the response of invertebrate communities to the combined effects of riverbed disturbance and sediment calibre. By combining traditional community metrics and trait-based approaches, I have found that communities which reside in rivers with gravel or cobble substrates respond along a disturbance gradient in a manner consistent with previous small-scale studies. Abundance and richness decreases, reducing the pool of traits present as the community becomes functionally more similar. The reduction in trait diversity was greater than expected for the decrease in taxonomic richness, implicating a role for environmental filtering in selecting for taxa with traits conferring greater resistance or resilience, such as short lifespans, aerial dispersal and smaller aquatic stages. Conversely, patterns were less clear or more complex in silt/sand as with increased disturbance propensity, communities became dominated by specific taxa that occurred in large abundances and were more functionally diverse, perhaps indicating that there are fundamental differences in what constitutes disturbance (cf. gravel/cobble). The distribution of burrowers and crawlers suggest that locomotion traits may be more readily predicted by the factors affecting particle entrainment.

The similarity between community response to disturbance in this study, at least in gravel/cobble bed channels, and previous studies (Death and Zimmermann, 2005; Bonada *et al*., 2007; Larsen and Ormerod, 2010; Doledec *et al*., 2011; Gutiérrez-Cánovas *et al*., 2015) is further evidence of common responses to disturbance across ecological communities. This novel approach, using a simple mechanistic model of particle entrainment and a national dataset, is the first study of its kind at such scale and resolution, although it is hoped that the increasing availability and resolution of nationwide datasets (e.g. LiDAR, Environment Agency Monitoring Data) will make the approach commonplace in the future.

4.7 Appendix

Table 4-4: Statistical significance (P-values) for the three smoothing terms and overall model R^r used to model community and functional metrics in the GAMs

Response Variable	**Predictor Variables (p-values)**			**R^2**
	Tensor Smooth of Dimensionless Shear Stress (τ^*) and Particle Reynolds Number (Re_p)	**Alkalinity**	**Distance from source**	
Species richness	<0.001	<0.001	<0.001	0.35
Total abundance	<0.001	<0.001	0.007	0.46
Rarefied richness	<0.001	<0.001	<0.001	0.10
Evenness	0.213	<0.001	<0.001	0.11
Functional Richness	<0.001	<0.001	<0.001	0.33
Functional Evenness	0.187	<0.001	<0.001	0.16
Functional Dispersion	<0.001	0.829	0.028	0.18
ses.FRic	<0.001	<0.001	0.399	0.14
Ses.FDis	<0.001	0.134	0.528	0.10

Table 4-5: Statistical significance (P-values) for the three smoothing terms and overall model R^2 used to model individual traits in the GAMs

Response Variable		**Predictor Variables (p-values)**			**R^2**
		Shields Regime Diagram	**Alkalinity**	**Distance from source**	
Lifespan	<1 year	<0.001	0.606	0.015	0.28
	>1 year	<.0.001	0.606	0.015	0.28
Number of Reproductive Cycles p/y	<1	<0.001	<0.001	<0.001	0.43
	=1	<0.001	<0.001	0.032	0.31
	>1	<0.001	<0.001	0.392	0.37
Aquatic Stage	Egg	<0.001	0.574	0.755	0.07
	Lava	<0.001	<0.001	0.050	0.28
	Nymph	0.435	0.066	0.128	0.03
	Adult	<0.001	<0.001	<0.01	0.44
Reproduction Method	Ovoviviparity	<0.001	<0.001	<0.001	0.38
	Isolated egg free	<0.001	<0.01	<0.001	0.19
	Isolated egg cemented	<0.001	<0.001	0.339	0.41
	Clutches cemented/fixed	<0.001	<0.001	<0.001	0.33
	Clutches free	0.048	0.039	0.181	0.02
	Clutches in vegetation	0.126	0.010	<0.001	0.07
	Clutches terrestrial	0.004	0.440	0.123	0.04
	Asexual	<0.001	0.607	<0.001	0.18
Dispersal Method	Aquatic passive	<0.001	<0.001	0.152	0.42
	Aquatic active	<0.001	0.562	<0.001	0.15
	Aerial passive	0.364	0.016	0.164	0.03
	Aerial active	<0.001	<0.001	<0.001	0.47
Locomotion Method	Flier	<0.001	0.52	0.13	0.07
	Surface swimmer	<0.001	0.647	0.223	0.05
	Full water swimmer	0.005	0.009	0.007	0.07
	Crawler	<0.001	0.552	<0.001	0.18
	Burrower	<0.001	0.193	<0.001	0.29
	Interstitial	<0.001	0.359	0.015	0.07
	Temporarily attached	<0.001	0.069	<0.001	0.11
	Permanently attached	0.005	0.905	0.299	0..04
Feeding Guild	Absorber	<0.001	0.462	<0.001	0.21
	Deposit feeder	<0.001	0.300	<0.001	0.14
	Shredder	<0.001	0.006	<0.001	0.23
	Scraper	<0.001	<0.001	0.022	0.36
	Filter feeder	<0.001	<0.001	<0.001	0.1
	Piercer	<0.001	0.645	0.103	0.06
	Predator	0.174	<0.001	0.231	0.10
	Parasite	0.692	0.171	0.310	0.01

5 Benthic invertebrate response to riverbed disturbance

5.1 Abstract

Riverbed disturbance, induced by the spatio-temporal variability of river flow, is known to be a primary control on habitat structure and physical diversity in fluvial systems. However, studies across large spatial scales and over multi-year time periods are rare. This study aimed to address this shortfall by quantifying the response of macroinvertebrate communities to riverbed disturbances at a national scale. Using a composite dataset of 118 locations based on annual monitoring data, I modelled community richness, persistence among years and the proportion of resistance and resilience traits using variables describing the riverbed disturbance regime and water quality. Evidence for a response to disturbance was limited to an increase in community persistence with greater disturbance: the other major result was a water quality signal that may have masked further community responses to physical habitat. As an initial step towards linking geomorphological disturbance and community composition through time, this study has shown that future efforts need to include small-scale experimental studies that are capable of accounting for water quality drivers, alongside such national-scale analyses, in order to isolate the response to physical disturbance.

5.2 Introduction

Disturbance has a key role in structuring ecological communities, and occurs both naturally and as a result of human actions (Connell, 1978; Sousa, 1984; Hobbs and Huenneke, 1992). It acts to change the state of an ecological community via chemical, biological or physical mechanisms, and can induce a response at all scales within an ecosystem (Resh *et al*., 1998; Lake, 2000). Classic ecological theory predicts that intermediate levels of disturbance may maximise species diversity, with inter-specific competition restricting diversity at lower disturbance and harsh environmental conditions limiting diversity at high disturbance levels (Connell, 1978; Townsend *et al*., 1997), although empirical evidence suggests that the relationship with disturbance is more complex (e.g. Mackey and Currie, 2001; Fox, 2013). Strikingly, there is strong evidence for a consistent response amongst species' ecological traits to more frequent or intense disturbance across ecosystems, with studies in terrestrial, aquatic and marine environments all showing evidence for increases in the prevalence of traits associated with resisting disturbance or rapid recovery following disturbance i.e. resistance or resilience traits (e.g. Townsend *et al*., 1997; Ding *et al*., 2012; Vinagre *et al*., 2017; Chapter 4). As ecosystems come under ever greater pressure from external factors such as climate change and urbanisation (Barker *et al*., 2016; Ummenhofer and Meehel, 2017), their response to and recovery from disturbance becomes of greater importance (Mouillot *et al*., 2013; Graham *et al*., 2015). Here, I aim to quantify the impact of riverbed disturbance by high flows on macroinvertebrate communities at a national scale and over a 20-year time period.

In freshwaters, disturbance is manifested as a change in the chemical, physical or biological environment that has the potential to kill or displace organisms, deplete resources such as food, and degrade or destroy habitat structure (Resh *et al*., 1988; Lake, 2000). These may be in the form of discrete 'pulse' events, such as floods, or prolonged 'press' or 'ramp' disturbances, such as channelization or the impacts of changing catchment land use (Lake, 2000). Biological disturbances include the introduction of non-native, invasive taxa, which can spread virulently and rapidly overwhelm native taxa (Kelly *et al*., 2003). Chemically-induced disturbances are often the result of wider physical or biological changes within the catchment, such as greater nutrient levels leading to eutrophication and reduced dissolved oxygen levels (Gulis *et al*., 2006) or afforestation with conifers reducing soil buffering to acid rainfall, leading to lower stream pH (Weatherly and Ormerod, 1987; Collier *et al*., 1989), as well as direct pollution events (Johnson and Finley, 1980; Mason, 2002). The close relationship between invertebrate communities and water quality induced disturbance has seen invertebrates used as a proxy for water quality in the UK (Metcalfe, 1989). The strength of the water quality signal is likely to mask subtler relationships between invertebrate communities and other disturbance gradients. Improvements in water quality in recent decades have allowed a recovery in invertebrate diversity (Vaughan and Ormerod, 2014), which may de-couple this relationship in some instances. Here, I use long-term monitoring data to study the temporal component of physical disturbance, extending beyond previous studies which have typically used space for time substitutions or short-term before/after comparisons. I also consider the relationship between improving water quality and invertebrate community resistance or resilience to physical disturbance, hypothesising that the increased community diversity will enable invertebrates to better withstand physical disturbance events.

Physical disturbances in freshwater environments principally involve changes in water or sediment (i.e. physical habitat) availability (Lake, 2000). Periods of drought can directly affect freshwater communities by reducing or eliminating suitable habitat and fragmenting stream continuity (Hynes, 1958; Extence, 1981; Bonada *et al*., 2006), and can also exacerbate pressures such as salinity, water temperature, low dissolved oxygen and resource competition (Larimore *et al*., 1959; Power *et al*., 1985; Gutierrez-Canovas *et al*. 2015). Catchment land use practices (e.g. intensive agriculture) and local bank erosion (e.g. cattle poaching) can result in excessive inputs of fine sediment into watercourses, causing burial of existing habitat and low near-bed dissolved oxygen levels (Sear, 1993; Larsen and Ormerod, 2010), whilst the removal of riparian vegetation reduces channel shading, leading to increased water temperatures (Quinn *et al*., 1992). Floods increase the flow velocity in a watercourse, therefore increasing the shear stress imparted on the river channel and any organisms which reside in, on or under the riverbed (Bathurst *et al*., 1979). This increased shear stress can directly or indirectly disturb organisms by forcibly removing them from their habitat (i.e. sediment) or by moving them and their habitat in combination (Gibbins *et al*., 2007). Floods can also cause indirect disturbance by removing food (e.g. periphyton) from the riverbed (Bond and Downes, 2000; Death, 2002), or by changing channel morphology (i.e. physical habitat) and the provision of refugia (Flecker and Feifarek, 1994). They are a classic example of a pulse disturbance, with a short-term, discrete event often having major effects on river ecosystems through multiple mechanisms (Woodward *et al*., 2016).

The severity of a flood can be split into three components: magnitude, frequency and timing, which could affect riverine communities in different ways (Olden and Poff, 2003). Future changes in land use and climate are predicted to exacerbate flood flows and sediment transport in the UK (Hannaford and Marsh, 2006). Evidence suggests that climate change forcing is already underway (Pall *et al*., 2011), although it is difficult to attribute individual flood events to these drivers (Robson, 2002; Stevens *et al*., 2016). It is often assumed that both the frequency and magnitude of flood events will increase in the future (particularly in the UK) but current evidence suggests that only flood frequency and timing are changing (Mallakpour and Villarini, 2015; Bloschl *et al*., 2017; Wasko and Sharma, 2017). Larger and/or more frequent floods are expected to result, at least initially, in more frequent and dramatic bed disturbances until channel morphology is modified to convey this change in flow regime, either by increasing bed armouring or increasing channel width (Goudie, 2006). The impact of these flow regime changes on invertebrate communities is currently unclear, but it is well known that communities are sensitive to inter-annual variations in climate (e.g. Bradley and Ormerod, 2001; Clews *et al*., 2010), although the relative contribution of riverbed stability to this has typically been ignored. Flood timing has been shown to directly influence invertebrate community composition and impact upon it for multiple subsequent seasons (Sagar, 1986; Quinn and Hickey, 1994; Lytle, 2003). Floods that occur during vulnerable life stages of a population are more likely to result in a decline in the population. It is therefore hypothesised that physical disturbances occurring in summer, when many invertebrates are active in the river channel, would have a greater impact upon community composition than disturbances that occurred in winter, when high flows (at least in the UK) are much more common and invertebrates are in dormant life stages.

Translating predicted changes to the flow regime into the effects on bed stability and disturbance requires a measure of the initiation of sediment transport. In alluvial rivers, those with riverbeds composed of loose sediment, these disturbance events are relatively frequent, occurring on average with the same period as bankfull discharge (Benda and Dunne, 1997b). Evidence suggests that bankfull discharge, which in unmodified channels has a return period of approximately two years, is the dominant discharge determining channel structure (Pickup and Warner, 1976; Williams, 1978; Andrews, 1980; Phillips and Jerolmack, 2016). Disturbance regimes vary through space, as catchment geology, relief and climate control flow regimes, hydrograph steepness and sediment calibre (e.g. a steep, impermeable catchment versus a lowland baseflow dominated catchment) and through time (Shaw *et al*., 2011). The initiation of disturbance is taken as the point at which bed load transport begins to occur in the channel. At this point, riverbed sediment begins to move downstream and rapidly transitions to full mobility of the riverbed surface under greater flows (Van Rjin, 1984). This initiation of sediment transport can be estimated using various methods, including critical shear stress, Froude number/sediment transport relations and critical specific stream power (see Chapter 2). Here, I chose critical specific stream power as it has the lowest data requirements (i.e. gradient, discharge, width and mean sediment size) and has been shown to be strongly correlated to the onset of bed load transport (Parker *et al*., 2011). Bed disturbance was defined as the point at which specific stream power exceeds the critical value.

Previous efforts to investigate the interaction between invertebrate communities and riverbed disturbance have mainly been limited to single reach or catchment scales due to time and data constraints (e.g. Death and Winterbourn, 1995; Townsend *et al*., 1997; McCabe and Gotelli 2000; Miyake and Nakano, 2002), although some larger scale studies have also been conducted (e.g. Kusnierz *et al*., 2015). They have provided evidence that with increasing disturbance, communities become less diverse (e.g. Death and Winterbourn, 1995) and have a greater proportion of organisms displaying resistance or resilience traits (e.g. high mobility, small body form, short lifespans and fast reproductive cycles; Townsend *et al*., 1997). More general studies of the role of flow regime in modulating invertebrate community structure have also been undertaken, using similar datasets to the current chapter but over shorter time periods and with fewer locations (e.g. Wagner and Schmit, 2004; Monk *et al*., 2006; 2007; 2008; Greenwood and Booker, 2015; 2016). These have found that extremes of high and low flow correlate with predictable changes in the invertebrate community (e.g. lotic-invertebrate index for flow evaluation (LIFE) score; Monk *et al*., 2006; 2007; 2008), that flood timing can influence invertebrate emergence (Wagner and Schmit, 2004) and that anthropogenic modifications to the flow regime can alter the dispersal ability of aquatic insects (Greenwood and Booker, 2016). The natural next step is to make an explicit link between the hydrology, sediment transport and mobility, and the invertebrate community.

This chapter builds on Chapter 4 by adding a temporal element to investigate community response to bed disturbance events over a 20-year timespan. Here, I want to understand how riverbed disturbance shapes the composition and function of benthic invertebrate communities, and whether this relationship has changed with improving water quality over the past 20 years (Vaughan and Ormerod, 2012; 2014).

Using a novel composite dataset of 118 sites with multiple years sampled (380 samples in total) from across England and Wales, including invertebrate communities, water chemistry, geomorphology and discharge from neighbouring monitoring locations, the relationships between riverbed disturbance and invertebrate diversity, traits and turnover are evaluated. The following hypotheses are tested:

- Invertebrate communities will be less diverse, exhibit a higher turnover of taxa through time and have a greater proportion of resistance and/or resilience traits where the riverbed is disturbed more regularly;
- Invertebrate communities are more sensitive to bed/hydrological disturbance in summer cf. winter; and
- Recovery from poor water quality increases community resistance to bed disturbance (i.e. there will be a smaller change in community composition between years in response to a similar level of river bed disturbance).

5.3 Methods

5.3.1 Data Sources

To capture information about river flow, channel morphology, water quality and invertebrate community composition, data were amalgamated from datasets held by the Environment Agency (EA), Natural Resources Wales (NRW), the National River Flow Archive (NRFA) and the Centre for Ecology and Hydrology (CEH). These datasets are described in detail in the following sections.

5.3.2 Macroinvertebrate data

Environment Agency Monitoring data

Macroinvertebrate data for the period of 1991 to 2011 were obtained from the Environment Agency's biological sampling network. Macroinvertebrate samples were collected in spring (March–May inclusive) using a standardized three-minute kick-sampling protocol (Murray- Bligh, 1999). A quality assurance scheme ensured that the error rate in the data remained near constant after 1990 (Vaughan and Ormerod, 2014). Data were extracted for 78 taxa, based upon the individual families and composite family groups used in the Biological Monitoring Working Party (BMWP) scoring system, but updated to reflect recent changes in taxonomy (Centre for Ecology & Hydrology, 2011; Table 5-5). All data were converted to presence–absence to avoid problems with changing taxonomy and different methods of recording abundance.

Trait data

Based on Chapter 4, five candidate ecological traits (Table 5-1) were selected from the invertebrate trait database of Tachet *et al*. (2002) to describe resistance and resilience strategies. The selected traits have been widely used to indicate relative resistance and resilience (e.g. Bonada *et al*., 2007; Larsen and Ormerod, 2010; Doledec *et al*., 2011; Gutiérrez-Cánovas *et al*., 2015). The trait data was assigned at the genus-level and had fuzzy-coded scores from zero to three indicating individual trait affinity within each trait group (e.g. individual scores for each reproduction method; Tachet *et al*., 2002). These were converted to percentage affinity to each trait category to standardise for potential differences in the fuzzy-coded scores (Gutierrez-Canovas *et al*., 2015). The sum of the individual categories for each trait group was 100%.

To match the invertebrate sampling data, the traits were aggregated to family level using a weighted mean for each individual trait within a trait group (Monaghan and Soares, 2012; Vaughan and Ormerod, 2014). The weights were the relative prevalence of each invertebrate genus across all locations in the RIVPACS data set (Wright, 2000; Chapter 4). The family-level traits were then standardised so that they summed to one across all of the individual traits within a trait group for each family. The RIVPACS data set has good coverage of the UK and its use of largely unmodified sites with good water quality ensures the robustness of the abundance data. Fourteen of the 78 families in the original dataset had either no or incomplete trait information and were excluded from the study. Excluded families did not fit into a particular category and included relatively rare taxa (e.g. Beraeidae and Hirudinidae) through to relatively common ones (e.g. Lepidostomatidae and Limnephilidae).

Table 5-1: Five candidate ecological traits (21 individual categories) for resistance/resilience to bed disturbance.

Trait Group	**Trait Categories**
Lifespan	<1 year, >1 year
Aquatic Stage	Adult, egg, lava, nymph
Reproductive Cycles per year	<1, =1, >1
Dispersal method	Aerial active, aerial passive, aquatic active, aquatic passive
Reproduction method	Asexual, clutches cemented or fixed, clutches free, clutches in vegetation, clutches terrestrial, isolated egg cemented, isolated egg free, ovoviviparity

5.3.3 Daily river flows

Daily mean discharge data and baseflow index were obtained from the NRFA (https://nrfa.ceh.ac.uk/) for 762 candidate gauging stations across England and Wales. The baseflow index is a measure of the proportion of the river runoff that is derived from stored sources. High permeability rock has a high baseflow, and rivers which flow over these high baseflow areas have a dampened flow regime and sustained flows, even in dry weather. Gauging stations with records that did not span the period of invertebrate samples, were greater than 5km from the nearest invertebrate sampling site and/or lacked reliable estimates of peak flows were excluded, leaving 118 gauging stations.

5.3.4 Water quality

Water quality data for 1991 to 2011 were obtained from the Environment Agency's water information monitoring system (WIMS). Phosphate, nitrate and biological oxygen demand (BOD) were recorded monthly using standard methods (Standing Committee of Analysts 1981, 1987, 1992). Median values were calculated at each sampling site for the 12 months preceding the start of the spring invertebrate sampling season (i.e. from March in the preceding year through to February in the current year). Where >50% of values were below detection limits, values were estimated using the regression on order statistics method in R's NADA package (Lee and Helsel, 2005). Years were excluded from each sampling site if they contained fewer than nine monthly samples.

5.3.5 River Habitat Survey

The River Habitat Survey (RHS) was developed in 1994 to characterize the physical character and quality of river habitats across the UK (Raven *et al*., 1998). It has since been used at over 25,000 sites in the UK and elsewhere across Europe. An individual RHS involves a survey of a 500-m length of channel with ten *spot-checks* that record features at 50-m intervals and a *sweep-up* section that records the presence, absence, or extensiveness (≥33% of channel length) of features within the reach (Raven *et al*., 1998). Features include the type and extent of channel vegetation, any modifications to the channel and the dominant substrate type. Finally, each RHS location has an accompanying estimate of channel slope, measured from 1:50,000 scale maps over a 1-km length centred on the mid-point of the study reach (Raven *et al*., 1998). Map-derived channel slope corresponds well with field measurements (Montgomery *et al*., 1998) and is often more accurate than slope derived from digital elevation models due to errors in channel length estimation as a result of pixel size (Clarke *et al*., 2008; Fisher *et al*., 2013).

RHS data for channel slope and bed material (spot checks) were used in the analysis. The bed material spot checks were converted into an average ϕ score based on approximate values for median particle size of each size class, using a similar method to Gurnell *et al*. (2010):

$$D_{50} = \frac{(-8 * BO - 7 * CO - 3.5 * GP + 1.5 * SA + 6 * SI + 9 * CL)}{(BO + CO + GP + SA + SI + CL)}$$

Where BO = boulder, CO = cobble, GP = gravel-pebble, SA = sand, SI = silt and CL = clay. Sites were limited to those with gravel or coarser beds, in order to comply with the channel width relation used to calculate specific stream power (Hey and Thorne, 1986), which only applies to gravel-bed rivers in the UK.

5.3.6 Site Selection

The use of four largely independent sampling schemes (invertebrates, chemistry, RHS and flow gauging) resulted in few locations where all information was available, but there were many occurrences where sampling sites were in close proximity. Combining data from nearby locations is common practice in studies based on river monitoring data (e.g. Naura and Robinson, 1998; Monk *et al*., 2006; 2007; 2008; Vaughan and Ormerod, 2012; 2014) and has proven to be an effective approach for utilising existing data sets (Vaughan and Ormerod, 2010). Potential study sites were selected based on the following criteria:

- Chemistry and RHS sites within 2km of the invertebrate sampling location, located on the same watercourse and with no major tributaries between them (verified by catchment area where possible, otherwise by a visual check);
- A gauging station within 5km of the invertebrate sampling location, with no major tributaries in between (where possible based on a check of upstream catchment area, or otherwise a visual check using GIS mapping).

These distances were chosen as they represented the best trade-off between geographic coverage and data integrity. Where multiple sites met the criteria to match to an invertebrate sampling site, sites were selected to provide the best temporal coverage of discharge and chemistry, and shortest distance to RHS site. Mean distances from an invertebrate sampling site to a gauging station, water chemistry site and RHS site were 1300m, 250m and 670m respectively.

The final data set comprised 118 regularly sampled sites (mean = nine years sampled) across England and Wales (Figure 2). They had catchment areas of 7 – 4325 km^2 and ranged from upland, high energy rivers such as the River Wye at Erwood, mid-Wales to lowland, low-energy rivers such as the River Mimram at Panshanger Park, Hertford.

5.3.7 Data Analysis

5.3.7.1 Quantifying Disturbance

To assess the impact of disturbance events on invertebrate communities a threshold at which disturbance occurs needed to be established. Various methods are capable of determining the onset of sediment transport (i.e. disturbance), such as the critical shear stress (Wiberg and Smith, 1987), sediment transport equations (Ackers and White, 1973; Yang, 1976; Mueller *et al*., 2005) and critical specific stream power (Bagnold, 1966; Parker *et al*., 2011). These methods vary according to their data requirements and applicability at different scales. For example, sediment transport equations typically require detailed information on flow velocities and/or sediment composition and as such, are only applied at reach scales or less (Andrews, 1979; Eaton and Lapointe, 2001). Critical shear stress requires a measure of flow depth which adds significant error to large-scale studies as flow depth is rarely measured at high flows other than at gauging stations, where the channel is usually overwide (underestimating flow depth in comparison to a natural section of channel). At catchment or regional scales, stream power has been the chosen method for predicting sediment transport or zones of erosion and deposition (Parker *et al.*, 2011; Bizzi and Lerner, 2012). It provides a simple means of estimating the energy available to do work in the channel, based on channel slope, discharge and, when calculated per unit area, channel width (Bagnold, 1977). Parker *et al*. (2011) attempted to improve the physical basis for using stream power by calculating dimensionless critical stream power, based on Einstein's (1950) dimensionless sediment transport equation, finding that it corresponded well with sediment transport rates measured in laboratory flumes (Shvidchenko and Pender, 2000) and empirical evidence that predicted critical unit stream power to be proportional to $D_i^{1.5}$ (Petit *et al.*, 2005). Here, I chose to use this critical specific stream power equation due to its low data requirements and applicability to high-energy, gravel-bed rivers that are common in England and Wales. The equation for critical specific stream power (ω_c) is:

$$\omega_c = \omega_{c*} * g(\rho_s - \rho_w).\sqrt{\frac{\rho_s - \rho_w}{\rho_w}.g.D_i^3}$$

where ω_{c*} is the dimensionless critical specific stream power (a laboratory derived constant of 0.1; Parker *et al*., 2011), g is the gravitational constant (9.81 ms^{-1}), p_s is the density of sediment (taken as 2650 kgm^{-3}), p_w is the density of water (1000 kgm^{-3}) and D_i is the diameter of the grain being entrained in metres, taken in this instance as the D_{50} calculated in Section 5.3.5. A disturbance was deemed to have occurred when the critical specific stream power was exceeded by the specific stream power. Specific stream power, the rate of energy expenditure per channel length, normalised by channel width, was defined as:

$$\omega = \frac{\rho g Q S}{w}$$

Where ρ_w is equal to the density of water (taken as 1000 kg m^{-3}), g is equal to the gravitational constant (taken as 9.81 m s^{-1}), Q is equal to discharge (m^3 s^{-1}), taken as the daily flow from 1990-2013 for each site, S is equal to average bed slope (m m^{-1}) as contained in the RHS data, and w is channel width in metres. Channel width (w) was estimated from the discharge using Hey and Thorne's (1986) equation from Knighton's (1999) study on gravel-bed rivers in the UK:

$$w = 3.42\, Q^{0.46}$$

Once the daily specific stream power was calculated for each of the 118 gauging stations, riverbed disturbance was identified as periods where the critical specific stream power (Parker *et al.*, 2011) was exceeded by the daily specific stream power. This daily specific stream power was likely to be a conservative estimate of when disturbance had occurred as average daily discharge is not the peak discharge of an event (Fill and Steiner, 2003).

To capture the frequency, magnitude and duration of disturbance at each site, the following metrics were calculated over the 12 months preceding an invertebrate sample:

1. Number of days when the riverbed was disturbed. A cumulative total of the annual number of days where the specific stream power exceeded the critical specific stream power;
2. The cumulative intensity of disturbance. A measure of the cumulative exceedance (daily exceedance = SSP / Critical SSP) above the critical threshold over the past year;
3. The peak intensity of disturbance. The largest daily event with the value recorded as a multiple that the critical power was exceeded by (i.e. SSP / Critical SSP); and

4. The number of discrete disturbance events. Events were counted as discrete if separated by at least 2 days where the critical threshold was not exceeded to ensure single storm events were only counted as one event.

Based upon work using related hydrological indices (Olden and Poff, 2003), it was expected that the disturbance metrics would display multicollinearity. A principal component analysis (PCA) was used to identify the relationships between them and provide a simplified disturbance index (PC1) for use in subsequent analyses (see Results for details of the PCA). To address Hypothesis 2 (summer vs. winter disturbance) the metrics were re-run for March to August (Summer) and September to February (Winter) only. These were then ordinated using the same PCA procedure, and seasonal PC1 scores estimated to indicate the disturbance regime at each site for summer or winter only.

5.3.7.2 Invertebrate community structure

The response of invertebrate community structure to riverbed disturbance was assessed using two metrics: i) taxon richness; and ii) Jaccard dissimilarity index between consecutive years. Taxon richness was simply a count of the number of families present for each sample. The Jaccard index (Jaccard, 1908) was selected to describe the dissimilarity between samples (in this case two invertebrate communities) as it is an established measure of persistence that has been used in several river studies (e.g. Milner *et al*., 2006; Collier, 2008). The index was calculated using the *vegdist* function in the vegan R package (Oksanen *et al*., 2017). This provided a measure of the dissimilarity in the composition between the communities in consecutive years, with a value of zero indicating that an identical set of families was present in both samples, and a value of one indicating that the two samples had no families in common.

5.3.7.3 Trait representation

An ordination analysis was used to provide a simple overview of how the prevalence of potential resistance and resilience traits varied among invertebrate communities. The aim was to provide a simplified representation of trait variation among communities for use in subsequent analysis (cf. analysis of individual traits; Chapter 4). The 877 invertebrate samples (across 118 sites) were ordinated on the five groups of candidate resistance and resilience traits (18 individual trait categories) using fuzzy correspondence analysis (Usseglio-Polatera *et al*., 2000; ade4 R package). The first axis (RS1) explained 39% of the variance and was selected as a resistance-resilience index for subsequent analysis (Figure 2-1; Table 5-2). It represented a trend from communities showing fewer resistance or resilience traits, with a higher proportion of taxa with long life spans and slower reproductive cycles (negative values), to communities in which short lifespans and fast reproductive cycles were more prevalent, consistent with expectations for greater resilience to disturbance (positive values; Odum, 1985). Other life history traits also varied along this axis, with taxa with active dispersal strategies, reproduction via cemented eggs and small aquatic stages all relatively abundant at negative values, and traits such as adult aquatic stage and ovoviviparous reproduction more common at positive values (Table 5-2). These secondary traits are consistent with a shift from insects to other invertebrate taxa (e.g. oligochaetes, crustaceans), which could also reflect a shift from smaller, faster flowing watercourses to larger, slower flowing ones. The second ordination axis, RS2, only explained 17% of the variance and so was discarded.

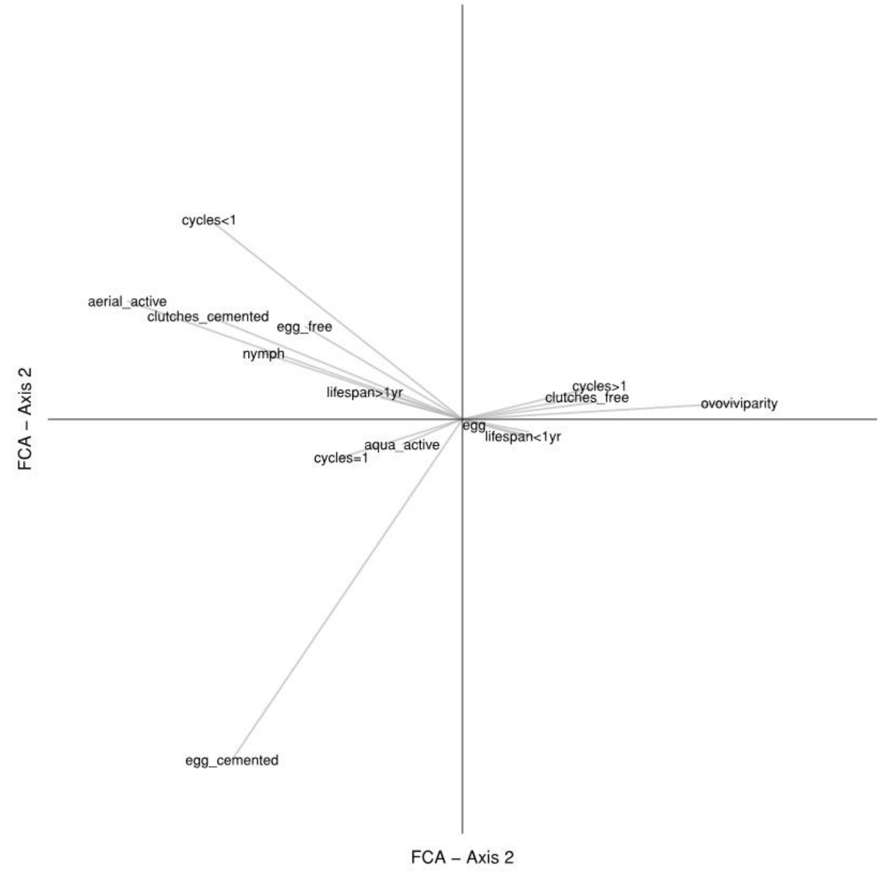


Figure 5-1: Fuzzy correspondence analysis of the 877 samples based on the five resistance/resilience trait categories (18 individual traits; Table 5-2).

Table 5-2: Loading coefficients for the first two axes of a fuzzy correspondence analysis conducted on the five resistance/resilience trait categories (18 individual traits). Three reproduction categories (asexual, terrestrial, in vegetation) were excluded due to low proportions skewing the FCA.

Traits		**CS1**	**CS2**
Lifespan	<1 year	0.41	-0.24
	>1 year	-0.66	0.39
Reproductive Cycles per year	<1	-1.70	2.83
	=1	-0.81	-0.54
	>1	0.92	0.48
Aquatic Stage	Egg	0.08	-0.08
	Lava	-0.55	0.31
	Nymph	-1.33	0.94
	Adult	0.48	-0.25
Reproduction Method	Ovoviviparity	1.86	0.23
	Isolated eggs free	-1.06	1.32
	Isolated egg cemented	-1.55	-4.84
	Clutches cemented or fixed	-1.71	1.46
	Clutches free	0.84	0.32
Dispersal Method	Aquatic passive	0.45	-0.18
	Aquatic active	-0.41	-0.36
	Aerial passive	0.91	0.24
	Aerial active	-2.25	1.68

5.3.7.4 Regression Models

Two different approaches to regression analysis were used to test the hypotheses: i) a cross-sectional approach, focusing on among-site differences in the invertebrate community at two time points, and ii) a longitudinal approach using the complete 21-year data set. Overall richness, the Jaccard index between years (persistence) and the index of resistance-resilience traits (RS1) were analysed in each case. For the first approach, the mean values of the three invertebrate variables at each sample site were regressed against the mean value of the site's disturbance index (PC1) using simple linear models (to address hypothesis 1). Phosphate, BOD, nitrate and temperature were also included in the models to control for variation among sites. Phosphate and BOD were log transformed and the fit of the models checked using plots of the residuals. To minimise the potential confounding effect of improving water quality over the study period (Parr and Mason, 2003; Vaughan *et al*., 2012; 2014), the analysis was repeated at two different 5-year periods, one early (1993-1998) and one late (2003-2008) in the study period (cf. averaging across the complete 21-year period). If the results were similar at both time periods it would provide evidence that any disturbance relationship was not altered by changing water quality.

The second approach modelled the three invertebrate variables for each sample site as a function of the disturbance index (PC1) and the first axis of a PCA of the water quality variables. The latter was run with phosphate, BOD and nitrate, and the first principal component explained 64% of the variance. Negative values of the component represented high water quality i.e. low concentrations of nitrate and phosphate, and low BOD. Water quality was summarised in this way to simplify the model and minimise potential convergence problems (e.g. due to collinearity). Generalised additive mixed models (GAMMs), using R's mgcv package, were used to relate the invertebrate data to disturbance and water quality, with identity links and Gaussian errors. Site was included as a random term in the model to account for multiple observations being taken from the same locations (through time). The disturbance and water quality PCA axes were modelled using a tensor product of thin-plate regression splines, with the degree of smoothing determined by generalized cross validation, which allows potential interactions between them to be modelled (Wood, 2006; see also Chapter 3). The fit of each model was checked by examining plots of the residuals. This approach was used to: (1) investigate whether there was a difference in response to summer vs. winter disturbance (hypothesis 2), by fitting the models twice, using disturbance PC1 for summer or winter, and (2) indicate whether the three response variables changed with improving water quality (hypothesis 3). To examine the effect of changing water quality on the relationships between invertebrates and disturbance, model predictions were generated with changing disturbance at both good and poor water quality. In the absence of other obvious values, 'good' and 'poor' were taken as the 25th and 75th percentiles of the water quality PCA axis (Harrell, 2001).

5.4 Results

5.4.1 Spatial distribution of disturbance

The four disturbance metrics varied widely across England and Wales, but did not show a simple relationship with the main topographical and climatological gradient from the upland north-west to lowland south-east (Figure 5-2A to D). Estimated bed disturbance was most frequent and intense in parts of the West Midlands (Severn & Wye) and in Somerset (Axe) catchments, whilst frequent but less intense disturbance was estimated in chalk streams in south east England, such as the Mimran, Pang and Frome. Elsewhere in England and Wales bed disturbance tended to be infrequent and of variable intensity. The model outputs indicated that some sites experienced bedload transport on average as many as 130 days per annum, a value which appears unreasonably high. These results are explored further in the discussion. A total of 33 sites (28% of dataset) with mean bed material size ranging from 11mm to 194mm had no estimated disturbances during the period 1990-2013. Of these, 28 sites had pebble or cobble beds (high critical specific stream power) and were located in upland areas of Wales, northern England or south-west England. The remaining five sites all had a baseflow index > 0.8 and were located in the Midlands or south-east England.

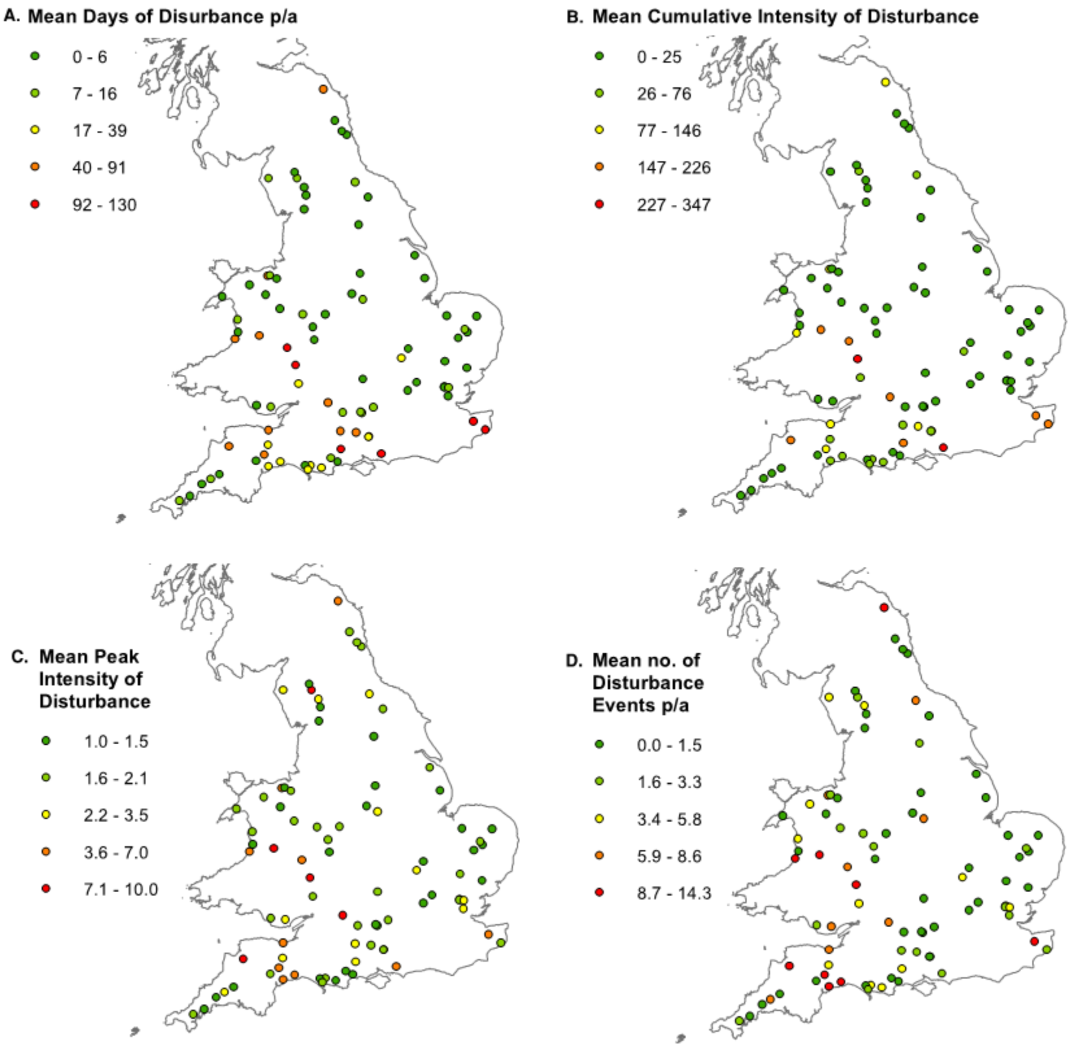


Figure 5-2: (A to D) Spatial distributions of four disturbance metrics calculated based on daily flow data and exceedance of the critical specific stream power threshold (Parker et al., 2011).

The four disturbance metrics were correlated with one another (mean Pearson's *r* = 0.58; range = 0.38 to 0.96). As a consequence, the first PCA axis explained 87% of the variance, with the second axis describing 10% (Table 5-3). Axis 1 (PC1) described a gradient in overall disturbance, with the duration, magnitude and frequency of disturbance events all increasing, with the four metrics showing very similar loading coefficients (Table 5-3). PC1 was negatively correlated with mean bed material size (Pearson's r = -0.53, p = 0.001): finer gravels tended to be disturbed frequently (i.e. typically multiple times per year), whereas cobbles were disturbed rarely (i.e. every several years). PC2 was strongly correlated with the baseflow index (Pearson's r = 0.62, p = 0.001) and described a gradient from catchments with little baseflow and a flashy hydrograph that experienced less frequent but high magnitude disturbance events, through to catchments with a large baseflow component that experienced more frequent, lower magnitude yet prolonged disturbances. The first axes of the PCAs for summer and winter disturbance had very similar loadings and variance explained to the overall PC1 axis, trending from low to high disturbance in all metrics (Table 5-3).

Table 5-3: Axes loadings and variance explained for a PCA of the metrics used to classify disturbance.

	Overall		**Summer**	**Winter**
PCA	**PC1**	**PC2**	**PC1**	**PC1**
Variance Explained (%)	87	10	72	78
Mean days of disturbance p/a	0.52	0.34	0.57	0.58
Mean cumulative intensity of disturbance	0.53	0.23	0.54	0.55
Mean peak intensity of disturbance	0.44	-0.89	0.57	0.58
Mean number of events p/a	0.51	0.19	0.59	0.56

5.4.2 Site-level (cross-sectional) analysis of invertebrate community response to bed disturbance

At a site level, there was some evidence that average river bed disturbance propensity was correlated with invertebrate community structure and temporal variability (Figure 5-3; Table 5-4). Only the model of Jaccard dissimilarity index (persistence) for the late time period had disturbance as a significant predictor variable ($p = 0.008$; Table 5-4C), but near-significant relationships were also observed for Jaccard dissimilarity at the earlier time point ($p = 0.069$) and RS1 at the later time point ($p = 0.054$). Water quality variables were significant in three instances: phosphate in both taxon richness models, and BOD in the Jaccard model for the first interval (Table 5-4).

For Jaccard dissimilarity, both models showed less turnover between years as the bed disturbance increased i.e. higher persistence (Figure 5-3). In the lowest disturbance conditions, an average of around 35–40% of the taxa in the invertebrate samples differed between consecutive years, which declined to around 20–25% in the highest disturbance conditions (Figure 5-3). The near-significant increase in RS1 with increasing bed disturbance at the second time point was consistent with the prediction that resistance and resilience traits would become more prevalent under such conditions. Taxon richness was highly variable at both time points.

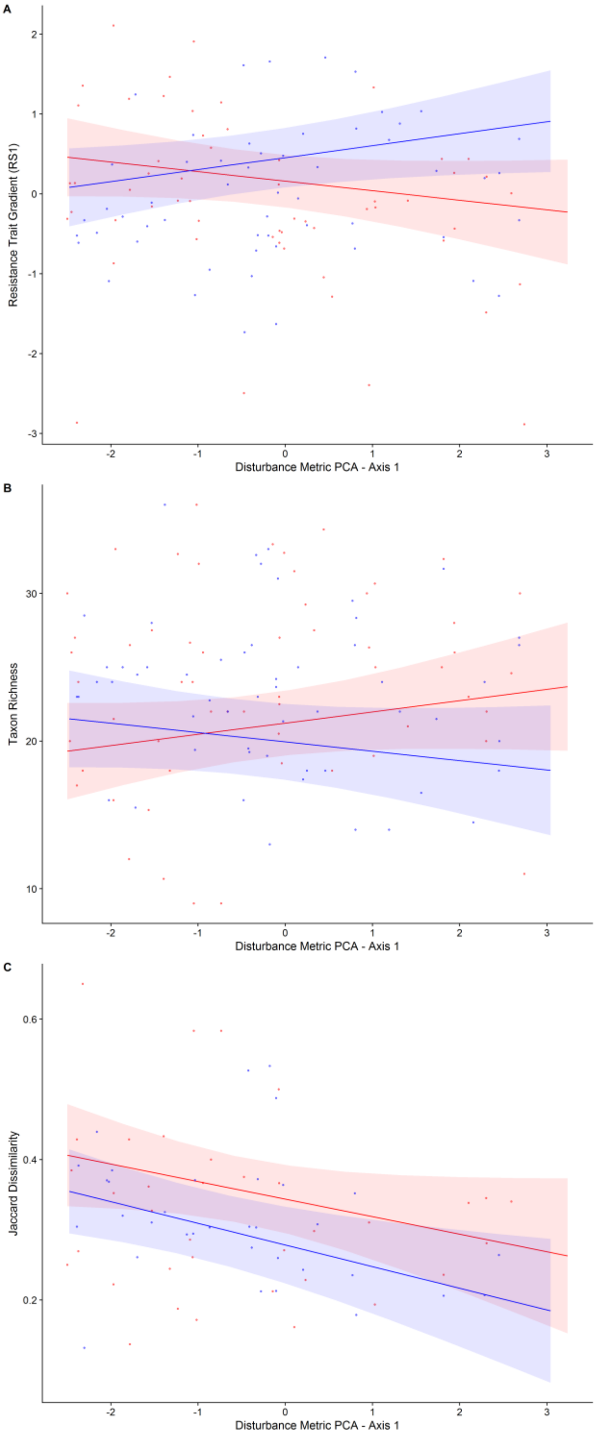


Figure 5-3: Predicted linear trends of the means per site of (A) resistance trait gradient (RS1), (B) taxon richness and (C) Jaccard dissimilarity index during the early (red) and late (blue) time periods with decreasing disturbance. Water quality held constant (mean values). Linear trends in (A) and (B) are non-significant (but included for interpretation), whilst the late trend in (C) is significant at p<0.01.

*Table 5-4: Linear regressions of (A) the resistance trait gradient (RS1), (B) taxon richness and (C) Jaccard dissimilarity index against disturbance and water quality variables for the early and late periods. Estimated coefficients, their standard errors and statistical significance from the models are shown. Significant predictors are in bold. * indicates predictor variables that were log transformed to meet model expectations.*

A. RS1									
	Early (Model r^2 = 0.31)					**Late (Model r^2 = 0.25)**			
	Estimate	**SE**	**t-value**	**P**		**Estimate**	**SE**	**t-value**	**P**
Intercept	-1.11	1.35	-0.82	0.415		-0.03	1.28	-0.02	0.984
Disturbance (PC1)	0.12	0.08	1.48	0.146		-0.14	0.07	-1.98	0.054
Phosphate*	0.42	0.22	1.90	0.063		0.57	0.23	2.52	**0.015**
BOD*	0.94	0.70	1.35	0.184		-0.14	1.04	-0.14	0.893
Nitrate	0.05	0.05	0.98	0.334		0.03	0.04	0.81	0.425
Temperature	0.09	0.13	0.65	0.516		0.04	0.11	0.43	0.673
B. Taxon Richness									
	Early (Model r^2 = 0.24)					**Late (Model r^2 = 0.18)**			
	Estimate	**SE**	**t-value**	**P**		**Estimate**	**SE**	**t-value**	**P**
Intercept	4.90	9.46	0.52	0.607		1.67	9.56	0.17	0.862
Disturbance (PC1)	-0.76	0.54	-1.42	0.163		0.61	0.49	1.24	0.222
Phosphate*	-5.26	1.52	-3.46	**0.001**		-4.01	1.64	-2.44	**0.019**
BOD*	-7.78	4.85	-1.60	0.115		9.49	7.16	1.33	0.191
Nitrate	0.44	0.36	1.22	0.227		0.07	0.27	0.25	0.804
Temperature	1.30	0.94	1.39	0.170		1.40	0.76	1.85	0.072
C. Jaccard Index									
	Early (Model r^2 = 0.19)					**Late (Model r^2 = 0.17)**			
	Estimate	**SE**	**t-value**	**P**		**Estimate**	**SE**	**t-value**	**P**
Intercept	0.60	0.22	2.77	**0.009**		0.25	0.19	1.32	0.198
Disturbance (PC1)	0.02	0.01	1.88	0.069		0.03	0.01	2.87	**0.008**
Phosphate*	0.06	0.03	1.78	0.085		-0.02	0.03	-0.73	0.473
BOD*	0.22	0.10	2.28	**0.030**		0.10	0.18	0.56	0.584
Nitrate	-0.01	0.01	-1.16	0.257		0.00	0.00	0.21	0.839
Temperature	-0.02	0.02	-1.04	0.306		0.00	0.01	0.02	0.985

5.4.3 Longitudinal analysis 1: The role of disturbance in summer versus winter

There was no evidence of a stronger response to disturbance in summer over winter for resistance traits or the Jaccard Index (Figure 5-4). The models of richness failed to converge and were excluded. Resistance traits (RS1) models for summer ($p < 0.001$, $r^2 = 0.22$) and winter ($p = 0.001$, $r^2 = 0.17$) disturbance both showed that resistance traits became more common as disturbance increased (Figure 5-4A; B), corresponding with the results of the linear models. The response of RS1 to increasing winter disturbance was non-linear and showed resistance traits initially increasing, then falling and then increasing again at peak levels of disturbance (Figure 5-4B), whilst in summer resistance traits increased linearly with disturbance (Figure 5-4A). The Jaccard dissimilarity index declined with increasing disturbance in both summer ($p = 0.434$, $r^2 = 0.01$) and winter ($p = 0.004$, $r^2 = 0.10$), although the predictor smooth in summer was non-significant. The decline was steeper in winter, 33% to 27% dissimilarity, than in summer, 30% to 29%, and was consistent with the trend of the linear models.

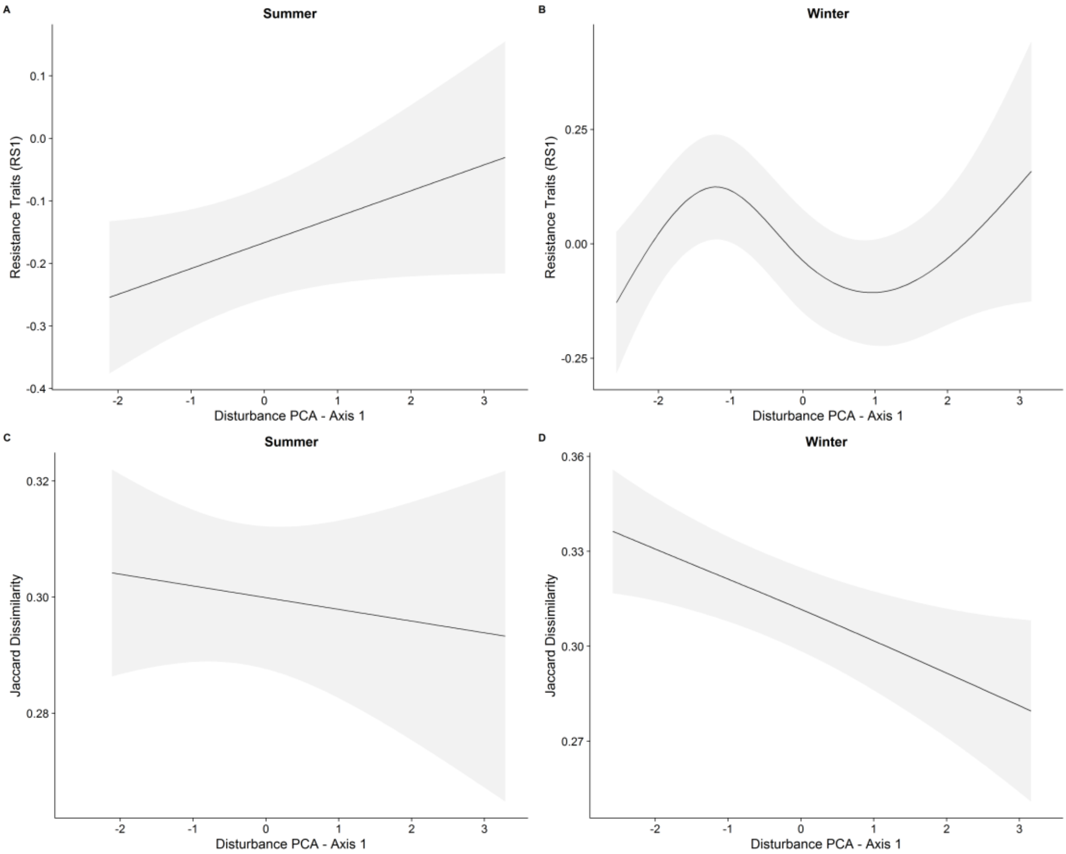


Figure 5-4: GAMM predictions for trends in resistance trait gradient (RS1) versus (A) summer and (B) winter disturbance, and Jaccard dissimilarity index versus (A) summer and (B) winter disturbance. Random effects are set to zero.

5.4.4 Longitudinal analysis 2: Interaction between water quality improvements and disturbance

Resistance traits (RS1; $p = 0.003$, $r^2 = 0.15$), richness ($p = 0.017$, $r^2 = 0.10$) and persistence (Jaccard dissimilarity; $p = 0.003$, $r^2 = 0.10$) were all related significantly to bed disturbance and improving water quality. Richness marginally increased with greater disturbance in poor water quality (by c. 1.5 families) but stabilised across the disturbance gradient with good water quality (Figure 5-5A). Resistance-resilience traits (RS1) responded differently to bed disturbance depending upon the prevailing water quality (Figure 5-5B). In poor water quality resistance-resilience traits became more prevalent with increasing disturbance, whilst in good water quality they became less prevalent (Figure 5-5B). In good water quality, Jaccard dissimilarity decreased from approximately 33% to 30% of taxa across the disturbance gradient, whilst the decline with increasing disturbance in poor water quality was steeper, from 34% to 28% of taxa (Figure 5-5C): similar responses to those of the site-average models.

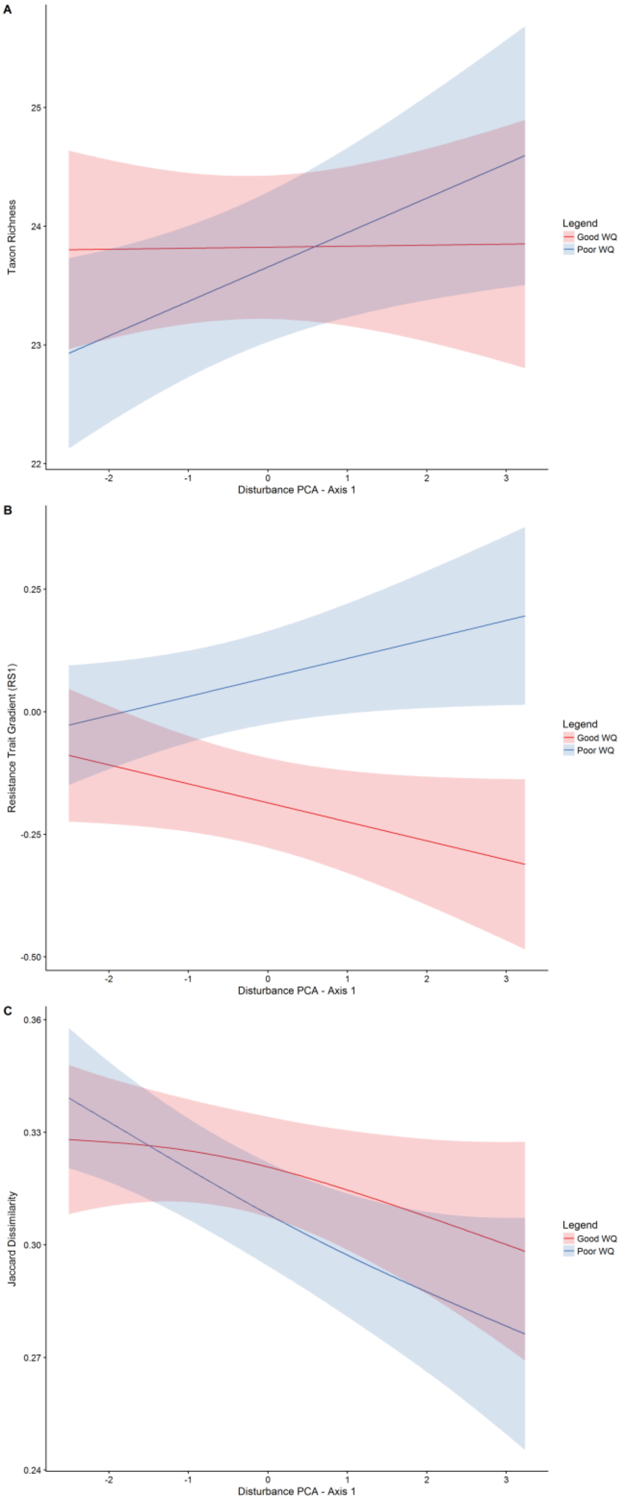


Figure 5-5: GAMM predictions for trends in (A) resistance trait gradient (RS1), (B) taxon richness and (C) Jaccard dissimilarity index for good (red) and poor (blue) water quality with increasing disturbance (x axis). Random effects are set to zero.

5.5 Discussion

Evidence for the role of riverbed disturbance in altering invertebrate community composition and function is restricted to a small number of studies (e.g. Death and Winterbourn, 1995; Townsend *et al*., 1997; McCabe and Gotelli 2000; Miyake and Nakano, 2002). These few studies, coupled with theoretical work on disturbance, suggests that bed stability could play an important role, and so a better understanding of this relationship is important if we are to make reliable predictions of future change to river ecosystems. Previous studies have for good reason focussed on the impacts of water quality (e.g. Vaughan and Ormerod, 2012; 2014) and it is only with improvements in water quality that the influence of physical modifications and channel change have become apparent (Newson and Newson, 2000). This study has investigated whether there is a riverbed disturbance signal in long-term ecological monitoring data using a novel composite dataset spanning England and Wales. The critical specific stream power equation (Ferguson, 2005; Petit *et al*., 2005; Parker *et al*., 2011) was selected as the threshold for disturbance due to its low data requirements and applicability to gravel-bed rivers, which are common in Britain. Despite the limitations of stream power in comparison to more detailed methods of predicting the onset of sediment transport (Gomez and Church, 1989; Ferguson, 2005), this approach represents a first step towards linking process-based, geomorphic theory with changes in the composition and function of invertebrate communities through time and at a national scale. The following section will discuss the limitations of the study before moving on to discuss the findings.

5.5.1 Limitations

The approach used here has four major limitations. Firstly, despite this approach involving largely unmatched spatial and temporal coverage, the use of a composite dataset that is applied in a manner different from its intended original use presents a series of limitations (Vaughan and Ormerod, 2010). Despite efforts to ensure that paired sites were in a similar location and considered river reaches with the same ecological, physical and chemical characteristics, the distribution of ecological communities and physical forms are known to vary at small spatial scales (Downes *et al*., 1993; Poff, 1997; Benda *et al*., 2004). Also, in a similar vein to the previous chapter, the available geomorphological data were particularly weak (e.g. simplistic channel substrate measures). Although bed material size could be estimated from the descriptive data in RHS, a quantitative measure of sediment size would have provided greater accuracy. Other shortcomings in the use of secondary data were (1) the lack of resolution in the family-level invertebrate data, potentially limiting the identification of patterns (i.e. divergent species' responses within a family could go unnoticed; Melo, 2005), and (2) incomplete trait information, leading to a potential bias towards well-studied taxa (Tyler *et al*., 2012) – the analysis here had to exclude 14 taxa (18%) due to lack of trait information.

The second limitation was that the threshold at which movement of sediment in the riverbed is considered to represent a disturbance to benthic invertebrates is poorly understood (Schwendel *et al*., 2010a; 2010b). Variations in the threshold of sediment transport, due to bed armouring (Gomez, 1983), fixed objects in the channel (e,g. large wood; Gurnell *et al*., 2002) or biotic influences (e.g. biofilms; Stone *et al*., 2008; 2011 or channel vegetation; Murray and Paola, 2003), introduces a high degree of uncertainty in predicting the onset of riverbed disturbance. In this study a disturbance to benthic invertebrates has been assumed to be represented by any movement of particles within the riverbed, in line with previous studies (e.g. Cobb *et al*., 1992; Townsend *et al*., 1997). Future studies should include experimentation to determine whether this assumption is correct of if a different level of physical movement is required to constitute a disturbance in ecological terms.

Thirdly, as floods can affect invertebrate communities in multiple ways (Naegeli *et al*., 1995; Olson and Townsend, 2005), it is difficult to identify the causal mechanism, even where a correlation between an expected stressor (e.g. bed disturbance) and the community response is observed. The approach used here of filtering by flows expected to have caused transport of riverbed material provides a first step towards a test of these causal mechanisms. To gain a full understanding, a similar approach to that used here needs to be combined with direct field observations of bed movement, manipulative experiments and more detailed measures of how invertebrate populations and resources change (e.g. with measures of basal food resources or food web structure).

Finally, the background conditions of largely poor water quality across the UK and a trend of improvement across the period of the study (Vaughan *et al*., 2012; 2014), increases the complexity of invertebrate responses and potentially masks underlying trends in community composition as a result of riverbed disturbance. The strong correlation between poor water quality and reduced invertebrate diversity and function (Whilm and Dorris, 1968; Lenat, 1988) presents a challenge when interpreting results. Here, there were several instances where the ecological relationships with disturbance varied according to the prevailing water quality. In addition to these observed relationships, the extent to which poor water quality could still be masking physical habitat effects is unknown. The changes in trait composition with improving water quality (Figure 5-5A) suggest that it may still be playing an ongoing role.

5.5.2 Spatial trends in disturbance

The metrics calculated here to describe the trends in sediment transport and riverbed disturbance across England and Wales correspond well with known variations in flow regime and river energy but do not display a simple upland lowland or north-west to south-east gradient (Hannaford and Marsh, 2006). Disturbance regimes with a long duration, moderate frequency and low peak intensity (Figure 5-2A; C; D), corresponded closely with high base flow rivers (e.g. Great Stour and the Wiltshire Avon; chalk streams in south eastern England). Conversely, active gravel-bed rivers such as the Wye, Clwyd, Axe and Dulas, were also found to be frequently disturbed but with higher peak intensities (Figure 5-2). This appeared to be a function of their relatively small bed material (gravel) in comparison to their specific stream power (>40 W m^{-2} at QMED), with high base flow rivers such as the Mimran, Pang and Frome having comparable bed material but much lower specific stream powers (< 20 W m^{-2} at QMED). The limitations of the approach were evident in the results of disturbance metrics, with some locations indicating that sediment transport occurred for up to 130 days a year, which is unlikely. The transport threshold overestimated disturbance where riverbeds were estimated to be composed of fine gravel. This was likely due to a combination of mean bed surface grain size being underestimated and the critical specific stream power threshold performing poorly where bedform structure contributed to overall bed stability (Church *et al*., 1998). A priority for future research should be to test the critical specific stream power threshold used here across a range of coarse grain sizes.

The high values of all four disturbance metrics in the active, mostly upland, gravel-bed rivers may be explained by their relatively unmodified form when compared to the other (modified) rivers in the dataset. Visual inspection of the data revealed that the 8% of sites with the highest disturbance PC1 scores all had RHS Habitat Modification Index scores of 2 or less (Raven *et al*., 1998). Where rivers have been modified by impoundments or for flood defence purposes, sediment supply and floodplain connectivity are reduced (Petts, 1980; Downs and Thorne, 2000), and a common geomorphic response of narrowing and deepening is evident (Church, 1995; Simon and Rinaldi, 2006). This response increases the energy directed at the riverbed rather than lateral channel adjustments (Lisle *et al*., 1993; Petit *et al*., 1996). In this scenario, bed material becomes significantly larger as finer material is transported away and not replenished (termed bed armouring), which stabilises the channel against greater shear stress (Gomez, 1983). Although the formation of a mobile armoured layer occurs naturally in many gravel-bed rivers, armouring can also occur in response to a reduction in sediment supply from upstream (e.g. due to anthropogenic modifications), forming a static armour layer, which would reduce the frequency of riverbed disturbance relative to its natural state (Mao *et al*., 2011).

5.5.3 Evidence for invertebrate community response to disturbance

Overall, there was evidence for a response of the invertebrate community to disturbance, but this appeared to interact with water quality, making interpretation of the results more complex. The prevalence of resistance/resilience traits declined with increasing disturbance in the early part of the time series (Figure 5-3A) and in the longitudinal model with good water quality (Figure 5-5A), contrary to predictions, but increased with disturbance in longitudinal models of summer or winter disturbance and water quality (Figure 5-4A; B) and poor water quality (Figure 5-5A), consistent with hypothesis 1. When focussing only on models with a statistically significant interaction between disturbance and water quality as the predictor variable (only the models of good and poor water quality), there appeared to be a recovery of insect taxa with improving water quality (decreasing resistance traits). EPT taxa, which make up a large proportion of the insect taxa in the dataset, are known to be highly sensitive to pollution (Barbour *et al*., 1992) and their recovery with improvement water quality could explain the trend shown in Figure 5-5A. This link between resistance traits and water quality was supported further by the positive correlations between RS1 and the three water quality variables, phosphate (Pearson's r = 0.45, p = 0.001), nitrate (Pearson's r = 0.42, p = 0.001) and biological oxygen demand (Pearson's r = 0.39, p = 0.001). The potential for water quality to affect RS1 is not surprising, as traits thought to confer greater resistance and/or resilience are often generic and applicable to multiple stressors, including physical and chemical disturbance. This can cause problems when trying to use traits to diagnose stressors (e.g. Schuwirth *et al*., 2015). Given the diverse set of locations at the national scale, and wide range in water quality both across England and Wales, and through time, a strong water quality effect was to be expected.

Taxon richness was the least sensitive metric to both disturbance and water quality. It increased with disturbance in the early period cross-sectional model and under poor water quality in the longitudinal model. One possible explanation for this result is the greater degree of re-oxygenation and cooler water temperatures in faster flowing upland locations, which were most prevalent at the upper end of the disturbance gradient. Both of these effects can act of offset poor water quality, such as high BOD (Verberk *et al*., 2016), and so might have promoted higher richness in these cases.

The Jaccard dissimilarity index consistently showed a trend of decreasing dissimilarity with increasing disturbance across the cross sectional and longitudinal models (Figure 5-3C; Figure 5-4C; 4D; Figure 5-5C). This indicated that the persistence of taxa was greatest at intermediate to high levels of disturbance, a trend noted by previous smaller-scale studies (Meffe and Minckley, 1987; Scarsbrook, 2002; Collier, 2008). Part of the explanation for this trend may be that the sites with the highest levels of disturbance (and therefore energy to transport sediment and create diverse physical forms) may also be the most spatially heterogeneous sites. Spatial heterogeneity has been shown to reduce the temporal variability (i.e. dissimilarity from year to year) in benthic invertebrate communities (Brown, 2003) by providing refugia for organisms (Townsend and Hildrew, 1994). In addition to this abiotic mechanism, the highest levels of disturbance are where the strongest habitat filtering is expected to occur (Townsend and Hildrew, 1994, Venn *et al*., 2011), selecting for a subset of taxa with traits that allow them to persist. The greater resistance of the selected taxa may feed up to the community level, creating a community with little variation in composition among years.

The results suggest that water quality still exerts significant control over invertebrate community composition, despite the improvements in recent decades (Langford *et al*., 2009; Durance and Ormerod 2009; Vaughan and Ormerod 2012, 2014). Therefore, future studies of the interaction between riverbed disturbance and invertebrate community composition will require a combined approach using large scale statistical analysis and small-scale experimental study, where other controls (e.g. water quality) can be held constant and the key processes and thresholds related to disturbance can be isolated.

5.6 Conclusion

The main aim of this chapter was to investigate the response of invertebrate communities to riverbed disturbance across spatial and temporal axes. A composite dataset spanning a 20-year time period, containing biological, chemical, hydrological and geomorphological data for sites across England and Wales, was combined with a simple, stream power model of the threshold of bed load transport. The results provide evidence for locations with greater bed disturbance showing increased community persistence, irrespective of water quality. Other trends may be masked by community-level response to water quality, both among-sites in the data set and over widespread improvements in recent decades. The response to water quality improvements has led to a reduction in resistance traits, hypothesised to be due to the recovery of pollution sensitive insect taxa (e.g. EPT). This study represents a first step towards linking geomorphological disturbance and community composition through time and has found that future studies need to combine this approach with small-scale experimental studies that are capable of isolating the response to physical disturbance from other drivers such as water quality.

5.7 Appendix

*Table 5-5: The 78 invertebrate families used for the analysis. Taxon list matches Vaughan and Ormerod (2014). Families with a * had missing trait information and were excluded from the study.*

Family	**Order**		**Family**	**Order**
Planariidae / Dugesiidae	Tricladida		Mesoveliidae*	Hemiptera
Dendrocoelidae	Tricladida		Hydrometridae	Hemiptera
Neritidae	Gastropoda		Gerridae	Hemiptera
Viviparidae	Gastropoda		Nepidae	Hemiptera
Valvatidae	Gastropoda		Naucoridae*	Hemiptera
Hydrobiida/ Bithyniidae	Gastropoda		Aphelocheiridae	Hemiptera
Physidae	Gastropoda		Notonectidae	Hemiptera
Lymnaeidae	Gastropoda		Pleidae*	Hemiptera
Planorbidae	Gastropoda		Corixidae	Hemiptera
Unionidae	Bivalvia		Haliplidae	Coleoptera
Sphaeriidae	Bivalvia		Paelobiidae*	Coleoptera
Oligochaeta	Oligochaeta		Dytiscidae/ Noteridae	Coleoptera
Piscicolidae	Hirudinea		Gyrinidae	Coleoptera
Glossiphoniidae	Hirudinea		Hydrophilidae/ Hydraenidae	Coleoptera
Hirudinidae*	Hirudinea		Scirtidae	Coleoptera
Erpobdellidae	Hirudinea		Dryopidae	Coleoptera
Astacidae	Decapoda		Elmidae	Coleoptera
Asellidae	Isopoda		Sialidae*	Megaloptera
Corophiidae*	Amphipoda		Rhyacophilidae/ Glossosomatidae	Trichoptera
Gammaridae	Amphipoda		Hydroptilidae	Trichoptera
Siphlonuridae*	Ephemeroptera		Philopotamidae*	Trichoptera
Baetidae	Ephemeroptera		Psychomyiidae/ Ecnomidae	Trichoptera
Heptageniidae	Ephemeroptera		Polycentropodidae	Trichoptera
Leptophlebiidae	Ephemeroptera		Hydropsychidae	Trichoptera
Potamanthidae	Ephemeroptera		Phryganeidae	Trichoptera
Ephemeridae	Ephemeroptera		Brachycentridae	Trichoptera
Ephemerellidae	Ephemeroptera		Lepidostomatidae*	Trichoptera
Caenidae	Ephemeroptera		Limnephilidae*	Trichoptera

Taeniopterygidae	Plecoptera		Goeridae	Trichoptera
Nemouridae	Plecoptera		Beraeidae*	Trichoptera
Leuctridae	Plecoptera		Sericostomatidae	Trichoptera
Capniidae	Plecoptera		Odontoceridae	Trichoptera
Perlodidae	Plecoptera		Molannidae*	Trichoptera
Perlidae	Plecoptera		Leptoceridae*	Trichoptera
Chloroperlidae	Plecoptera		Tipulidae	Diptera
Platycnemididae	Odonata		Simuliidae	Diptera
Coenagrionidae	Odonata		Chironomidae	Diptera
Calopterygidae	Odonata		Mesoveliidae	Hemiptera
Cordulegastridae	Odonata		Hydrometridae	Hemiptera
Aeshnidae	Odonata			
Libellulidae	Odonata			

6 General Discussion

6.1 Synthesis

6.1.1 Overview

The main aim of this thesis was to provide greater understanding of the interaction between freshwater ecology and hydromorphology (i.e. physical habitat), with a focus on benthic invertebrates. In particular, by employing simple, process-based geomorphological models, it aimed to adopt a stronger conceptual underpinning than simple species-habitat correlations. Specific knowledge gaps identified in the literature review (Chapter 2) were the focus of subsequent chapters and included: (i) predictions of the spatial distribution of distinct physical habitats (i.e. bedforms) using simple models of relative riverbed mobility (Chapter 3), (ii) an assessment of the effects of bed material and riverbed stability upon the composition and functional diversity of invertebrate communities (Chapter 4) and (iii) an investigation of invertebrate community response to riverbed disturbance through time (Chapter 5).

The results of these chapters have combined to provide new insights into the interaction of physical processes and ecological communities in river systems. As predicted, simple measures of the interaction between energy and grain size were able to discriminate well between different physical habitat forms, despite evidence for channel modification influencing the natural processes. Invertebrate communities were found to be strongly connected to dominant bed material and some evidence was found for increased flow energy (i.e. disturbance propensity) limiting the diversity (taxonomic and functional) of communities, particularly in coarse-bedded rivers. Evidence of riverbed disturbance acting as a temporal control on invertebrate community composition was limited: this may have been due to the ongoing effects of water quality.

These findings broaden current understanding of ecology-hydromorphology interactions in river systems, particularly at large scales, and point to new tools that could be developed to direct future river management and restoration efforts. For example, a combination of the approaches taken in Chapter’s 3 & 4 would allow for the design of river restoration schemes (i.e. bed material calibre, types of bedforms) to be tailored to introduce applicable habitat for the species of interest. The approach taken in Chapter 4 could also be developed into a tool to rapidly assess the position of a site within the wider habitat template. This would provide river managers with a way of classifying habitats with relatively low data requirements to select those where improvement schemes would be most beneficial.

6.1.2 The distribution of physical habitats

Bars were chosen as a case study for assessing the ability of simple sediment transport models to predict physical habitat, as they are closely linked to transport processes, are important habitat for a range of organisms, and are recorded in detail in River Habitat Survey i.e. different bar types and vegetation cover (Eyre *et al*., 2001; Environment Agency, 2003). In this instance a very simple model of specific stream power and mean bed material size was used to validate this possibility, which was a key assumption for the rest of the thesis. Overall, bars were found to be readily predictable at a national scale, with the success of predictions largely determined by how common the bar type was. Un-vegetated bars were more readily predictable than vegetated, likely due to their greater connectedness to the flow and sediment transport regime, whilst alternate bars were successfully predicted most often, followed by point and mid-channel bars. There was evidence for a threshold of specific stream power (30 W m^{-2}) above which bars became most common, which was hypothesised to approximate the minimum energy required to transport gravel-sized material. Bar prevalence was overestimated in rivers with significant modifications or distinct flow regimes (e.g. high baseflow chalk streams). It is apparent that the rivers where bar occurrence was overestimated due to channel modification (Chapter 3) broadly match the rivers identified as having oversized bed material (i.e. rivers that experience little to no bed load transport/disturbance) in Chapter 5. Physical modification is offered as an explanation for both results, with impoundments and flood control structures known to cause reductions in sediment supply (lack of sediment for bar building; Petts, 1980; Brookes *et al*., 1983), which leads to channel incision and bed armouring (lack of bed load transport / disturbance; Gomez, 1983). The findings of Chapter 3 indicate that river managers need to consider that catchment context of a river reach if interventions to restore or protect physical habitat are to be justified and effective in the long-term.

6.1.3 Process-based models linking habitat with community composition

The high taxonomic resolution (species-level) and good spatial coverage of the RIVPACS dataset provided a unique opportunity to conduct a first-step study of the links between sediment transport processes and invertebrate communities across Britain (Chapter 4). The Shields regime diagram was chosen as the physical model for this study as it provided a better link to process (e.g. bed load and suspended load transport) than the model used in Chapter 3. The composition and function of invertebrate communities was found to vary between rivers with gravel/cobble and silt/sand substrates. Greater transport ability was found to reduce invertebrate community richness, abundance and functional diversity in gravel/cobble substrates, with traits indicative of greater resistance or resilience, such as short lifespans, aerial dispersal and smaller aquatic stages also becoming more prevalent. In silt/sand substrates, patterns were more complex as communities with highly-abundant taxa became dominant with increasing transport ability, perhaps indicating that there are fundamental differences in what constitutes disturbance (cf. gravel/cobble). The results from gravel/cobble channels are consistent with other studies of disturbance within rivers (e.g. Bonada *et* al., 2007; Larsen and Ormerod, 2010; Gutiérrez-Cánovas *et al*., 2015), as well as smaller scale studies of river bed mobility (Death and Winterbourn, 1995; Townsend *et al*., 1997; Miyake and Nakano, 2002), all of which have tended to focus on gravel-bedded channels. These responses also fit with theoretical expectations across different ecosystems (Odum, 1985), providing further evidence of common responses to habitat variability (i.e. disturbance) across ecosystems. Further work is needed to assess whether communities in silt/sand channels are consistently more resistant/resilient to disturbance, or whether the approach used here failed to capture the important characteristics of disturbance in those rivers.

6.1.4 The temporal role of disturbance

To supplement the initial chapters which considered spatial interactions between geomorphology and ecology, the temporal aspect of disturbance and its impact on invertebrate communities was considered in Chapter 5. Critical specific stream power was selected as the indicator for riverbed disturbance due to its low data requirements and its link to the initiation of bed load transport in gravel-bed rivers (Petit, 2005; Parker *et al*., 2012; 2015). This method was selected over the Shields diagram (Chapter 4) as there is some ambiguity around the threshold of bed load transport represented by the regime diagram (Mueller *et al*., 2005). Taxon richness, the Jaccard index (persistence) and the prevalence of resistance and/or resilience traits were modelled using cross sectional and longitudinal methods, with predictor variables representing disturbance regime and water quality. The results supported the predictions of an increase in community persistence at locations with larger or more frequent bed disturbance, in line with previous studies (Meffe and Minckley, 1987; Scarsbrook, 2002; Collier, 2008). However, links to richness and resistance-resilience traits were equivocal, possibly due to water quality continuing to out-weigh the effects of physical habitat in many streams.

6.2 Implications

The results of this thesis have several implications for the study of geomorphology – ecology interactions in rivers. The first, based on Chapter 3 in particular, is that physical habitat characteristics can be predicted with relative success using simple mechanistic models, consistent with a few existing studies (e.g. Bizzi and Lerner, 2012; Vaughan *et al*., 2013). The focus on bars has provided a greater understanding of the limits of and controls on their distribution, whilst also providing a proof of concept for using models of this type to predict channel forms. This approach should promote further integration of the traditionally separate disciplines of ecology and geomorphology, a key requirement for the protection and restoration of river systems into the future (Vaughan *et al*., 2009).

Secondly, process-based models offer a robust method of predicting community diversity and function (Chapter 4). Understanding the factors affecting the predictability of ecological systems, and reducing those uncertainties, is a research priority across ecology, and capturing processes – rather than just patterns – is thought to be an important part of this (Petchey *et al*. 2015). By getting closer to first principles for both physical habitat and biology, the latter via the use of ecological traits, process-based models should also generalise more successfully in a changing environment (e.g. climate; Urban *et al*., 2016). This could provide important advances for both pure and applied fields.

Finally, the process-based models used to link fluvial geomorphology and ecology in this thesis are very simple (cf. fully-parameterised sediment transport equations; Bagnold, 1966; Engelund and Fredsøe, 1976). Barriers to more widespread use of mechanistic modelling in ecology and other disciplines include a limited understanding of the underlying processes and the complexity and/or expense of collecting data to calibrate process-based models. As a group, the sediment-transport models used in Chapters 3–5 were simple and had minimal data requirements: their data requirements, advantages, limitations and potential applications are summarised in Table 6-1. All three models have wider applications for river management and restoration planning but further development, including field verification to enhance their links to geomorphic processes and threshold would greatly increase their power.

Table 6-1: A summary of the process-based models used in this study, with their data requirements, advantages, limitations and potential applications.

Model	**Data requirements**	**Advantages**	**Limitations**	**Examples of potential applications**
Specific stream power & Mean bed material size (D50) (Chapter 3)	Channel slope, discharge, channel width, bed material composition.	Easy to calculate. Majority of data can be derived in a GIS. Allows for rapid predictions of presence of bars with little input information.	No explicit link to geomorphological processes.	- Identifying river reaches that do not conform to predictions (e.g. potentially modified) to rapidly filter large scale data and predict reference conditions. - This application would allow river restoration projects to be prioritised at a regional scale and could also be used at a local scale to inform practitioners undertaking river restoration design.
Shields regime diagram (Chapter 4)	Flow depth, channel slope, bed material composition.	Well established link to sediment transport processes. Can be applied across wide range of channel substrates.	Difficult to interpret for non-expert user. Lack of field testing. Threshold approach makes it sensitive when considering disturbance.	- Identifying locations with highest sensitivity to fine sediment impacts (i.e. coarse substrate channels with low flow energy). - When combined with RIVPACS dataset it could be used for rapid comparison between observed vs expected community (similar to RIVPACS/RICT tool but also considering physical habitat rather than water quality. This could be used to indicate where existing disturbance regimes are impacting upon invertebrate communities.
Critical specific stream power (Chapter 5)	Channel slope, discharge, channel width, bed material composition.	Evidence for correlation with initiation of sediment transport. Majority of data can be derived in a GIS.	Limited to gravel-bed rivers. Limited field testing. Threshold approach makes it sensitive when considering disturbance.	- Identifying zones of erosion and deposition along a length of river (Parker *et al*., 2015).

6.3 Limitations

This study has four key limitations, the first three of which are at least partly related to the national scale at which it was conducted. This national scale is, concomitantly, one of the strengths and novel aspects of the study, allowing questions to be asked across spatial extents far exceeding those of conventional research funding (Vaughan and Ormerod, 2010). The first stems from the use of secondary datasets in Chapters 3–5, all of which had broadly the same limitations: primarily the lack of robust geomorphic measures. For example, the measurements of mean bed sediment size used to model bedform distribution (Chapter 3), substrate type (Chapter 4) and the threshold of disturbance (Chapter 5) were reliant on estimates from percentage coverage or dominant substrate type in the RIVPACS and RHS datasets, whilst the inconsistent measurements of channel width included in the datasets were excluded in favour of more reliable flow-width relationships (Hey and Thorne, 1986; Thayer, 2017). Other weaknesses included using family-level resolution for the invertebrate time series data (Chapter 5), which may mask important results (Melo, 2005), and daily mean discharge records, rather than capturing peak discharges for characterising bed disturbance (Chapter 5). There was also error introduced by the spatial mismatches between sampling locations from different schemes.

The second limitation centred on the quality of the physical models. The thresholds used to indicate the initiation of sediment transport in the critical specific stream power and Shields regime diagram models are generally derived from laboratory flume studies (Brownlie, 1981; Petit, 1994; Parker *et al*., 2012), and field testing of them is limited to a small number of studies (e.g. Petit, 2005; Parker *et al*., 2007; Parker *et al*., 2015). These thresholds typically do not account for variations due to bed armouring (Gomez, 1983), fixed objects in the channel (e,g. large wood; Gurnell *et al*., 2002) or biotic influences (e.g. biofilms; Stone *et al*., 2008; 2011 or channel vegetation; Murray and Paola, 2003). Better, more mechanistic methods of predicting sediment transport and channel form that account for some of this variability are available (Ackers and White, 1973; Yang, 1976; Mueller *et al*., 2005) but their data requirements exceed that of the available data and their ease of calculation and interpretation is such that non-expert users (e.g. river managers, ecologists) would be unlikely to apply them.

Thirdly, the influences on river ecosystems at a national scale are manifold, including factors such as climate, water quality, vegetation and land use in addition to physical habitat (Vaughan *et al*., 2009), whilst local-scale biotic influences (e.g. biofilms; Stone *et al*., 2008; 2011) may also have a significant contribution. Trying to account for these factors whilst focusing on physical habitat is a major challenge, and may contribute to the small proportions of the variance usually explained by ecological models (Moller and Jennions, 2002). Although additional data were available on factors such as average water quality on a national scale, so that it was possible to control for their influence to some extent, it is likely that they made it harder to resolve the role of sediment transport and bed disturbance.

Finally, all of the chapters relied on correlative approaches, rather than addressing causation directly. This is a generic problem with observational studies, but especially with complex phenomena such as floods, where there are manifold changes to the river environment, including water quality, habitat area or volume, and hydrological components in addition to bed mobilisation. Although ecological relationships with bed disturbance were found here, and attempts were made to control for factors such as water quality, a combination of detailed, direct observations and experimental manipulation would be needed to ascribe causal relationships with a higher degree of confidence.

6.4 Future areas of study

The results of this study have highlighted several gaps in understanding where future efforts should be directed. Most importantly, future studies should investigate whether the invertebrate responses to riverbed stability noted here are replicated in other settings. Although Britain accounts for a tiny proportion of global river length, it has a diverse range of freshwater invertebrates and geomorphology that were captured by the national datasets used here, yet river ecosystems in other climatic (e.g. tropical, arid) and geologic (e.g. active mountain belts, lowland plains) settings may respond differently (Montgomery, 1999; Boulton *et al*., 2008; Gallardo *et al*., 2014).

The consistent approach used throughout this study to link physical processes and ecological communities based on simple, process-based models has the potential to be developed into a series of tools for use in evidence-based river management. Greater understanding and tools at the multi-catchment scales at which river basin management is now planned, at least in the UK and Europe, is a key research priority (Vaughan *et al*., 2009). The process-based models developed here allow for sites to be placed in context against a baseline understanding of the likely bedforms that are typically present (e.g. bars; Chapter 3) or invertebrate community composition (Chapter 4) using a relatively small number of geomorphic variables (i.e. sediment size, channel gradient, discharge and channel width/depth). At present, physical habitat restoration has a relatively low level of success (Palmer *et al*., 2010) and significant benefits could be derived from the use of process-based models to predict geomorphic processes, sustainable channel forms and the resulting biological communities. A first step of any future developments should be to validate the results of this thesis at field sites and/or using a laboratory flume. Such studies would enable an assessment of the potential errors inherent to these studies due to the use of secondary data and give validation to practitioners who may wish to make use of these approaches.

Much of the novelty in this thesis has come from approaching the ecology with better coverage of geomorphic processes. Obvious next steps would be to take a similar approach with the ecology. Adding a phylogenetic dimension to studies of ecological communities may provide complementary information to taxonomy and ecological traits into the role of fluvial geomorphology, and provides a window onto evolutionary processes. For example, measuring phylogenetic dispersion can extend the understanding of the roles that environmental filtering and inter-specific competition play in structuring communities relative to functional diversity measures alone (e.g. Helmus *et al.,* 2007; Violle *et al*., 2011; Cisneros *et al*., 2014). Stronger filters (e.g. greater river bed disturbance) are expected to decrease phylogenetic dispersion, leading to a community of more closely related taxa, whereas stronger inter-specific competition is predicted to generate the opposite pattern. Work is already underway to study the relative roles of phylogeny and habitat filtering in the formation of community trait assemblages.

There is also potential to extend the approach used here to simple models of ecological process, such as metabolic processes and community assembly rules (Woodward *et al*., 2016). These future studies are likely to benefit from ever improving trait information with greater coverage and resolution than that used here (e.g. Schmidt-Kloiber and Hering, 2015), along with national datasets of greater duration, such as the routinely sampled biological and chemical data used here, that continue to be supplemented and made more open to public/research use (Environment Agency, 2017). There is an opportunity for statutory environmental bodies to consolidate their sampling network such that chemistry, biology, flow and even geomorphology are monitored at the same locations within the river network. This would greatly increase the perceived reliability and number of useable locations within these datasets for applications beyond routine monitoring and allow the scale of research studies to be greatly increased with little time/cost implications. To identify the causal mechanisms of disturbance by high flows, future approaches should look to combine large scale study with experimentation that allows other drivers (e.g. water quality) to be held constant over the period of interest.

Finally, future efforts could look to investigate how the geomorphology-ecology links identified in this study are likely to change based on predictions of future conditions. With the pressures faced by freshwater ecosystems expected to continue to increase as a result of climate change, water resource use and land use change (Palmer *et al*., 2008*;* Vorosmarty *et al*., 2010), this understanding is vital for undertaking effective mitigation or restoration to protect these ecosystems and the services that they provide.

6.5 Conclusion

In short, the data presented here show evidence of an implicit link between freshwater community composition and function, and the distribution of physical habitats. Despite large improvements over recent decades, water quality still appears to be a key control in terms of community structure. Both traditional and functional measures of community diversity showed a response to changing bed material calibre and stability across large spatial scales, consistent with other studies of habitat stability in rivers and other ecosystems. Despite this spatial response, there was limited evidence of temporal variability in communities as a result of riverbed disturbance, perhaps because water quality continued to suppress the physical habitat signal. These results advance current understanding of the role of physical habitat distribution and stability in limiting invertebrate community composition, although more research is required to identify whether riverbed disturbance regimes have a greater influence on invertebrate communities as water quality stressors continue to decline. An understanding of this relationship between physical and biological processes is of importance if management and restoration efforts are to be successful into the future, particularly as pressures on river ecosystems are predicted to continue to increase. The wide availability and continued expansion of the datasets used in this study permits further development of the approaches used here to create a series of tools, at a scale relevant for river managers, that allow for the management decisions to be based on a scientifically robust understanding of both hydromorphology and ecology.

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