

Evidence

Threats and controls on the distribution of exposed riverine sediments and their associated Coleopteran fauna in England and Wales

Report – SC060038/R

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Miranda Kavanagh
Director of Evidence

Executive summary

This report presents the conclusions of a three year investigation into the controls on the distribution of English and Welsh exposed riverine sediments (ERS), their associated specialist Coleopteran fauna and the impact of river management activities. The habitat has been identified as at risk from anthropogenic pressures, and due to the high levels of rarity observed for many of its reliant species, it is important to fully understand how best to protect and enhance existing distributions. It is intended that the outcomes of this investigation feed into future management and restoration strategies, ensuring that these extend out of the channel to include the adjacent floodplain.

Known threats to the resource are reviewed before the current distribution of the ERS resource in England and Wales is presented. A subset of rivers is investigated to establish which natural (geographical and geological) and anthropogenic (impoundment, large-scale water abstraction) influences best explain observed distributions. The ERS resource is shown to have strong geographical limitations to its distribution, confined to rivers originating at high altitudes and typically within catchments containing glacial/alluvial deposits. Consequently the habitat shows its highest concentrations in the English north, Wales, and the English south west. It is mostly absent from the midlands, east and south of England, areas which have undergone extensive historical urbanisation and river modification. Rivers in these areas are also strongly influenced by groundwaters, reducing their flashiness and therefore the frequency of high flow, habitat forming events. The frequency of high flow events, and the stream power (indicated by channel slope) are shown to be the strongest predictors of average ERS area and density within the rivers included in the modelling processes. Anthropogenic pressures on the rivers (particularly the presence of large-scale abstraction in the headwaters) are shown to negatively impact on ERS occurrence downstream.

A combined approach of population sampling and trait-based analyses is used to model the importance of landscape controls on observed distributions of specialists across five ERS-rich rivers in Wales. Species fall into distinct, morphologically defined groups with associated distributions. Highly mobile species appear least reliant on a complex, highly connected mosaic of habitat patches, although there is a distinct split between headwater and lowland species in modelled distributions. Less mobile (and often rarer) species are dependent on well connected, headwater habitat, and there is an indication that where habitat isolation occurs, emigration is suppressed causing localised heightened densities. This requirement has the potential to increase their vulnerability to local extinction events.

Long-term data from the upper river Severn are analysed to investigate the presence of trends in population structure according to changes in flow characteristics. The implications of these data in the context of climate change are discussed. Larger, active ground beetle species show a strong, positive population response to high flows, particularly in the previous year. This supports previous observations that some species are able to rapidly take advantage of newly deposited or reworked habitat. Smaller, fossorial rove beetles show a positive response to low flows (indicating stability), but there appears to be a threshold at which this stability becomes less advantageous (perhaps due to other physical stresses that it imposes, such as reduced humidity or higher temperatures). Finally, the larger rove beetles benefit most from periods of moderate flows, although if these are prolonged the response becomes negative.

Fundamental ecological processes are investigated to establish the functional role of specialists and their contribution to floodplain ecosystems. Data are used to investigate food webs within the ERS habitat, the strength of connection with adjacent channels and changes in the structure of the food web at local and catchment scales. The same morphological traits that are associated with distributions also influence prey selection. Strong dispersal abilities allow greater use of aquatic prey, whilst reduced abilities or levels of specialism are associated with higher uptake of terrestrial prey. These prey 'choices' become exaggerated under different flows and along a downstream gradient. There is also a strong seasonal switch between terrestrial and aquatic prey in all species studied.

Finally, a proof of concept study of genetic microsatellite markers is presented for the abundant ground beetle species, *Bembidion atrocaeruleum*, showing future potential for development of wider dispersal and population recovery studies. Six polymorphic loci are identified across five discreet Welsh populations, with varying levels of connectivity. Variation between these populations indicates this is a path worth pursuing to investigate how stenotopic ERS species respond to isolation, varying scales of disturbance and habitat restoration.

The key points of this research project are that ERS distributions in England and Wales today are best predicted by natural factors; where prolonged anthropogenic pressures have affected river systems the resource is largely absent. Distributions of specialist beetles are inherently tied to adaptations that predict dispersal potential and these dictate the importance of well-connected habitat and the optimal lateral and longitudinal positioning of species. In turn, these traits drive the functional role of species across these scales, suggesting that the consequences of habitat loss are different for different functional groups. Loss of headwater habitat has the potential to reduce local diversity and directly impact rarer species, with a moderate reduction in resource processing. Loss of habitat in lowland areas will have a major functional impact, potentially removing a key vector of cross-ecotone subsidies.

Due to the historic losses of ERS in English and Welsh rivers, an understanding of the remaining resource and its utilisation by specialist invertebrates is vital for maintenance of current distributions. The sensitivity of ERS to channel and flow modifications, and the dependence that complex invertebrate assemblages have on a well-connected, longitudinally structured habitat mosaic should be considered at an early stage for any works involved changes to flow or channel.

The absence of before and after population studies suggest future research should concentrate on restoration projects, establishing the potential of these to enhance sediment supply, re-establish ERS and the timescales over which ERS specialist populations may recover.

This report identifies the rivers and geographical areas where ERS are abundant ensuring that the resource is recognised before potentially damaging hydrological or geomorphological changes are undertaken. If structural projects are proposed, the current resource within the river, the likely consequences of the proposed work and the potential of the catchment to maintain ERS can quickly be established. Impacts on different groups of specialist Coleoptera and associated functional roles can also be suggested based on likely changes in habitat provision, based on the position of the resource within the river corridor and the dispersal potential of target species.

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1 Introduction

1.1 Report Structure

The report presents an overview of the ecological value and current understanding of exposed riverine sediments (ERS) functioning, along with known threats to their stability and distribution. Following a statement of the study aims and objectives, the results are summarised in five short sections:

- i) discussion of the habitat distribution within England and Wales;
- ii) models of species distributions and the importance of habitat connectivity;
- iii) long term population trends, with reference to climate induced changes to hydrology;
- iv) an overview of prey selection by specialist Coleoptera and how this translates to ecological function, and
- v) a brief overview of a proof of concept genetics study.

The report ends with a series of recommendations for conserving ERS and their associated species, whilst acknowledging their vulnerability to even moderate anthropogenic disturbance.

The full methodologies and data analyses behind this summary document, along with the database of identified coarse ERS, are provided as technical appendices (A1-5).

1.2 Introduction

ERS are a common morphological form associated with natural and near natural river systems globally and defined as:

“exposed within channel fluvially deposited sediments (gravels, sands and silts) that lack continuous vegetation cover, whose vertical distribution lies between the levels of bankfull and the river’s typical base flow”.

(Bates and Sadler, 2005 p.3)

The unique pressures associated with the habitat (extremes of temperature, inundation threats, high habitat turnover, low primary productivity) support a highly specialised invertebrate fauna (Sadler and Bates, 2008). The habitat is however highly susceptible to anthropogenic disturbance and has been declining (or lost) across much the English and Welsh river network (Brewer et al., 2000, Gilvear, 1993, Petts and Gurnell, 2005). In consequence, the associated invertebrate fauna (particularly river shingle beetles), already constrained by its high levels of specialism, has exhibited parallel declines (e.g. Sadler et al., 2005).

The vulnerability of the habitat and associated species has been recognised through the creation of a specific habitat action plan (Environment Agency, 2002) and UK Biodiversity Action Plans for the rarest species (Anon, 1999). Furthermore, of the 131 invertebrate species with a high level of affinity to ERS, 66% have been designated some level of conservation status (nationally scarce, or Red Data Book) (Sadler and Bates, 2008).

This is the first study that addresses the controls on the distribution of both habitat and specialists in England and Wales. It demonstrates why present geographical

distributions of habitat occur, as a result of terrain, geology and absence of human impacts. Specialist distributions are shown to be highly complex at both local and regional scales, with shifts occurring in assemblages laterally and longitudinally. The response of species to inundation pressures, along with the extent to which they are reliant on aquatic food sources is shown to explain these variations. Simultaneously, it appears that the rarer species are highly reliant on a complex and well connected mosaic of habitat patches (as a result of relatively poor mobility), confining their distribution to areas where this occurs naturally and has not been reduced by hydrological modifications.

With the results of this study, it is clear that both the ERS habitat and its associated river shingle beetle populations are highly responsive to changes to the hydrology and channel morphology of the rivers where they are found. Assemblages demonstrate spatial complexity at catchment scales, underlining the importance of considering downstream implications of proposed alterations to river systems. This study also suggests that there is strong potential for including ERS in channel restoration considerations, given that enhanced habitat complexity and connectivity is likely to benefit associated specialist invertebrates.

1.3 Study aims and objectives

The dual aims of this study are i) to establish the extent and controls of the coarse ERS habitat within England and Wales, providing a baseline for future conservation and restoration work in relation to engineering works and activity that alters the river's flow regime and ii) to understand how the ecology of specialist ERS beetles is influenced by the landscape they inhabit, particularly in terms of the dominant influences on river flows and prey availability. A better understanding of these ecological processes will also help in a greater understanding of current observed distributions of ERS invertebrates.

These aims will be met by:

- The creation of a database of the main ERS deposits in all English and Welsh rivers and assess the hydrological, geographic or geological factors that may predict their occurrence.
- Assessing the role of variable hydrology in altering assemblages of specialist beetles.
- Modelling the influence of landscape factors and anthropogenic alterations to habitat on specialist beetle distributions.
- Exploring the underlying ecological processes that can be identified for specialist beetles, particularly their role in floodplain foodwebs.
- Examining the potential of genetic microsatellite markers as a tool for investigating dispersal within and between catchments.

1.4 Study Background

Definition of exposed riverine sediments

ERS has become (within the UK) an accepted term to describe various geomorphological features associated with natural or near-natural rivers, where variable flows rework and erode sediments, arresting successional processes. Sediments are supplied via i) downstream transportation and ii) erosion and

mobilisation of the lateral floodplain. A formal definition has been established by the Environment Agency, classing ERS as:

“exposed within channel fluvially deposited sediments (gravels, sands and silts) that lack continuous vegetation cover, whose vertical distribution lies between the levels of bankfull and the river’s typical base flow”.

(Bates and Sadler, 2005 p.3)

This definition incorporates a longitudinal gradient of habitat forms from headwaters to estuary and broadly mirrors the convention of riverine sediments exhibiting a reduction in grain size with downstream transportation (Brookes, 1994, Surian, 2002) notwithstanding variations resulting from tributary inputs (Benda et al., 2005, Knighton, 1980) or local geological changes (e.g. Rice, 1957). ERS represent a transient terrestrial habitat formed, modified and destroyed by natural riverine processes (Ward and Stanford, 1995), their formation being a product of the interaction between discharge, slope and sediment supply whose spatial variations dictate ERS distribution along the river’s length (Gurnell et al., 2009). Figures 1 and 2 show examples of riparian and in-channel ERS from the rivers Severn and Wye respectively.



Figure 1.1: Extensive riparian deposits of ERS on the River Severn, at Llandinam, mid Wales, exhibiting characteristic lack of perennial vegetation and deposits of coarse woody debris, which influence the ongoing erosion and deposition processes.



Figure 1.2: Within channel ERS on the River Wye, downstream of Glasbury, mid Wales. These deposits followed an extreme flooding event in the winter of 2007, which caused channel alterations and extensive reworkings of existing ERS. Note willow growth in middle distance.

1.5 Threats to the habitat

The current extent of ERS within English and Welsh rivers is known to be reduced relative to historic levels. Although no comprehensive data exist, it has been demonstrated that the large scale engineering projects of the 19th and 20th centuries (especially impoundments) caused substantial losses of ERS (e.g. Brewer et al., 2000). There is also evidence that in lower altitude rivers channel modification can result in an absolute loss of the habitat; immediately following engineering work on the River Soar in Leicestershire, ERS were still present (Lott, 1993), but are absent two decades on. Studies on European systems indicate that such large-scale impoundments and modifications fundamentally alter the behaviour and geomorphology of previous complex braided systems (Bravard, 2010); and continue to detrimentally impact faunal assemblages (Paetzold et al., 2008, van Looy et al., 2007) and their capacity to recover after extreme events (Lambeets et al., 2008).

The known threats to ERS persistence (see Table 1 for summary), for example regulation (via impoundment or water abstraction), channel engineering (e.g. straightening, deepening) and substrate extraction, are pervasive within English and Welsh rivers, indeed no river can be described as wholly natural. Consequently, current ERS distributions have been modified by prolonged anthropogenic suppression and the resource is missing from many rivers, especially at lower altitudes. New large-scale engineering projects are rare, and where floodplain works are undertaken, the resource is already largely absent. Similarly, substrate extraction licences are no longer issued (although current licences do not expire for 30 years) (Bates and Sadler, 2005). Current ERS distribution is therefore (partly) a product of these long-term pressures. An important consideration in the future conservation status of associated invertebrate fauna is assessing the extent and distribution of the resource, preventing future losses of habitat and, if possible, expanding its range. As such, this report contains an overview of extant English and

Welsh ERS and categorises the rivers with which it is associated, demonstrating the natural controls on the habitat's distribution and outlining the implications of anthropogenic activity on these controls.

Table 1.1: Summary of anthropogenic activities known to influence persistence of ERS within river systems, indicating the consequences and scale of activities.

Activity	Impact	Consequences	Scale	reference
Impoundment	Negative	Channel incision Sediment capture Flow moderation Hydropeaking	Catchment	(Petts, 1984)
	Positive	Scour deposits	Reach	
Channel straightening	Negative	Channel incision Sediment flushing	Segment	(Brookes, 1994)
Bank stabilization	Negative	Lateral movement reduced Channel incision	Segment	(Liebault and Piegay, 2002)
Dredging	Negative	Removal of sediments Increased flows	Reach	(Elosegi et al., 2010)
Water abstraction	Negative	Reduced downstream reworking	Catchment	(Brunke, 2002)
Flood defences	Negative	Lateral movement reduced Sediment flushing	Segment	(Bravard, 2010, Parsons and Gilvear, 2002)
Gravel abstraction	Negative	Local disturbance Downstream sediment supply reduced	Reach / segment	(Gaillardot and Piegay, 1999, Kondolf et al., 2002)
Bank vegetation structure	Negative / positive	Lateral movement reduced/enhances	Segment	(Millar, 2000, Trimble, 1997)
Livestock poaching	Negative	Nutrient enrichment Sediment compaction and silting	Reach	(Bates et al., 2007a)
Weir removal	Positive	Restoration of longitudinal sediment supply Increased flow variability	Reach / catchment	(de Leaniz, 2008)
Reconnection with historic floodplain	Positive	Restoration of lateral sediment supply Greater channel complexity	Reach / catchment	(Caruso, 2006)
Restoring braiding	Positive	Spatially variable flows allow sediment deposition	Reach /catchment	(Jahnig et al., 2009)

Scale definitions: Reach 10^1 m, Segment 10^2 m, Catchment 10^3 m (from Frissell et al., 1986)

1.6 Conservation status of ERS Invertebrates

Current distributions of the Coleopteran fauna associated with ERS have been broadly described for England and Wales (Bates and Sadler, 2004, Eyre et al., 2001a, Eyre et al., 2000, Eyre et al., 2001b, Sadler and Bell, 2002). Historic losses and future pressures on the ERS resource are important due to the high levels of rarity exhibited by many of the associated species; of the 131 specialist Coleoptera found on UK ERS, 86 have been accorded a level of conservation status (Fowles, 2005, Hyman and Parsons, 1992a, Hyman and Parsons, 1992b), with 5 of these included in the river shingle beetle BAP (Anon, 1999). The statuses of individual species were reviewed by Bates and Sadler (2005), with a caveat that further work on both the distributions and ecology was necessary. Since then, our understanding of microspatial distributions (Bates et al., 2007b, Henshall et al., 2011) and inundation responses (Hering et al., 2004, Lambeets et al., 2008, Paetzold et al., 2008) has been much increased.

1.7 Key landscape and ecological factors

Habitat resilience

Although individual ERS patches are inherently transient, where systems are in equilibrium loss of habitat is balanced by the deposition of new patches locally. This process is dependent on the maintenance of sediment supplies via downstream transport and lateral erosion, which are in turn reliant on variability in the magnitude and duration of flows.

Habitat connectivity, flooding and dispersal potential

The repeated reworking of ERS habitat requires high levels of adaptation by stenotopic species, which can loosely be split into two strategies: tolerance (via avoidance or survival) and flight (relocating away from floods). The flight strategy also allows rapid dispersal and colonisation of new habitat units. Strong variations in dispersal potential have been seen in ERS associated species (Bates et al., 2005) and poor abilities may cause local extinctions (Stelter et al., 1997). Variation in ERS distributions means similar levels of habitat connectivity, which will benefit species differently according to their dispersal abilities

Food Webs

Natural floodplains characteristically facilitate substantial and reciprocal exchanges of nutrients and food resources. It is as processors of these resources that specialist Coleoptera provide a fundamental ecological role, with predators, herbivores and detritivores all utilising large aquatic subsidies (Bastow et al., 2002, Paetzold and Tockner, 2005). Known variation in inundation tolerance, coupled with assemblage resilience in this patchily distributed habitat is likely to influence the efficiency of this processing and further dissemination of resources into the floodplain. By investigating variation in food web structure, according to flooding, functional grouping and location in the catchment, the relative importance of specialists as processors and contributors to floodplain ecosystems can be established.

2 Summary of key findings

2.1: The English and Welsh sand/gravel ERS resource. The controls and influences on its distribution.

See Appendix A1 for Extended Technical Report

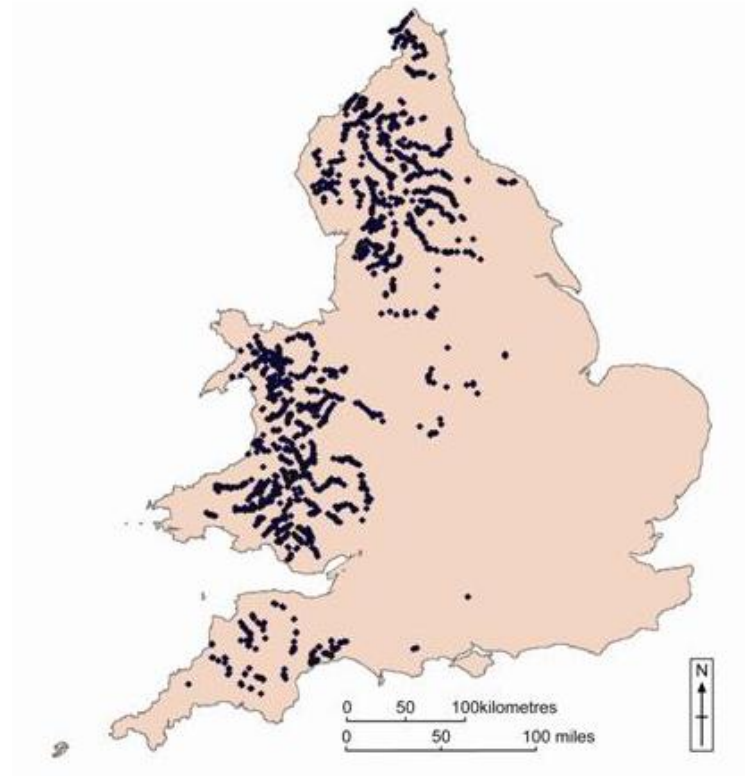


Figure 2.1: Distribution of observed or mapped ERS deposits in England and Wales, with each data point representing discrete areas of single or multiple habitat as of 2010.

English and Welsh ERS (as of 2010) is now mapped (Figure 3; Appendix 6), providing the location of visible (or recorded on OS maps) river shingle deposits and available in the Access database on the appended cd. This resource enables the ERS content of individual rivers to be checked. The grid references in the database may indicate individual habitat units, or the centre of multiple dense distributions within a reach.

Distributions are predominantly confined to Wales and the north and south west of England – characteristically high altitude, high rainfall areas which create the erosive flows needed for reworking of sediments within the catchment. The seasonality of flows is similar across sampled rivers, with highest flows in autumn and winter, but maintaining stochastic year-round high-flow events of variable duration. Analysis of

geology within the catchments of representative rivers indicates that ERS dominates in areas where glacial or alluvial substrates are present (supplying the sediments for reworking by associated high flows). The resource is largely absent from the Midlands, the south and East Anglia – a combination of buffering groundwater influence on hydrology, reduced substrate availability and anthropogenic pressures and geology?

The strongest predicting factors in ERS distributions at the <1km scale are the level of very high flows (the highest 10% in any given river) and the slope of the river. The former, which is a measure of magnitude, predicts the overall area of ERS, the latter (a proxy for stream power) predicts the density of habitat patches within the river. However, there is evidence that the presence of large-scale abstraction within the headwaters is associated with a reduction in the area of ERS downstream, the consequence of long-term alteration to the flow regime, with a reduction in magnitude.

Key Points

- The levels of ERS provision in any river can now be assessed using the database of mapped English and Welsh resource.
- Current distributions of ERS are largely predicted by natural factors. Significant anthropogenic alterations to river channels remove the resource entirely, or in the case of historic modifications, rivers have achieved a new stable equilibrium state (e.g. upper River Severn below Llyn Ciwyedog).
- The consequences of anthropogenic alterations to river hydrology and morphology have been well described elsewhere (see Table 1). Where engineering/management work is proposed, within a specific river, both the current ERS and its potential ERS provision should be considered in the light of these known consequences
- It is important to remember that in the long term most channel modifications that alter natural morphology necessarily alter natural flow velocity and variability, which reduces or removes entirely ERS deposits at catchment scales. This represents the key problem of ERS conservation where anthropogenic needs are paramount, and suggests that conservation and management efforts should be concentrated where these are not in conflict with land use requirements.
- In restoration schemes, the capacity of rivers to sustain ERS can be predicted by examining their hydrological, geographical and geological profile.

2.2 Hydrological controls on specialist species abundance

See Appendix A2 for Extended Technical Report

The complexity of species assemblage behaviour and requirements is demonstrated by the differing and distinct responses to differing flow events (Table 1). Larger, strongly dispersing species (usually predatory ground beetles) benefit from high flow, habitat restructuring events. Species of similar size but with reduced dispersal abilities (e.g. larger rove beetles) show highest numbers during periods of moderate flows. Smaller, fossorial species (smaller rove beetles) respond positively to both a low number of low flow (Q95) levels but also to very low individual flows. Predicted changes in abundance (per 4m²) are given in table 1. These different responses indicate that weather-driven changes in flow regimes predicted under current climate scenarios may fundamentally alter assemblage make up and biotic mass of ERS specialists at catchment scales. Any such long-term change would potentially alter both the functional capacity of the assemblage and the dynamics of nutrient transfer from stream to floodplain (see no. 3).

Table 2.1: Average abundances per sample (4 m²) predicted by strongest modelled environmental variables. Highest predicted abundances in bold.

Ground beetles

Maximum summer flow (m³/sec) in preceding year

Flow	10	15	20	25	>25
Abundance	22	25	37	24	13

Small rove beetles

i)Number of Q₉₅ events (low flow) in previous years

Events		0	3	6	9	12
Abundance	25	32	21	12	13	

ii)Minimum flow in previous year (m³/sec)

Flow	0.5	0.6	0.7	0.8
Abundance	24	24	20	15

Larger rove beetles

i) No. Q₅₀ days in previous years

Days		140	160	180	200	220
Abundance	2	5	7	3	2	

ii) No. Q₅₀ events in previous years

Events		10	12	14	16	18	20
Abundance	7	8	9	8	1	1	

*These responses are specific to the assemblage sampled from Llandinam Gravels only and should be seen as indicative of responses by these groups to local hydrology: Q data taken from Dolwen flow gauge, Q₁₀: 16.2m³/s; Q₅₀: 3.755m³/s; Q₉₅: 0.951m³/s

2.3 Explanation of observed assemblage structure within the Severn/Wye catchments

See Appendix A3 for Extended Technical Report

Generally speaking, the most complex and dense distributions of ERS are found in a river's higher reaches, where floodplains first appear, fed by low order streams, this decreases downstream until the habitat typically is represented by single, isolated patches, separated by kilometres rather than metres. There may also be a raised disconnect resulting from reach-scale loss of patches caused by adjacent land-use and channel modifications.

In this context, observed species distributions have strong relationship variables describing the connectedness (or not) of the habitat and the morphological adaptations of species studied (Figure 4 shows varying responses). Variation in assemblage structure occurs along rivers containing ERS, with highest levels of diversity and rarity associated with complex, high density lower stream order habitat. However, lowland habitat supports its own distinct assemblage adapted to the changing hydrology. This assemblage also appears to model greater densities, increasing the functional capacity of the fauna as both predators and potential prey items (Table 2 shows predicted numerical responses of functional groupings to significant distance and density variables). Downstream areas of habitat (occurring as isolated, single patches) are most vulnerable from anthropogenic changes to flow and channel alterations, but are indicated as having the potential to support highest levels of specialists (although not diversity). As a rule of thumb loss of lowland habitat therefore has the greatest potential functional impact on this riparian ecosystem. Proximity to urbanised or valuable agricultural land increases the likelihood of management to reduce flood risk and lateral channel movement, which in turn decreases overall connectivity and habitat provision.

Species with strong dispersal potential occur along the gradient, but the most able dispersers are most associated with downstream habitat. Less able dispersers (and often rarer species) are most strongly associated with headwater habitat. Headwater habitat also possesses more diversity, with strong, moderate and less able dispersers co-existing. Although headwater habitat is less at risk from anthropogenic changes (e.g. large scale engineering works and flood relief schemes being rarer in sparsely populated areas); the vulnerability of local populations to extinction events is greater. Consequently, pressures such as poaching and substrate removal, which reduce quality and density of habitat, may potentially reduce headwater diversity.

Table 2.2: Predicted abundances according to (i) longitudinal positioning and (ii) habitat density modelled from observed assemblage data.

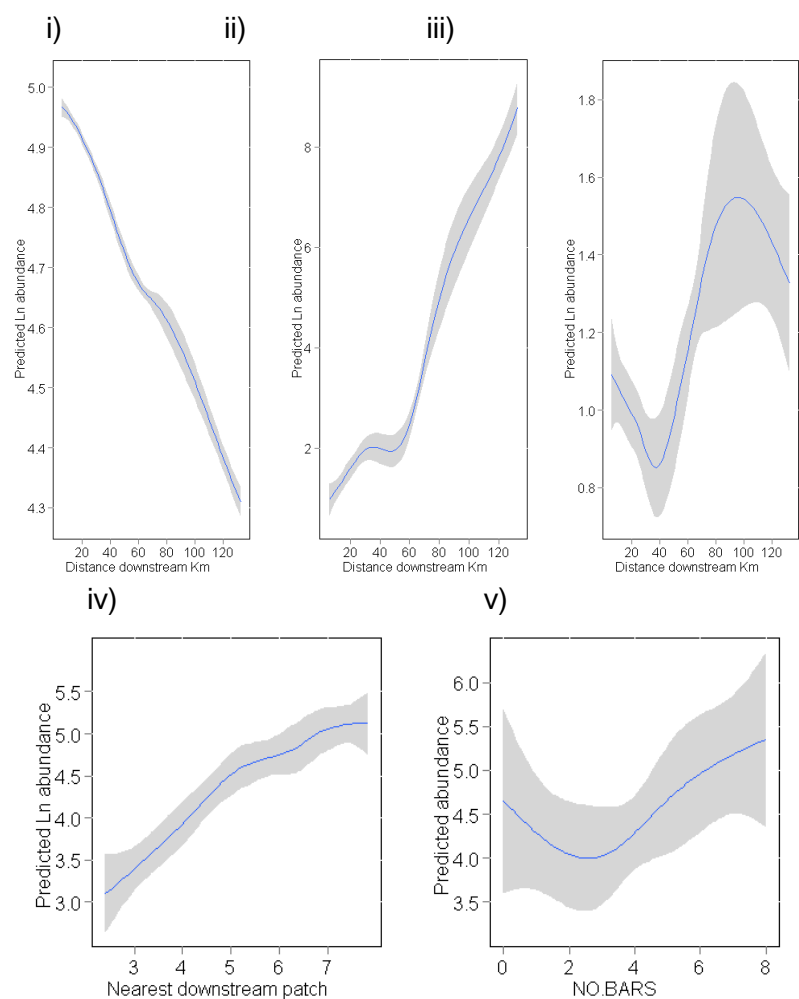
i) Predicted changes in abundance according to distance of sampling point from headwaters

Distance	20km	40km	60km	80km	100km
Grp 1a	148	134	100	109	88
Grp 1b	3	7	2	90	403
Grp 2	3	2	3	4	5
Grp 3	90	70	60	55	45

ii) Predicted changes in abundance according to number of habitat patches within 1km

Patches	0	2	4	6	8
Grp 1a	115	115	121	128	134
Grp 3	90	54	69	148	221

Figure 2.2: Predicted abundances of specialist beetles responding to strongest modelled environmental variables i) headwater ground beetles and distance downstream; ii) lowland species and distance downstream; iii) low affinity species and distance downstream; iv) specialist, non-ground beetles and distance to nearest downstream habitat and v) the number of bars within 1km.



Key points

- The threats to ERS specialists and consequences of loss are distinct and related to preferential longitudinal positioning.

- Headwater species occupy a dense and locally abundant form of the habitat. Unless large-scale impoundments or similar engineering works are undertaken, the overall habitat provision is relatively 'safe'. However, the assemblages found in these areas have high levels of rarity with more species possessing reduced mobility.
- Loss or reduction in quality of individual patches risks loss of populations of rarer species. As an example, the only known record of the endemic rove beetle *Thinobius newberyi* on the river Severn is from a single ERS patch at Llandinam (personal communication, S. Henshall, Buglife), which lies within extensive ERS deposits that have been sampled continuously over a decade.
- Damage caused by substrate removal or cattle poaching should therefore be prevented in areas of high quality ERS, where these are known to possess diverse specialist assemblages.
- Conversely, lowland habitat occupies land more commonly required for human use and more likely to require flood defences or erosion control. Although more infrequent, the high abundances predicted for these isolated patches gives them a large, local functional role. Here the rarity of the habitat, rather than associated species is the concern, and the almost certain loss of these patches following channel or flow alteration and the consequences for the functional ecology of the floodplain should be understood and considered in the relevant planning and consenting processes.

2.4 Food web development and functional role of specialists

See Appendix A4 for Extended Technical Report

Dispersal-enhancing traits improve species' ability to survive or rapidly escape inundation, reducing the 'risk' of utilising habitat areas at the stream edge subject to rapidly varying flows. This narrow strip within ERS is frequently the most productive, due to high levels of emerging and stranded aquatic insects. Analysis of dietary composition across functional groups indicates that the uptake of this resource can be directly linked to the strength of dispersal potential and the optimal longitudinal positioning within the river catchment, with strong-dispersing, lowland species deriving up to 80% of their diet from emerging aquatic invertebrates. Conversely less-able dispersers, associated with headwater habitat derive up to 80% of their prey from terrestrial prey (e.g. collembola and aphids). The 'risk' of stream-edge positioning with reduced dispersal abilities effectively denies this grouping access to the primary nutrient source in ERS, but also permits multiple functional niches within the habitat, reducing interactions and potential competition.

These patterns are reinforced at the patch-scales, with inundation frequency and extent having marginal impact on the uptake of aquatic prey by highly mobile species (indicating an ability to continue functioning as shoreline predators under high flows), less well adapted species (e.g. *Bembidion tetracolum*) show a rapid switch to terrestrial prey under even moderately higher inundation pressures.

A strong seasonal switch in prey is shown in all predators, with terrestrial prey indicated as the primary food source for all species. Although it has long been understood that ERS specialists utilise inland overwintering sites (to avoid

prolonged, high winter flows), this is the first time that it has been demonstrated that they remain at least partly active in these sites, to the extent that their feeding can alter their isotopic signal.

These three consumption patterns are indicated in the conceptual models presented in Figure 5:

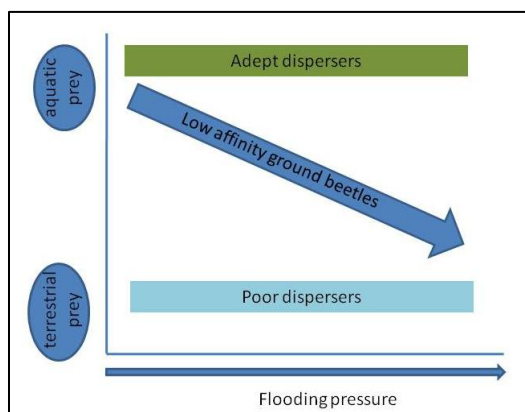
- 1) Adept dispersers utilise aquatic prey regardless of inundation pressure, whereas poor disperser consistently utilise terrestrial prey. Species with low affinity to ERS only utilise aquatic prey when inundation pressures are low.
- 2) All species show a seasonal switch in prey choice, indicating that autumn-early spring is dominated by terrestrial prey, reflecting choice of overwintering habitat away from the river channel.
- 3) The proportion of aquatic prey in adept dispersing species increases with distance downstream, but the assemblage structure also changes with increasing abundances of species best adapted to downstream hydrology; species better adapted to flashier, headwater influenced flows appear unable to utilise the aquatic resource efficiently outside of these conditions.

Key points

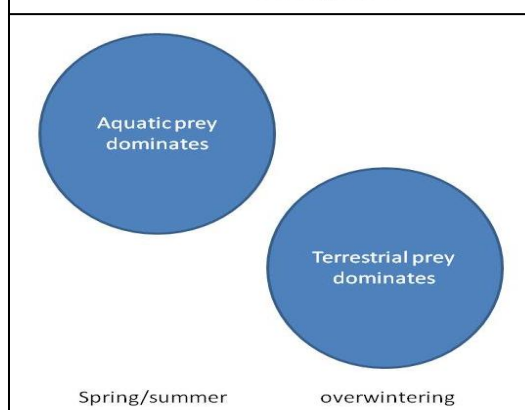
- Prey selection indicates high functional diversity within Coleopteran species utilising ERS, particularly in headwater habitats, this reinforces the groupings indicated by morphological traits and modelled distributions.
- The scale of Coleoptera as vectors for transferring nutrients from aquatic to terrestrial ecosystems is greatest in lowland habitat, an indication both of adaptation, abundance and relative stream productivity.
- The seasonal shift in prey choice stresses the importance of maintaining viable overwintering habitat adjacent ERS where Coleoptera can both escape prolonged high flows, and continue to find suitable prey items when feeding.

Figure 2.3: Trends in prey selection by ERS beetles according to

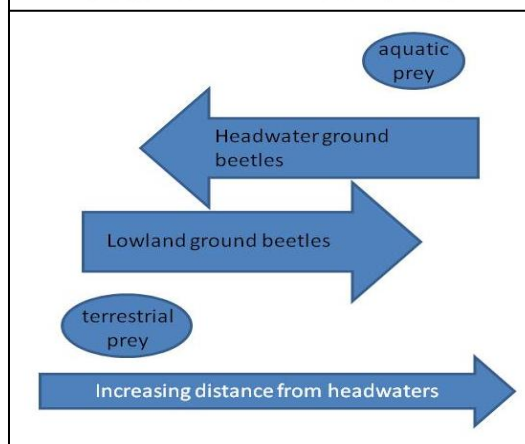
i) flooding pressure



ii) season



iii) distance downstream



2.5 Overview of genetic proof of concept study.

See Appendix A5 for Extended Technical Report

The pilot study was to test the viability of using DNA microsatellite markers to investigate dispersal and post-inundation recovery in ERS species. An abundant, widely distributed ground beetle (*Bembidion atrocaeruleum*) was selected for study. Following identification of polymorphic microsatellites, genetic variation between populations from the rivers Severn, Tanat, Banwy, Vyrnwy and Wye was investigated. The presence of significant variation indicated that there is enough between-population difference to continue the development of this tool for

further research. The research team are currently assessing the viability of increasing the library of usable microsatellite loci, and it is envisaged that upon completion of this assessment, the results will be used to develop further research programmes on catchment-scale dispersal pathways.

3 Key recommendations and conclusions

Table 3.1: Key recommendations and area of river improved

Action	Benefitting area
Identify key locations of vulnerable species and ensure catchment scale resource protection	All
Reduce/prevent livestock poaching	Headwaters
Ensure lateral channel mobility when not in conflict with other land uses	All
Identify ERS presence downstream of major works and incorporate assessment of value in decision making processes	Lowland
Reduce bankside vegetation development	All
Continue to reduce substrate extraction	All
Reduce/remove weirs	Lowland
Include ERS restoration/recovery in river restoration projects	Lowland
Study assemblage recovery potential in restored sections	All

- In the short-term, known locations of species targeted in the grouped action plan for river shingle beetles should be collated. Potentially negative land-uses or proposed changes to flow/sediment can then be managed with these species in mind.
- Current ERS distribution is the result of underlying natural processes and long-term (decadal – centennial) alteration of natural river regimes by anthropogenic causes.
- The 2010 database allows the resource to be monitored at multiple scales; we do not know if current habitat levels are stable, and so the database provides a tool to monitor changes over time.
- Many channel modifications are driven by increasing urban and land use pressures. Where ERS is present (or downstream) in reaches of proposed work, the likely impact of work can now be assessed, and the value of ERS conservation included in the planning and implementation process.
- The natural processes that predict ERS within a river are identified. Where these are present in a river undergoing restoration, the re-establishment of ERS should be included as a measure of the project's success.
- The potential for ERS specialists to recolonise restored habitat has not been explored in this country. As such, monitoring of such projects should include locally relevant species as indicators of success.
- Variations in dispersal potential and resource utilisation strongly reinforce the message that ERS assemblages operate on complex lateral and longitudinal scales. As such the inland and downstream consequences of channel alteration are reiterated. Given the large scale resource processing undertaken by studied species, and their further role as prey items for numerous terrestrial vertebrates and other invertebrates, this key ecological process needs to be preserved wherever possible. The connectivity of catchments and their floodplains is not always visible, but any disconnect will seriously impair the health and diversity of associated ecosystems.

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Glossary

<i>Allele</i>	a variation in a gene code which will produce a differing effect in expression e.g. eye colour
<i>Coleoptera</i>	Beetles
<i>Ecotone</i> terrestrial.	boundary between different ecosystems e.g. aquatic and
<i>Diapause</i>	Essential developmental period in insects, typically over winter, characterised by lack of activity. Also provides a survival mechanism for prolonged cold.
<i>Emergence</i>	macroinvertebrates in transition from aquatic larval stage to terrestrial / aerial adult stage.
<i>Fennoscandia</i>	Geographical region comprising Scandinavian peninsula, Finland, Karelia and the Kola peninsula.
<i>Fossorial</i>	organisms living below the surface.
<i>Functional response</i>	Environment induced changes in resource use by an organism or species that potentially alter local ecosystem dynamics e.g. prey choice or spatial positioning.
<i>Heterozygosity</i>	level of differing alleles at chromosomal loci between individuals.
<i>Homozygosity</i>	level of genetic similarity.
<i>Hydro-peaking</i>	artificial, high flow events resulting from deliberate releases of impounded water.
<i>Macroptery</i>	level of flight ability.
<i>Microsatellite markers</i> variation.	areas of genetic code common within species, but exhibiting
<i>Phytophagous</i>	insects that feed on plant material
<i>Polymorphic loci</i>	variable sections of genetic code that are used to investigate relatedness within/between populations.
<i>Stenotopic</i>	restricted to a small range of habitats/ecological conditions.
<i>Trait</i>	a species-specific physical or behavioural attribute which influences its utilisation of the habitat and resources.
<i>Vector</i>	organism that consumes prey from allochthonous source, thereby transferring nutritional content to a different habitat/ecosystem.
<i>Subsidy</i>	external nutrient source supplementing that originating from primary production of an ecosystem.

Appendix A1:

THE ENGLISH AND WELSH RESOURCE, THE CONTROLS AND INFLUENCES ON ITS DISTRIBUTION

Introduction

Exposed riverine sediments have been defined as “*exposed, within channel, fluvially deposited sediments (gravels, sands and silts) that lack continuous vegetation cover, whose vertical distribution lies between the levels of bank-full and the typical base flow of the river*” (Bates et al., 2005 p.5). ERS represent a transient terrestrial habitat formed, modified and destroyed by natural river processes (Church, 2002, Ward and Stanford, 1995), their formation being the product of the interaction between river discharge, slope and sediment supply (e.g. Vandenberg, 1995). The frequency with which the sediments are remobilised and transported is a product of flow and power (Bettess, 1994, Carling, 1992), and the combined influence of these two forces will vary spatially (according to geomorphology) and temporally (with changes in hydrological response), and these variations will dictate the channel form (including presence of ERS) (Gurnell et al., 2009). Crucially, the available sediments must possess sufficient erosive potential (under local hydrological conditions) to allow mobilisation that maintains the channel instability (Lisle et al., 2000). Powerful high flow events mobilise available sediments from both within channel and (where lateral transfer occurs) from the adjacent floodplain (Surian and Cisotto, 2007), resulting in characteristic ‘wandering channels’ (Church et al., 1987), deposits of ERS in the riparian zone, and a wider floodplain at varying stages of successional development: creating a ‘shifting steady state mosaic’ (van der Nat et al., 2003). Where the channel is constrained (e.g. steep, incising, headwater channels), lateral turnover is reduced, relative to non-constrained channels (e.g. braided channels) (Ward et al., 2002). ERS are reliant on turnover rates high enough to mobilise deposits and scour vegetation. Where inundation and sediment remobilisation are infrequent, successional processes stabilise recently exposed sediments returning them to a familiar, terrestrial, vegetated form that is resilient to further erosion (Asaeda et al., 2010, Gurnell et al., 2001).

These interactions of flow, power, sediment supply, transportation and resistance form a level of equilibrium within channels, where downstream transportation is counteracted by upstream and lateral replenishment. This natural equilibrium state makes ERS vulnerable to anthropogenic alterations to the river channel and flow, which may upset the balance of erosion and deposition (Gurnell et al., 2009). The long-term consequences of human impacts are reduction or loss of ERS. For example, impoundment may reduce the magnitude of restructuring flow events (Brandt, 2000) and interrupt sediment transport (Petts and Gurnell, 2005); and substrate extraction and land use changes may reduce sediment supply into the river channel, typically reducing channel complexity and habitat diversity (Gaillardet and Piegay, 1999, Kondolf et al., 2002, Liebault and Piegay, 2002). Impoundment and sediment extraction have been suggested as one of the principle causes for the shift in many European rivers from historic braided forms to present day single channels (e.g. Bravard, 2010, Hohensinner et al., 2004). As rivers enter downstream urbanised areas, channel straightening, deepening and bankside protection flood defences combine to diminish the potential for ERS occurrence (Florsheim et al., 2008).

Given these controls, ERS are considered as indicative of a river system maintaining some degree of naturalness and equilibrium with the landscape through which it passes; and, in this state, ERS deliver unique ecosystem services (Paetzold et al., 2005). Their role as a habitat resource for specialist and often rare invertebrates and birds has been well established (Anderson and Hanssen, 2005, Drake et al., 2007, Lambeets et al., 2009, Sadler et al., 2004, Yalden, 1986). Increasingly, these specialist inhabitants are being shown to be dominant vectors transferring nutrients between aquatic and terrestrial ecosystems, through predation (Paetzold et al., 2005) and herbivory (Bastow et al., 2002), to the extent that they may impact on emergence success of adult aquatic invertebrates (Paetzold and Tockner, 2005).

As a consequence of associated levels of rarity and the ecosystem services provided, the English and Welsh resource has been assigned its own habitat action plan (Environment Agency, 2002), although knowledge of its distribution is very limited, particularly the coarser forms associated with lower order, higher power streams. In the UK there has been a marked reduction in the amount of ERS in the last century (e.g. Brewer et al., 2000), concomitant with global degradation and loss of floodplain environments (Tockner and Stanford, 2002) and increasing recognition of the need to identify and

conserve the resource (Ulyshen and Horn, 2010). Work is needed to establish what variables control and affect their distribution, to ensure future conservation.

This research package will:

1. provide the first systematic, modern (2010) assessment of the extent and distribution of ERS in England and Wales.
2. characterise geographical and hydrological features of ERS rich systems.
3. model the physical and anthropogenic factors determining the complexity and abundance of ERS at the England and Wales scale.

Methods

To achieve the research aims, we undertook a sequential compilation and analysis of extant English and Welsh ERS. Remote sensing was used to identify the extent and distribution of the resource, before the hydrographs of ERS-rich rivers were characterised according to flow regime shapes and magnitude. These characteristics were then linked to physical and anthropogenic variables to model factors predicting ERS distributions and densities.

Aerial imagery and ERS distribution

Identification of ERS used modern (2010) aerial photography cross-validated with high resolution Ordnance Survey maps to overcome issues of photograph interpretability for high flows (i.e. ERS inundation) and tree canopy cover of the river channel. The coordinates of visible ERS patches or systems were recorded prior to plotting in a geographical information system (ArcGIS) and entry into a database (Microsoft Access, contained on appended cd) for archival purposes. For the purposes of mapping and database compilation the coordinates of each site represented the central point of the observed ERS. Where multiple habitat units were observed, the coordinate represented the middle of the central unit.

River flow regime analysis

From regions of England and Wales with high ERS densities (identified from the mapping exercise), a total of 44 rivers were selected to characterise long-term annual river flow and identify any relationship with ERS coverage. For these rivers, a more detailed analysis of ERS present was undertaken, with every visible or recorded gravel/shingle bar identified and its size recorded. This provided a dataset of high resolution, river-specific ERS distribution and density. Event-based flow variation is built into generalised linear modelling (below), with the frequency and timing of high flow Q_{10} events used as an indicator of frequency of disturbance events (selected based on field observations of high flows and patch submersion). Long-term mean daily flows were extracted from the National River Flow Archive (NRFA) by the Centre for Ecology and Hydrology. Data were obtained from stations closest to headwaters with a complete (or >90%) record over a common 30-yr period from 1988-2008. To standardise against variable catchment size, monthly averages of daily flows (mm month^{-1}) were calculated to characterise the seasonality annual regimes; with the restructuring potential of flows greater in the winter when sediments lack stabilising annual vegetation. For the purposes this analysis the timeframe for the regime classification was defined as one month after the month of minimum flow (July). Additional information on catchment geology and anthropogenic modifications (impoundment by large, headwater dams and water abstraction) were derived from the NRFA to interpret flow regime classification results.

When assessing spatial and temporal variations in river flow regimes, it is important to identify both the size (magnitude) and timing (shape) of discharges over the annual cycle. A hierarchical cluster analysis based method was applied to classify these two key attributes of annual flow regimes. The regime shape and magnitude classification procedure was developed by Hannah et al. (2000), and has been evaluated in several applications (Bower et al., 2004, Hannah et al., 2005, Harris et al., 2000, Kansakar et al., 2004, Monk et al., 2008). The shape classification identifies stations with similar regime forms, regardless of magnitude; whereas the magnitude classification is based on four indices (i.e. the mean, minimum, maximum and standard deviation) derived from long-term mean monthly values for each station, regardless of timing. The comparison of solutions for seven hierarchical, agglomerative clustering algorithms (i.e. average linkage between and within groups, complete linkage, single linkage, centroid, median and Ward's Method) revealed that different algorithms identify different groups (Bower et al., 2004). Ward's Method produces the most robust clusters with parsimonious membership. Dendrograms and agglomeration schedules are used to identify robustly the number of clusters to retain (Griffith and Amrhein, 1997).

Generalised linear modelling

Following exploration of data for co-linearity and the presence of outliers (none were found) (Zuur et al., 2010), generalised linear models (GLM) were run using a suite of potential explanatory variables (Table 1) against ERS abundance (L_n total habitat area km, transformed to allow comparison between rivers of different sizes) and complexity (total number of habitat units km) (McCullagh and Nelder, 1983). Variables encompassed geographical (geology, local physical characteristics and location), hydrological (flow regime, including frequency of high flow events) and anthropogenic influences within the catchments (impoundment and water abstraction). Values for individual gauging stations are shown in Table 2. Significant explanatory variables were identified using both forwards and backwards selection to identify best-fit models (Table 3) (Zuur et al., 2007). Visual model validation was conducted; and histograms of residuals were used to test normality and plots of residuals against explanatory variables established independence (after Zuur et al., 2010).

A suite of possible models was derived using Akaike's Information Criteria (AIC), ranking these according to their AIC value and Akaike weight (Akaike, 1974, Burnham and Anderson, 2002). A 95% confidence set of models was identified starting with those holding the greatest weight, and repeatedly adding the model with the next highest weight up to 0.95. Both the most parsimonious models, and those lying within the 95% confidence range, are presented (Table 4).

Results

The results are presented in the same sequential order as the methodological approach, with initial English and Welsh distributions identified, prior to the hydrological characteristics of the associated rivers. Potential models for ERS presence and complexity within rivers are then explored.

Spatial distribution of ERS and river flow regimes

Aerial imagery and cross-validated map data identified 1,670 areas of substantial ERS along English and Welsh rivers. Ground truthing on reaches from five Welsh rivers (Severn, Wye, Banwy, Vyrnwy and Tanat was also undertaken). When mapped (Figure 1), ERS are shown to be confined largely to three areas: the north of England (in rivers originating along the Pennine spine), the south-west of England, and much of Wales.

The flow regime classification yielded five groupings for both shape and magnitude classes (as described below), which were cross-tabulated to define an overall (composite) regime for each river and overlain on the map as ERS occurrence (Figure 1). The underlying geology, anthropogenic influences and hydrological characteristics associated with these rivers are provided in Table 2. Common to all classes was a strong seasonality to flow variation with a clear winter peak but variations in the timing and rapidity of onset of flow maxima (Figure 2), and lowest flows in mid-summer.

Five shape classes were identified with differences in flow seasonality (Figure 2) as follows:

- Class A. A stepped autumnal increase, with a steep rising limb in September - October, followed by a more gradual rise to a January peak and a steep recession limb from February (18 stations).
- Class B. A steep rising limb from September - October, with a broad peak through the winter before a gradual recession from February to March (4 stations).
- Class C. A prolonged and steep rise from September to sharp January peak, the spring decline is similar, but more gradual than Class A (9 stations).
- Class D. A gradual autumn increase, with a plateau in October - November. The January peak is distinct, but not as sharp as Classes A and C. The spring decline is steep to the summer minimum (8 stations).
- Class E. A steep rising limb in autumn from September to December, with a broad peak until February. A steep recession limb, although there is some indication of a February - March step (12 stations).

Five magnitude regimes were identified and described using the indices (Figure 3):

- Class 1. Low mean and seasonality with the lowest values for all indices (14 stations).
- Class 2. Intermediate mean and seasonality with second lowest values for all indices (2 stations).
- Class 3. Moderate, consistently placed in the mid-range for the indices (10 stations).
- Class 4. High but with lower maximum flow than Class 5 (6 stations).
- Class 5. Very high with consistently highest magnitude across all categories, most notably maximum flow (13 stations).

Some general trends appear for shape and magnitude classes. Shape class A is confined to Wales (Figure 2), and Classes B and D to northwest England. Classes C and E are spread across all regions, with no clear underlying pattern of distribution. Magnitude groups show less geographical fidelity, with Classes 2 and 3 showing a westerly distribution, and Class 5 spread across all of the regions (there is some indication that higher magnitudes are associated with mid- and south Welsh rivers, rather than north Welsh). Class 4 is confined to mid Wales, but is represented by only two rivers (the Vyrnwy and Ystwyth). The only composite shape-magnitude classes showing geographical fidelity are A3 (gradual rising limb, moderate magnitude), confined to Wales and E5 (broad winter peak, highest magnitude) to the English midlands, with one example in mid Wales (the Ithon).

Predicting ERS abundance and complexity

Generalised linear models were derived using catchment, hydrological and anthropogenic influences as predictors for: (1) Ln of the average m^2km^{-1} of habitat (i.e. ERS area scaled by river length to characterise 'abundance') and (2) the average number of habitat units per km of river (i.e. ERS density to characterise 'complexity'). The absence of water abstraction in the headwaters, was shown to have the strongest positive influence on the abundance of ERS ($F = 8.483$; $df = 43$; $p = 0.006$), appearing as the sole explanatory variable in the optimum and only significant model. Other elements appear in models lying within the 95% confidence interval, but none are significant. Habitat density was influenced most strongly by gradient of the river channel (L_n m per km) ($F = 14.75$; $df = 43$; $p = < 0.001$) (Table 3). There are fewer models within the 95% confidence interval and gradient is consistently the only significant factor, although geology (indicative of sediment availability) occurs in over 50% of them. The suite of potential models lying within the 95% confidence interval is presented in Table 4, along with AIC scores and weightings.

Discussion

The aims of this research were to assess the modern extent of ERS resources in England and Wales, characterise the physical and hydrological features common to ERS-rich systems and to model the physical and anthropogenic factors that can be used to predict ERS complexity and abundance for individual rivers.

Distributions and hydrological characteristics

In achieving these aims, we have compiled a unique database of English and Welsh ERS, using both photographic and map data to cross-validate distributions and ensure that records are up to date (as of 2010). Using this comprehensive database, we are able to confirm findings of coarser resolution studies that have suggested the regional patterns of distribution (Eyre and Lott, 1997); however, for the first time, these data pinpoint distributions within individual rivers, providing a potentially valuable resource for conservation and management purposes, indicating specific reaches of high value and at risk from major channel alterations.

Characterising the physical factors and hydrological regimes associated with high levels of ERS abundance provides a strong evidence base for understanding current distributions in terms of shared, natural characteristics. These characteristics (i.e. high flow regime seasonality, glacial and alluvial substrates, and montane headwaters), provide the fluctuating flows, sediment availability and stream power potential that are essential for ERS-maintaining levels of disturbance within riparian corridors (Bettes, 1994, Carling, 1992). They also provide suggestions for the absence of ERS across much of England, with lower altitudes and a greater influence of groundwater in river hydrology. By empirically modelling the observed distributions of habitat, we have demonstrated that whilst there is an overriding natural control on the complexity of the habitat (predicted by the rate at which a river descends from headwaters to confluence/estuary), anthropogenic suppression of total habitat by large-scale water abstraction or impoundment is a principal modifier of ERS habitat.

The analysis of ERS occurrence in relation to location and flow regimes provides new information on the English and Welsh regions in which the resource prevails. Strong regional variations in river hydrology have been shown for the whole UK (Bower et al., 2004, Laize and Hannah, 2010) and England and Wales (Monk et al., 2006) with west-east gradients related to higher terrain in the west (eastern rain shadow), greater westerly precipitation-bearing weather systems' influence and lagged, buffered flow responses in the southeast (underlain by major groundwater aquifers). By applying regime classification to a subset of ERS rich rivers, we assessed variation between ERS forming flow regimes in terms of seasonality and magnitude. The classification process identified distinct regimes; however, when these are applied to modelling the drivers behind ERS density and abundance, no regime class was identified as significantly influential. This suggests that the seasonal regimes are less informative than quantifying shorter term flow fluctuations for predicting ERS prevalence. However, our classification method has identified a suite of typical river types with abundant ERS. The observed variations may also have an influence on the timing of ERS re-working (and associated ecology), as earlier autumn peaks/late spring peaks will induce strong regional variation in the clearing and emergence of annual vegetation, which in turn has the potential to influence life-cycles of resident species.

Modelling local distributions

This research necessarily concentrates on presence, rather than absence, of the ERS resource. The strong regional constraints and membership of a broad hydrological 'suite' indicate a set of physical parameters necessary for the presence of these coarse gravels and shingles within a catchment. To understand finer-scale processes it is necessary to define variations that subdivide the broad membership, allowing us to add in natural and anthropogenic variation between rivers.

We included the complexity-predicting river gradient as an indicator of stream power (Knighton, 1999), which relates partially to the erosive and sediment transporting potential of the river (Vandenberg, 1995). Given its scale, this is necessarily a desk-based study; we cannot include data on reach-scale stream power and sediment calibre, and so use gradient as an indicator of potential.

Channels do not exist as steady and consistent slopes from headwater to estuary, rather there is a continuum of changing geomorphological forms (nickpoints, gorges, rapids, pools, riffles, glides etc.), all of which have differing local sediment erosion and transport potential (Church, 2002). The more rapid the slope change, the more likely that geomorphological complexity will exist as individual reaches have greater potential to erode, transport and deposit sediment (Arscott et al., 2002, Ward et al., 2002, Barker et al., 2009). In addition to spatial patterning, temporal variation in disturbance-inducing flows will be accentuated in steeper sections with more stream power (Allan, 1995).

Significant flow regulation by anthropogenic water abstraction and impoundment is believed to suppress the magnitude of high, restructuring flows, stabilising substrates through vegetation growth and increase their resilience to previously erosive flows (Brunke, 2002). Equally, the sediment entrapment caused by impoundment alters the erosion/deposition balance. It is wrong to think of ERS as purely a function of local hydrology reworking sediments, indirect impacts of variable flows and catchment changes are equally important. If such human flow modification is prolonged, successional development of ERS becomes permanent, removing sediments from the lateral erosion/deposition equilibrium necessary for ERS persistence: no longer a 'shifting mosaic steady state' (van der Nat et al., 2003).

Conservation and management issues

Interest in understanding and conserving ERS distributions in the UK stems from their role as a unique habitat supporting, for instance, specialist invertebrate communities with high levels of rarity (Sadler et al., 2004, Plachter and Reich, 1998, Stelter et al., 1997, Bates et al., 2009, Henshall et al., 2011). Typically these invertebrates are dependent on the habitat for one or more stages in their lifecycle and, as such, their observed distributions are inherently tied to current ERS distributions.

In characterising and modelling the factors that explain extant distributions of the ERS resource, the role of historic anthropogenic pressures is difficult to assess. Studies have shown decreases in ERS provision at reach scales where rivers are subjected to major engineering works (Petts et al., 1993, Petts and Gurnell, 2005). Within our English and Welsh database, coarse ERS is absent from many rivers and we have to exercise some care in stating that this is solely a result of underlying physical characteristics, particularly as the data indicate ERS is mostly absent from the heavily urbanised English Midlands and south east. There is evidence from our database that ERS have vanished from an entire river system after engineering. Two decades after engineering works on the River Soar, Leicestershire, UK (Lott, 1993), the resource observed then is no longer discernible. In large swathes of the river network it may therefore be plausible to suggest that observed absences are a consequence of reduced underlying potential, compounded by anthropogenic pressures. However, it is beyond the scope of this study to model historic changes in the habitat density, and as such this remains a caveat of our research.

The extreme fragility of and bleak outlook for global floodplain ecosystems has been highlighted (Tockner and Stanford, 2002). Attempts to reconnect rivers with their historic floodplains are becoming increasingly common in an attempt to at least partially arrest this decline. Reconnection delivers an increase in ERS associated processes (e.g. flow induced disturbance, sediment availability, lateral channel mobility); therefore, increased habitat density may be indicative of the success of such restoration programmes (Elosegi et al., 2010, Gilvear and Willby, 2006). Dispersal abilities are highly variable amongst associated specialist species (Bates et al., 2006), so the ability of new habitat to achieve full functional capacity will be dependent on the availability of remnant populations to provide pioneer individuals.

We have demonstrated a plausible desk-based methodology for assessing the current distribution and predicting factors of ERS habitat complexity and abundance. Remote sensing affords the opportunity to identify large quantities of habitat at increasingly fine scales as technology improves and becomes more affordable (Campbell, 2002) which, when coupled with the detail available from Ordnance Survey data create a best estimate of the distribution and complexity of the ERS resource. Our 'snapshot' of the ERS resource has clear potential to provide a useful dataset for tracking reach and catchment scale changes in habitat provision over annual and decadal time frames (e.g. Parsons and

Gilvear, 2002). Presently, it acts to identify the rivers and regions where the habitat is abundant and which may be most impacted by major hydrological or geomorphological alterations. Characterisation of hydrological, geological and geographical commonalities adds further to our understanding of current distributions, and modelling of geomorphological and anthropogenic controls provides insight into local processes and potential threats. This represents the first national scale assessment and cataloguing of the ERS resource, which given its role in supporting numerous rare, even endemic, species, represents an important increment in our knowledge. Specific regions, regimes and catchments are identified as of value for ERS provision, and highlight the areas of the river network that are important for further study and protection.

Conclusions

We suggest that this study provides useful information for both river management and restoration proposals, providing indicators of habitat potential for individual rivers. Moreover, whilst we have explained several resource structuring processes, there remains a gap as to how these processes impact on the conservation concerns associated with the habitat, particularly in terms of habitat loss, fragmentation and restoration potential for species of interest. This represents an important next step for research. Finally, the impact of predicted climate change on regional precipitation levels and timings (Burt and Holden, 2010, Museth et al., 2011, Rodda et al., 2010) may fundamentally alter catchment hydrology in England and Wales, but what long-term impacts this may have on the ERS are unclear, with potential for both net gains and loss.

By their very nature, ERS are never static; we suggest that this research should be viewed in those terms and invites revisiting, not least to study the degree and rate of change in distributions of the resource over coming years against a backdrop of any climatic and management changes that may occur. Increasing anthropogenic pressures on floodplains and rivers could easily accelerate the loss of ERS and their associated fauna; equally, the changing hydrology envisaged under some future climate scenarios may increase floodplain turnover and ERS density. With an increasing understanding that floodplain biodiversity brings with it strong functional capacity, the initial step of first identifying the habitat and understanding its distribution is invaluable for targeting its conservation.

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Tables

Table 1: Variables (explanatory and response) included in the general linear modelling selection process

Variable	Description	
Shape class	Classification rivers according to standardised annual hydrographs	Explanatory
Magnitude class	Classification of rivers according to clustered magnitude of flow (mm month^{-1})	Explanatory
Regime class	Amalgamated shape and magnitude classifications	Explanatory
Region	Grouping of rivers by region (Wales, SW, NE, NW and English midlands)	Explanatory
Incline	The rate of descent of the river from headwaters to discharge or confluence. A proxy indicator of stream power potential	Explanatory
No Q_{10} events	Average annual number of discharge events when the Q_{10} threshold was exceeded – as an indicator of frequency of disturbance	Explanatory
Abstraction	Presence or absence of major headwater abstraction for anthropogenic requirements	Explanatory
Impoundment	Presence or absence of headwater dam	Explanatory
Natural	Presence or absence of anthropogenic alteration of hydrology/channel	Explanatory
Geology	Underlying rock/sediment provision	Explanatory
L_n no of habitat units km^{-1}	Measurement of complexity of habitat provision	Response
L_n total area of habitat km^{-1}	Measurement of overall habitat provision	Response

Table 2: List of rivers used for generalised linear modelling and regime characterisation, with associated geological (as defined by the National River Archive), hydrological and anthropogenic variables.

Region	Hydrometric Area Group	River	Regime Class	Catchment Geology*	Abstraction	Impoundment	Natural	Average Annual Q ₁₀ events	Average No. habitat units/km ⁻¹	L _n average area/km ⁻¹	L _n slope /km ⁻¹
Mids	Trent	Trent	E5	Coal Measures / boulder clay	Y	Y	N	14.87	0.06	4.27	-0.08
Mids	Wye (Hereford)	Lugg	C5	Alluvial	Y	N	N	4.95	1.53	5.4	1.51
Yorks & NE	Coquet	Coquet	C5	Igneous/sandstone	N	N	Y	13.91	0.85	8.08	1.76
Yorks & NE	Ouse (Yorks)	Derwent	E5	Clays/shales & limestone	Y	Y	N	9.52	0.34	5.08	0.66
Yorks & NE	Ouse (Yorks)	Swale	C5	Glacial	N	N	Y	13.64	1.42	8.08	1.81
Yorks & NE	Ouse (Yorks)	Wharfe	D1	Boulder clay	N	Y	N	18	1.53	7.25	1.74
Yorks & NE	Ribble	Ribble	D3	Boulder Clay	N	N	Y	15.59	1.16	6.88	1.23
Yorks & NE	Tess	Tees	D1	Boulder Clay	Y	Y	N	17.64	0.81	7.06	2.05
Yorks & NE	Tweed	Tweed	E3	Shale/alluvial	Y	Y	N	12.1	1.49	7.31	1.04
Yorks & NE	Tyne	South Tyne	B1	Millstone grit / boulder clay	N	N	Y	23.86	1.62	8.56	2.11
Yorks & NE	Northumberland Wear	Wear	C5	Alluvial/boulder clay	N	Y	N	18.36	1.85	7.66	2.12
NW	Eden (Cumbria)	Eden	D1	Boulder clay/sandstone	Y	Y	N	18.86	0.62	6.62	1.57
NW	Eden (Cumbria)	Irthing	D5	Boulder clay	Y	Y	N	18.18	1.25	6.78	2.19
NW	Esk (Cumbria)	Esk	B2	Tuff/granite	N	N	Y	19.33	1.65	6.71	3.69
NW	Esk (Dumfriesshire)	Liddel Water	D1	Shales & boulder clay	N	N	Y	20.91	1.87	7.34	1.84
NW	Ouse (Yorks)	Calder	E5	Millstone grit	Y	Y	N	12.48	1.68	7.42	1.88
NW	Ribble	Hodder	A1	Millstone grit / boulder clay	N	Y	N	19.35	1.79	7.66	1.92
NW	Tees	Greta	E3	Millstone grit / boulder clay	N	N	Y	19.13	1.82	7.01	2.55
NW	Wyre & Lune	Brock	B3	Millstone grit / boulder clay	N	N	Y	19.43	2.54	6.18	3.02
NW	Wyre & Lune	Lune	D1	Boulder clay	N	N	Y	17.09	2.36	9.19	2.05
NW	Wyre & Lune	Wenning	D3	Coal Measures / boulder clay	Y	N	N	17.35	1.89	6.83	1.89
NW	Wyre & Lune	Wyre	B1	Millstone grit/glacial	Y	N	N	21.1	2.95	7.27	3.3
SW	Exe	Exe	C3	Sandstone	Y	N	N	7.86	0.3	5.29	1.52

SW	Exe	Otter	C5	Alluvial	Y	N	N	14	2	6.58	2.22
SW	Somerset rivers	Axe	C5	Sandstone/limestone	Y	N	N	16.83	1.65	4.72	0.96
SW	Tamar	Tamar	E3	Shale/sandstone	Y	Y	N	15.09	0.32	4.29	0.83
SW	Tamar	Tavy	E1	Granite	N	N	Y	12.61	0.59	6.68	3.52
SW	Taw & Torridge	Torridge	E3	Shale/Sandstone	Y	Y	N	13	0.5	6.05	1.05
Wales	Conway & Clywd	Elwy	E5	Boulder clay	Y	Y	N	9.83	2.29	6.72	2.04
Wales	Conwy & Clywd	Conwy	A2	Igneous	Y	N	N	19.43	0.87	6.77	2.21
Wales	Dee (Cheshire)	Dee	A2	Igneous/limestone	Y	Y	Y	8.68	0.98	6.51	0.93
Wales	Loughor	Tawe	A2	Coal Measures / boulder clay	Y	N	N	19.91	0.54	6.36	1.84
Wales	Mid Glamorgan	Neath	A2	Millstone grit / boulder clay	Y	Y	N	17.61	1.49	7.41	3.08
Wales	Mid-Glamorgan	Afan	A2	Peat/Boulder clay	Y	N	N	14.57	1.94	5.93	3.46
Wales	Severn	Dulas	E3	Shales, slates & boulder clay	N	N	Y	11.3	1.21	6.63	3.7
Wales	Severn	Severn	A3	Boulder Clay	Y	Y	N	10.68	0.98	7.6	1.3
Wales	Severn	Vyrnwy	E4	Boulder clay	Y	Y	N	12.22	1.63	7.16	1.19
Wales	Taff	Cynon	A1	Millstone grit /alluvial & boulder clay	N	Y	N	15	1.48	6.09	1.59
Wales	Towy	Bran	A1	Alluvial	Y	N	N	11.35	3.62	7.36	3.02
Wales	Towy	Cothi	A1	Mudstone/sandstone	N	N	Y	12.43	1.59	7.55	1.94
Wales	Usk	Usk	C5	Alluvial/boulder clay	Y	Y	N	6.91	0.98	7.41	1.01
Wales	Wye (Hereford)	Ithon	E5	Shales	N	N	Y	11.68	2.07	6.78	1.55
Wales	Wye (Hereford)	Monnow	C5	Sandstone/mudstone	N	N	Y	10.48	0.68	5.9	2.22
Wales	Wye (Hereford)	Wye	A1	Igneous/marl	Y	Y	N	14.46	0.89	7.37	1.35
Wales	Ystwyth	Ystwyth	A4	Shales	N	N	Y	18.73	2	8.26	2.88

Table 3: Primary generalised linear models for predicting ERS area ($\text{m}^2/\text{km}^{-1}$) and density (habitat units/ km^{-1}) using hydrological and landscape variables.

Model	adjusted r^2	F	df	Variable	p-value
Area	0.145	8.483	43	Abstraction	0.006
Density	0.238	14.75	43	Ln drop/ km^{-1}	< 0.024

Table 4: Generalised linear models lying within the 95% confidence interval (with Akaike's Information Criteria scores and weighting) explaining average area (Ln) of ERS habitat per km (a) and average number of habitat units per km (b). Significant elements of models are marked *.

Magnitude	Region	Slope	Q10	Abstract	Dam	Geology	Natural	AIC	Weight	CI
a)										
				✓*				180.13	0.289	0.289
			✓					180.96	0.191	0.479
		✓		✓				181.76	0.128	0.608
			✓	✓				181.88	0.120	0.728
				✓	✓			182.1	0.108	0.835
				✓		✓		183.9	0.044	0.879
	✓							184.08	0.040	0.919
	✓			✓				185.6	0.019	0.938
			✓	✓		✓		185.63	0.018	0.956
b)										
		✓*						119.54	0.283	0.283
		✓*	✓					121.22	0.283	0.566
		✓				✓		121.95	0.196	0.762
		✓		✓		✓		123.54	0.089	0.851
						✓		124.94	0.044	0.895
	✓	✓*						125.97	0.026	0.921
						✓	✓	126.2	0.023	0.944
	✓	✓				✓		126.63	0.019	0.963

Figure 1: Distribution of major areas of English and Welsh ERS resource. [Black points represent discreet habitat areas at reach scales, and may indicate single or multiple habitat units. Also indicated (coloured symbols) are positions of gauging stations used for modelling subset, with regime class indicated (Shape A-E; magnitude 1-5). Symbol shapes are common to regime shape classes, colours to magnitude groupings.

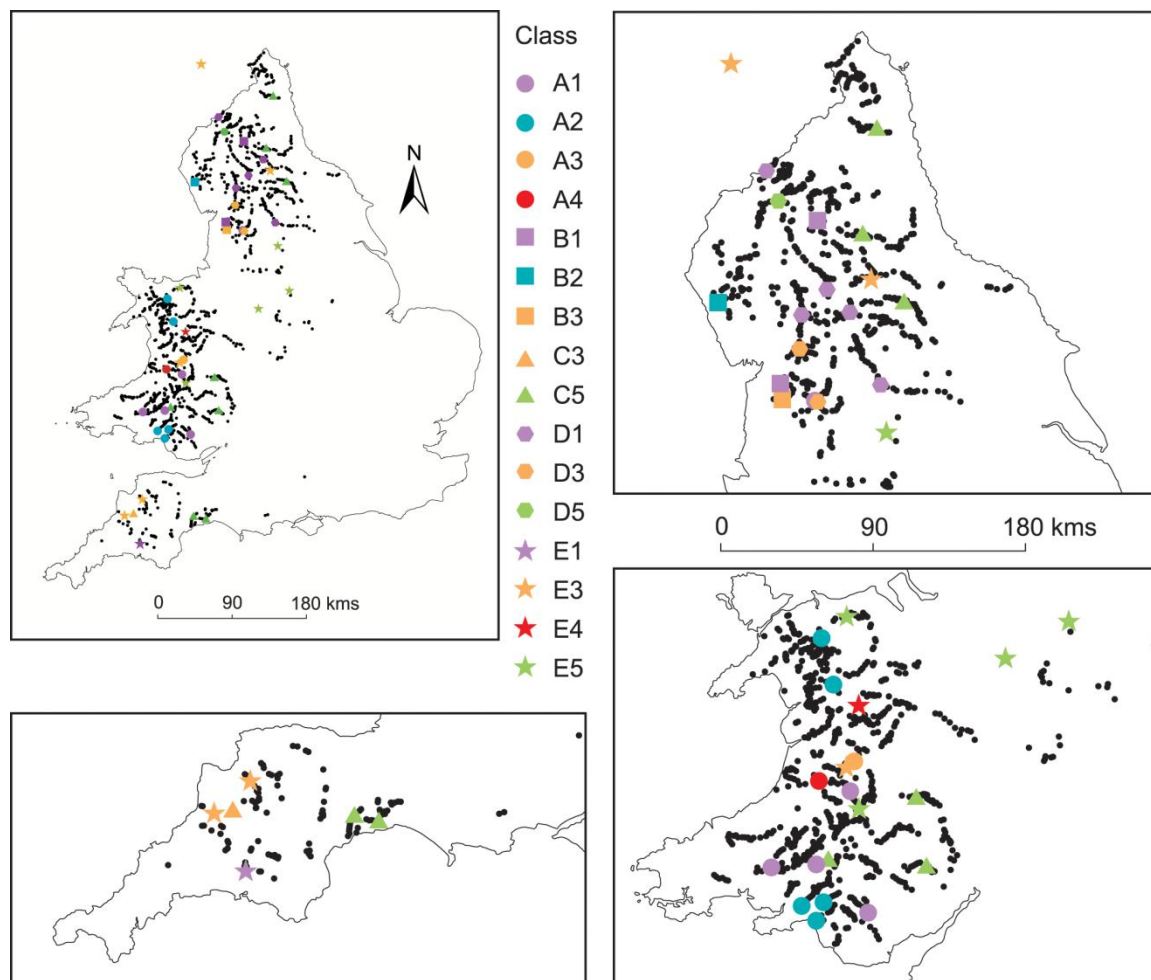


Figure 2: Grouping of flow regimes of 44 rivers classed by shape [data standardized as z-scores]. Regimes are shown over the hydrological year (July-June) and show variations in the timing of seasonal changes in flow between classes.

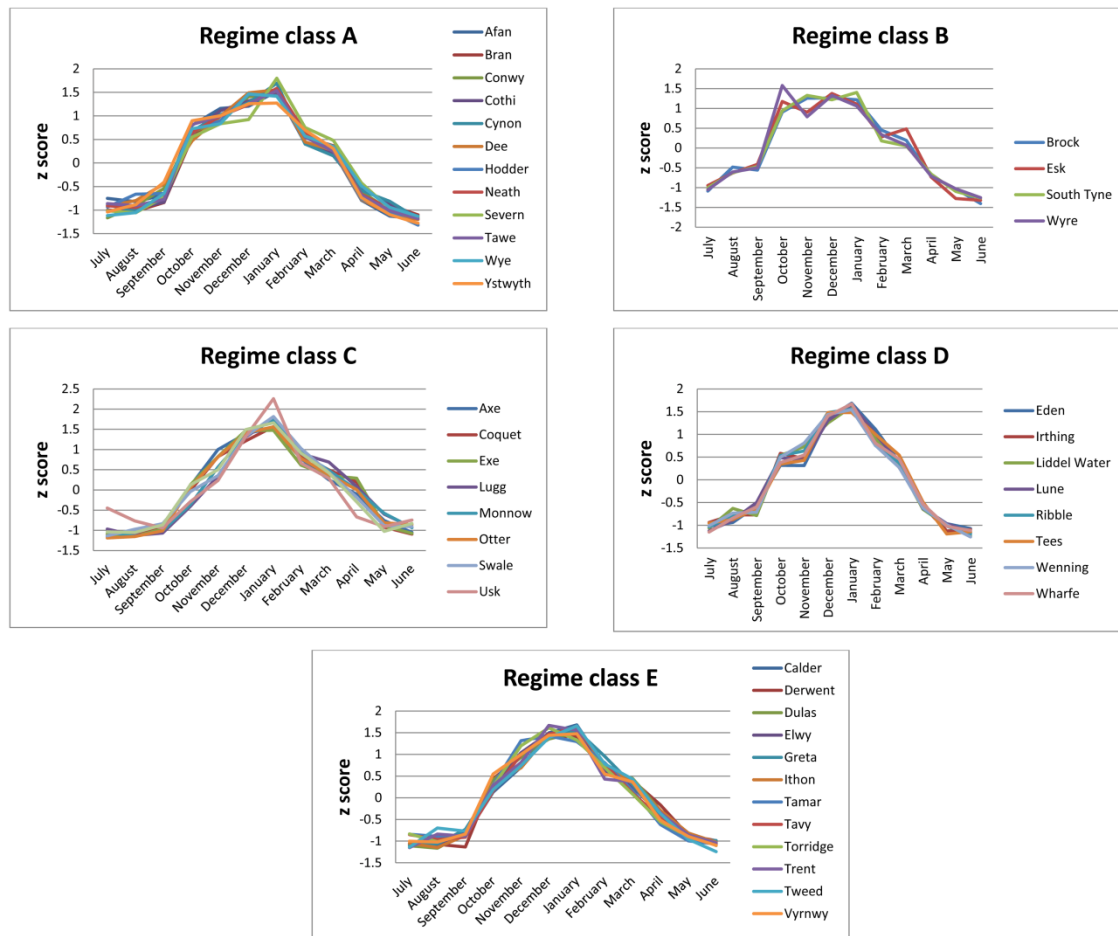
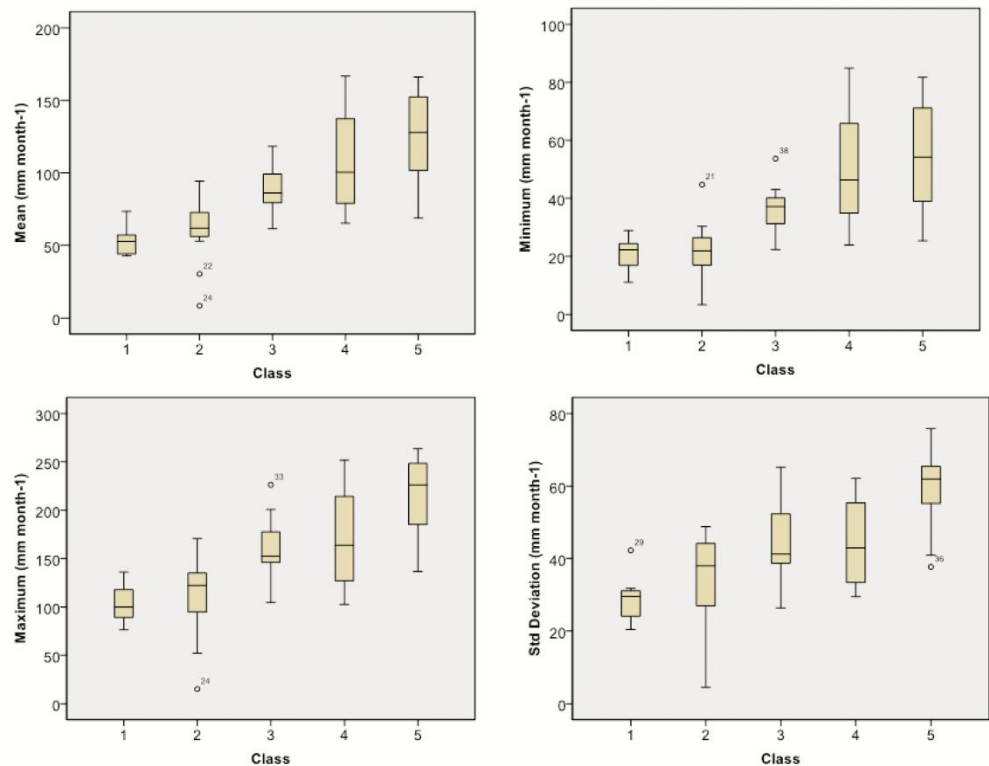


Figure 3: Box-and-whiskers plots of flow regime indices (mean, minimum, maximum and standard deviation) for magnitude classes derived from 44 sample rivers.



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Appendix A2:

**HYDROLOGICAL CONTROLS ON ERS SPECIALIST SPECIES
ASSEMBLAGES**

Introduction and discussion

Floodplain habitats represent one of the most pressurised freshwater systems (Tockner et al., 2006), with direct anthropogenic impacts (Tockner and Stanford, 2002) compounded by changing flow regimes associated with climate change (Easterling et al., 2000). Unmodified they have the potential to provide substantial ecosystem services through the provision of biogeochemical and hydrological processes (Burt and Pinay, 2005, Klaar et al., 2009), as well as acting as a substantial biodiversity store (Anderson and Hanssen, 2005, Sadler et al., 2004). A key process occurring is the exchange of nutrients between stream and terrestrial zones (Nakano and Murakami, 2001, Baxter et al., 2005), with abundant invertebrate fauna acting as an important vector (Kato et al., 2003, Paetzold et al., 2005). Highly adapted to the disturbed environments associated with floodplains (Desender, 1989), many of these invertebrates are significant predators of emerging adult aquatic macroinvertebrates, taking up to 80% of their diet from this source (Hering and Plachter, 1997). Recent work has demonstrated however that there are strong variations in the level of this uptake, driven by the strength of traits utilised to reduce inundation pressures (O'Callaghan et al., 2013). The frequency and magnitude of flood events is increasing globally (Milly et al., 2005, Schiermeier, 2011). Using a long-term data set of invertebrate and river discharge data, we model responses of different functional groups of specialised invertebrates to changing flow regimes, highlighting the importance of antecedent flows on subsequent generations. We found that heightened flows, which rework floodplain habitats and reset them to early successional stages, benefit larger, ground beetle species. These possess strong dispersal mechanisms and show highest levels of aquatic prey selection (O'Callaghan et al., 2013). Smaller rove beetle species, which typically utilise interstitial pockets between gravels, model strong negative responses to frequent low flows, but conversely, positive responses where there are high impact (in duration and extent) low flows. Larger rove beetles, known to utilise habitat further removed from the stream edge, model strongest response to moderate flows. These data indicate that under scenarios with larger flood events, the ability of floodplains to absorb aquatic subsidies may increase, if these events continue to benefit larger predatory species. However, assemblages of specialised rove beetles in floodplains frequently contain high levels of rarity (Eyre et al., 2001, Sadler et al., 2004). If climate scenarios predicting warmer, drier summers with increased storminess prevail, the overall conservation value of floodplains may decline, as habitat is subjected to frequent shifts between very high and very low flows.

Inherently dependent on the structuring potential of high flows and suitable sediment supply, floodplains exist in a state of shifting equilibrium, where erosion is balanced by deposition, creating high local variation in successional development (van der Nat et al., 2003). Equally, the organisms associated with these regimes are presumed to be adapted to the levels of disturbance that maintain this catchment-scale equilibrium, although there is strong evidence that tolerance varies strongly between orders and species (Greenwood and McIntosh, 2008, Hering et al., 2004, Lambeets et al., 2008). Equilibrium and adaptation are long-term processes, resulting from a stability in the behaviour of the system over time; predicted changes in rainfall patterns, more frequent and intense summer storms for instance, may alter the responses of high altitude, surface-fed catchments, which characteristically have high levels of disturbed floodplain habitat. With so much of the life-cycle of floodplain invertebrates structured by flow-related environmental cues, the impact of changing patterns has the potential to alter the functional capacity of this group.

Strategies for utilising disturbed habitat can essentially be split into two; avoidance, by positioning above the level of usual inundation threat (Bates et al., 2007b), or acceptance, utilising rapid and efficient dispersal abilities to respond to inundation cues and escape flooding, recolonising re-emerging habitat as flows subside (Desender, 1989). These two, simplified strategies have major impacts on prey selection, with the former largely restricted to terrestrial prey items, and the latter able to optimise uptake of the stream-derived subsidy (O'Callaghan et al., 2013). Differing spatial

positioning suggest that susceptibility to extreme events will vary, and indeed, individual high flow events are known to drastically reconfigure assemblage composition (Hering et al., 2004, Lamberts et al., 2008). Longer-term patterns, and subsequent possible impacts on functional potential have not been established. Our data represents a unique long-term overview of changing community composition, taken from the river Severn, UK between 2002-2010. As far as we aware, this is the only dataset of its kind.

Our samples were taken from a near continuous stretch of disturbed, semi-natural floodplain between Llandinam and Caersws, mid-Wales, UK. The exposed gravel bars have been sampled annually from 2003- 2010 (with data missing in 2005 and 2007), by researchers from the University of Birmingham using standardised methods (Andersen, 1995). The hydrological information on river discharge is provided by a gauging station immediately upstream of Llandinam and supplied by the National River Flow Archive (NRFA). The sampling years contained extremes of both high and low flows, with the floodplain undergoing major reworking and channel alteration during the study period. For the purposes of continuity, only data from patches present throughout the study period were included, giving a total of ten habitat patches. Although the general pattern is for highest flows to occur in autumn and winter, unusually high flows also resulted in occasional summer inundation of the flood plain in some years (Figure 1).

Consistently the most abundant grouping were specialised ground beetles (total records 8,547, of which 6,090 were a single, highly adapted species, *Bembidion atrocaeruleum*), often an order of magnitude above that of smaller, often cryptic rove beetles (total records, 1,604). These larger, active species typically incorporate the rapid dispersion behaviour which favours inundation flight (Bates et al., 2006). They also demonstrate the high uptake of aquatic prey items (O'Callaghan et al., 2013). The trend over the period for this group has been a significant decline (Figure 2a), with a spike in records in 2003 (a year of below average flows, with one high flow period in May, although the previous year had seen extremely high winter flows). The rove beetles exhibit an opposite, non-significant trend over the period, increasing in abundance (Figure 2b). Their peak year was 2008, a year of prolonged stable flows, although the preceding year had very high summer flow in July (approaching normal winter levels).

When the response of functional groupings to hydrological variability was modelled, different variables consistently explained observed abundances of each grouping, although always it was antecedent flows which influenced observed abundances (Table 1). Weighted models of small, fossorial rove beetle responses consistently featured low flows from the previous year (Q95 events and the flow minimum) with a strong negative response (Figure 2). Conversely, weighted models of ground beetle responses consistently reflected the importance of high flow events, again, those that occurred in the previous year (Table 2). Crucially, there is an optimum level of high flow event frequency and duration, after which the community response is negative. The third functional group modelled was of larger rove beetles, which are surface dwelling predators, typically found further from the stream edge than ground beetles. Their models revealed strongest positive responses to moderate flows (again, from the previous years), with an optimum, intermediate level of frequency and duration (figure 3), prolonged stability induces a negative response. These varying responses to changes in flow are in addition to those ecological variables already known to predict distributions, including sediment size (Andersen, 1978), behaviour (O'Callaghan et al., 2013), local humidity (Henshall et al., 2011), cattle poaching (Bates et al., 2007a) and anthropogenic originating pressures such as hydro-peaking (van Looy et al., 2007), all of which are relevant to this section of the river Severn. We may assume then that observed abundances have been pre-structured by these factors, and that some of the variation we see between years can be explained by flow variation.

The mechanisms by which these variations enforce the community changes can be related to habitat provision, dispersal potential, resource utilisation and availability. By applying these to envisaged changes to discharge in coming decades, we may suggest how community structure and function could alter over this time frame. Mobile ground beetle species are believed to use to the cues of rising water levels to initiate flight (Bates et al., 2006), either inland, away from rising waters, or in search of other habitat patches. This ability allows high survival rates during flooding, but also enhances colonising abilities. Typically, species of invertebrates with low dispersal potential become vulnerable to local extinctions as individual patches are reworked or isolated by high flows (Stelter et al., 1997). The low dispersal trait reflects the positive response in models of ground beetles to high flows. That these flows occur in the previous year indicates a response to newly reworked habitat becoming available, which is colonised and numbers are enhanced. This pattern matches that witnessed by Hering et al (2004), where a 100 year flood initially reduces abundance of flood plain beetles, but is followed by a rapid surge in numbers of *Bembidion* species, as active colonisers. It is known that the capacity of these predatory species to take up aquatic subsidies is large (Hering and Plachter, 1997, Paetzold et al., 2005) to the point that it can suppress the numbers of adults successfully emerging (Paetzold and Tockner, 2005). Consequently, any establishment of a flow regime which repeatedly enhances their success within the environment will, long-term, increase the importance of this vector as a transfer pathway for stream-originating nutrients. However, the indication that there is an optimum magnitude and (more weakly) frequency of these events suggests that should high flow events surpass a certain level (around 20 m³/sec at this site, which although above the Q10 exceedence level may still occur within the active spring/summer period), populations start to decline.

The larger rove beetle assemblages show a different response, with optimum responses to moderate flows in the previous year. Although possessing high levels of affinity to the habitat, it appears that their adaptations allow utilisation of the habitat but that these are not sufficient to override the pressures of high flows. Evidence has previously suggested that their diet is dominated by terrestrial prey items, indicative of the use of more stable areas of habitat (O'Callaghan et al., 2013). Again though, beyond an optimum level (approximately 150 days of Q₅₀ flows in the previous year) predicted numbers begin to decline. It may be that this is the level of stability at which successional processes become established, with increased vegetation and terrestrialsation of individual patches serving to exclude species adapted to the disturbed floodplain.

Finally, the mixed response of small rove beetles to low flows presents interesting questions. Typically possessing strong affinity to the habitat, their size and lifecycle means that very little is known about species in this group. Whilst the larger ground and rove beetle species in the study are around 5mm, species in this grouping are at most 2mm. Although winged, many of these species live within the gravel, and their food items are less certain; size limitation precludes them from consuming most emerging macroinvertebrates, and it is likely that they are more reliant on detritus and algae (an area that requires further supporting research). Both lower numbers and uncertain feeding strategies make this grouping less important as a functional component of the community (as far as we are aware), but crucially it contains many of the rarer species found in floodplain assemblages, for instance two high-fidelity species endemic to the UK, *Meotica anglica* and *Thinobius newberyi*. Modelling indicates a strong negative response to frequent low flows but there are positive trends in response to high magnitude and duration low flow events. This apparently contradictory response is curious, but may be indicative of a preference for stability, repeated low flows will necessarily be characterised by frequent changes in flow, which will require shifts in positioning and may impose unknown pressures. Where low flows are prolonged and exaggerated, not only is more habitat available, but pressures associated with inundation are removed. The uncertainty in the causes of modelled responses and the high levels of rarity within this grouping indicate that this is clearly an area that merits further research.

Future climate scenarios feature increases in both high rainfall events (which may benefit ground beetles) and longer drought periods which may impact the smaller rove beetles. Current moderate flows are unlikely to be the norm under either scenario. The indication of an optimum level of disturbance for ground beetles suggests that under the most extreme scenarios, they may not benefit from increased inundation levels. The work on post-flooding recovery indicates that extremely high flows effectively reset local communities to pioneer assemblages, and whilst strong dispersal abilities promotes rapid recolonisation, if these events increase in frequency, the recovery times will be shortened between events. Our data indicate several scenarios are possible for these key functional assemblages. Larger ground beetles may benefit, and increase their uptake of aquatic insects, facilitating greater transfer of resources into the floodplain; if summer droughts become the norm, then rarer, smaller species may benefit. Although the functional consequences of this are as yet uncertain, this potential outcome of climate change may aid conservation efforts. However, if low flows are interspersed by increased storm events, there may be further increases in rarity. Under all scenarios, the shifts are away from moderate flows, and as such we may expect larger rove beetles to be negatively impacted. This study is necessarily based on data from a single catchment; we argue that, given the vulnerability of floodplain habitats, there is an urgent need to compare these data with other systems, to establish the extent and applicability of the observed trends to geographically disparate systems.

Methods

The upper River Severn beneath the reservoir Llyn Clywedog is characterised by extensive semi-natural floodplains, with a wandering river channel. Although the flow is regulated via releases from the reservoir, the flow regime retains a flashiness that gives a high variability to discharge, caused by the steep, high altitude and predominantly surface water fed catchment. The floodplains are largely used for sheep and cattle grazing, with an area of nature reserve at Llandinam Gravels (SO022874). There are also large areas of wet woodland and gorse within the floodplain. Major sediment mobilisation occurs during high winter flows, with stochastic high summer flows occasionally matching winter flows, although annual vegetative growth reduces erosion in these periods. The stretch of river between the villages of Llandinam and Caersws has been studied continuously between 2002 – 2010 with simultaneous river discharge data available from a gauging station maintained for the National River Flow Archive at Dolwen (SO003858).

Specialist beetles were sampled three times during the summer of each year (except 2005 and 2007 when high flows restricted access to the gravel bars). At each habitat patch, standardised hand searching of a 2x1m area of gravel at the stream edge was undertaken at an upstream and downstream position, with adult beetles being taken by pootering, the armoured layer being excavated to ensure fossorial species were captured. Searching continued until all individuals had been taken. Individuals were immediately killed in ethylene glycol and returned to the laboratory at the University of Birmingham for identification to species level. (Andersen, 1995)

Records of species with affinity to the habitat were then pooled for each habitat patch and year for statistical analysis, grouped according to functional potential (based on dispersal and spatial positioning related characteristics).

Hydrological variables were defined from a suite of high, mean, moderate and low flow criteria in the year of sampling and from the previous year (to establish the impact of events on subsequent generations. The wide range of variables was reduced via Variance Inflation Factors, which allowed identification of most important hydrological variables in each flow category. Population responses to different flow scenarios (with sediment calibre also included due to its known influence

(Andersen, 1978)) were then modelled using an information theoretic approach (Whittingham et al., 2006, Whittingham et al., 2005), generalised additive mixed modelling were run to account for non linear responses, with Akaike's information Criteria and weighting used to rank all plausible models within a 95% confidence interval. From these suites of models, a probability estimation of the importance of individual components was derived by summing the weights of all models containing each element and retaining those which summed over 65.

Figures

Figure 1: Illustrative examples of interseasonal flow inundation risk within habitat patches. The image on the left was taken during a low flow period in April 2009, when adult invertebrates are moving back to floodplains following inland overwintering. The image on the right is the same patch during an atypical season of very high rainfall taken in July 2009. The entire habitat area is submerged during the period of greatest adult invertebrate activity



Figure 2: Trends in populations over time on the left, rove beetle populations showing a non-significant increase, on the right, ground beetles demonstrate a significant decline during the sampling period.

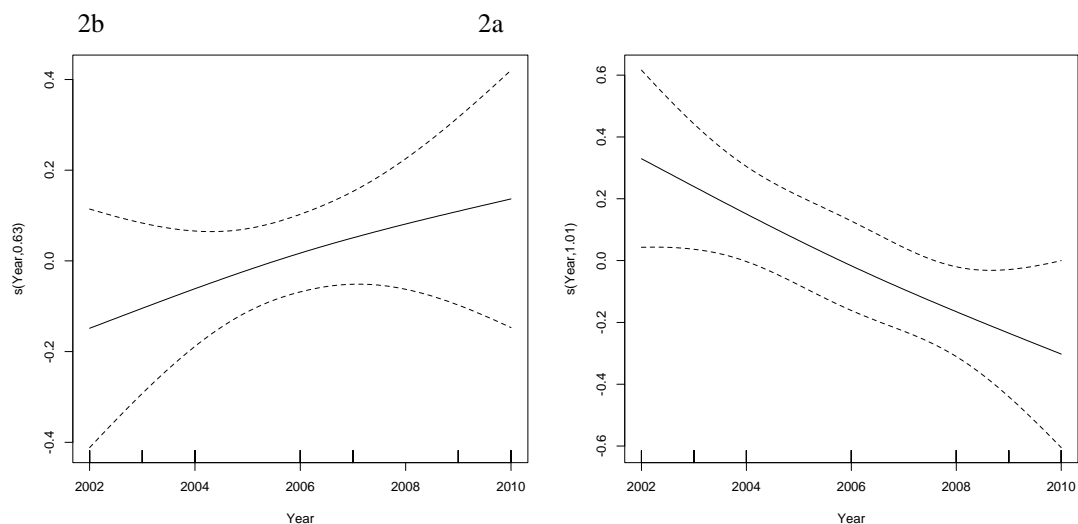


Figure 3: Plot of predicted abundance of specialist ground beetles to maximum summer flow events in the previous year, showing an optimum magnitude of around 20 m³/sec.

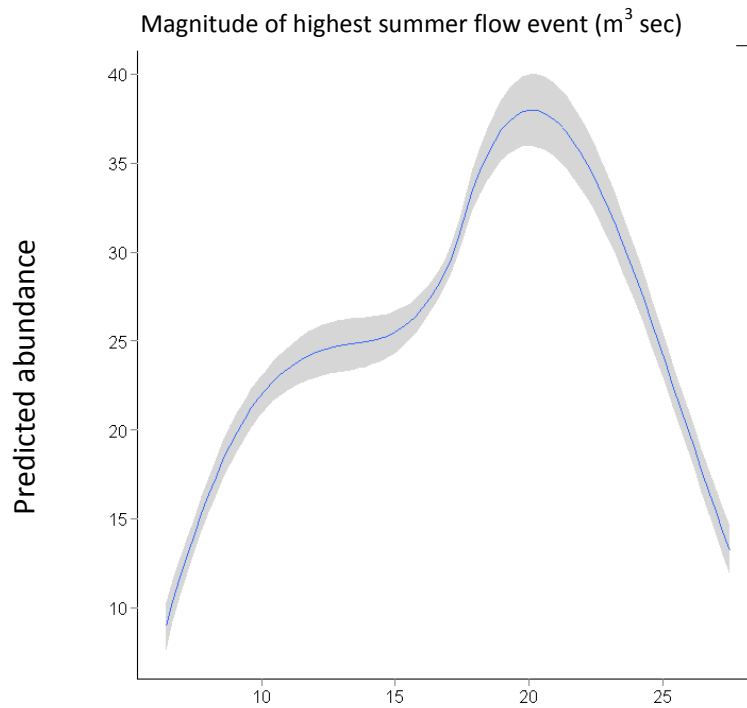


Figure 4: Plots of predicted abundance of specialist smaller rove beetles according to probable variables of the number and extent of low flow events in the previous year, showing a negative response to frequent low flows although high impact (extent and magnitude) low flows show a level of positive response

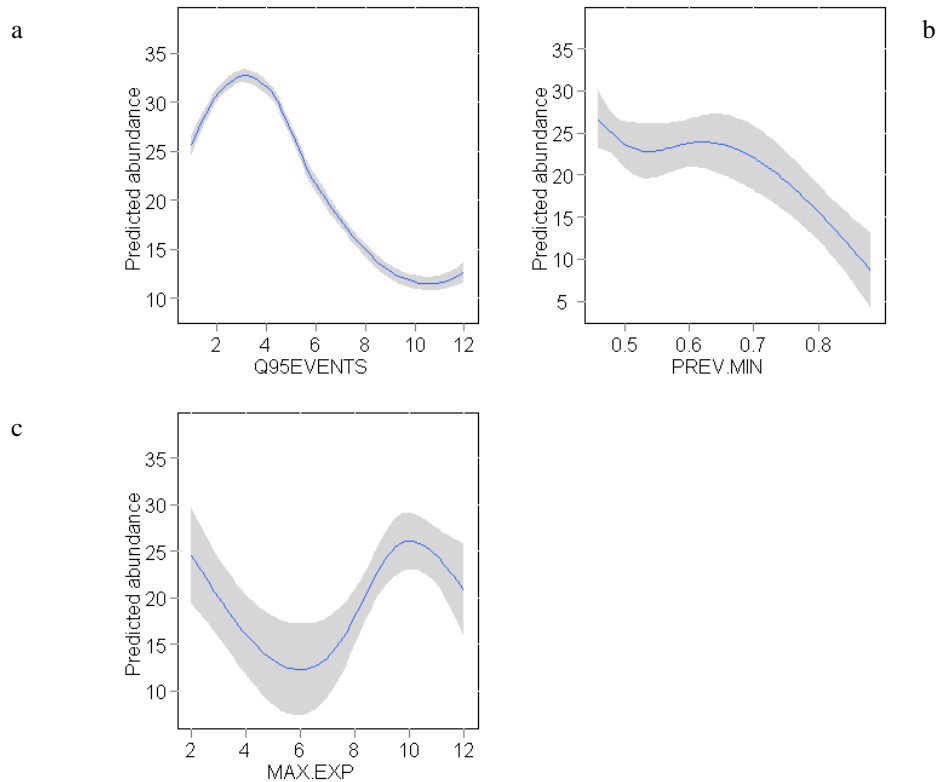


Figure 5: Plots of predicted abundance of specialist larger rove beetles according to identified probable variables, indicating positive responses to both (a) duration and (b) frequency of moderate flow rates and (c) negative response to prolonged or reduced moderate flows.

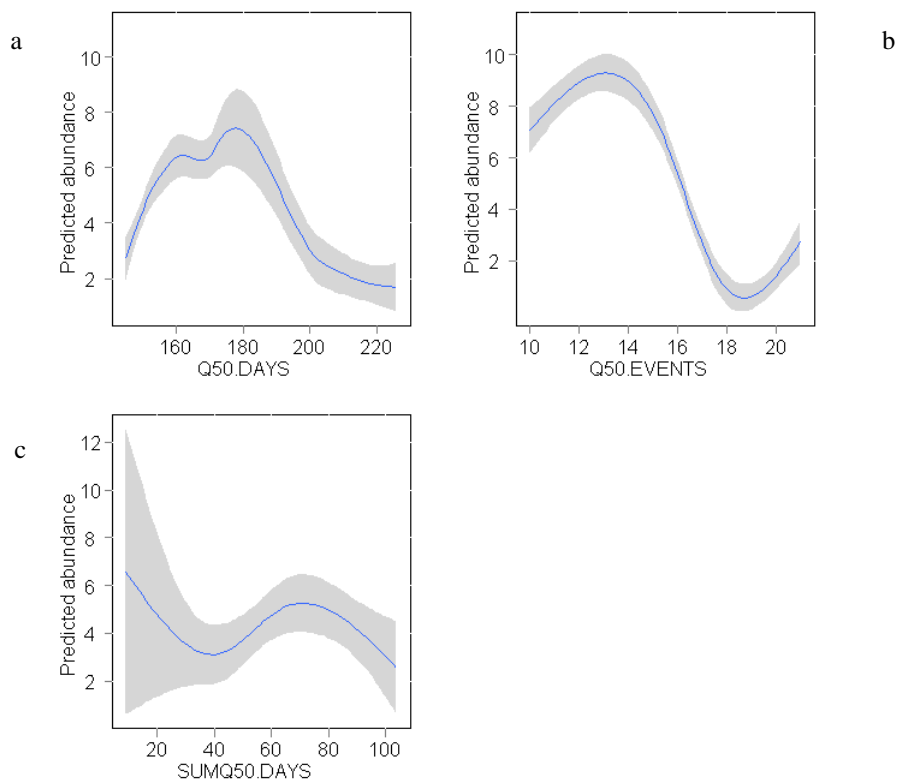


Table 1

Supplementary model information, showing weighted model components within 95% confidence intervals for a) ground beetles, b) smaller rove beetles and c) larger rove beetles.

a) Ground Beetles

						Weight	CI
max sum*						0.161	0.161
max sum*					Max_phi	0.098	0.259
max sum*				med_phi		0.075	0.334
max sum*			sumq10 events			0.074	0.409
max sum*	max prev					0.073	0.481
max sum*		Q_10 events				0.057	0.539
max sum*	max prev				Max_phi	0.043	0.582
max sum*			sumq10 events		Max_phi	0.042	0.623
max sum*			sumq10 events	med_phi		0.038	0.661
max sum*	max prev		sumq10 events			0.037	0.698
max sum*		Q_10 events			Max_phi	0.034	0.732
max sum*	max prev			med_phi		0.034	0.766
max sum*	max prev	Q_10 events				0.032	0.798
max sum*		Q_10 events	sumq10 events			0.032	0.831
max sum*		Q_10 events		med_phi		0.027	0.858
max sum*	max prev		sumq10 events		Max_phi	0.02	0.878
max sum*	max prev		sumq10 events	med_phi		0.019	0.897
max sum*	max prev	Q_10 events			Max_phi	0.018	0.915
max sum*	max prev	Q_10 events	sumq10 events			0.016	0.931
max sum*	max prev	Q_10 events		med_phi		0.0157	0.946
max sum*		Q_10 events	sumq10 events		Max_phi	0.014	0.96

b) Small rove beetles

						Weight	CI
q95_events*	max_exposure	previous_minimum*				0.368	0.368
q95_events*	max_exposure	previous_minimum*			Med_Phi	0.255	0.622
q95_events*		previous_minimum*				0.151	0.774
q95_events*		previous_minimum*			Med_Phi	0.118	0.891
q95_events*	max_exposure	previous_minimum*		Max_Phi		0.016	0.908
			Csum_q50_days*			0.0161	0.924
	q50_events	sum_q50_days	Csum_q50_days*			0.015	0.94
			Csum_q50_days*		med_Phi	0.009	0.948
	q50_events	sum_q50_days	Csum_q50_days*		med_Phi	0.007	0.955

c) Larger rove beetles

						Weight	CI
q50_days*	q50_events*	sum_q50_days*				0.411	0.411
q50_days*	q50_events*	sum_q50_days*			Med_Phi	0.146	0.557
	max_prev*	Q_10_events*				0.063	0.62
max_sum	max_prev*	Q_10_events*				0.058	0.678
q50_days*	q50_events*	sum_q50_days		Max_Phi		0.047	0.725
max_sum	max_prev*	Q_10_events*	sumq10_events			0.043	0.768
	max_prev*	Q_10_events*	sumq10_events			0.034	0.802
q50_days	q50_events*	sum_q50_days*	Csum_q50_days			0.034	0.836
	max_prev*	Q_10_events*			Med_Phi	0.022	0.857
max_sum	max_prev*	Q_10_events*			Med_Phi	0.02	0.877
	q50_events*	sum_q50_days				0.017	0.894
max_sum	max_prev*	Q_10_events*	sumq10_events		Med_Phi	0.015	0.909
q50_days	q50_events*	sum_q50_days*	Csum_q50_days		Med_Phi	0.013	0.922
	q50_events*	Q_10_events*	sumq10_events		Med_Phi	0.012	0.934
max_sum	q50_events*	Q_10_events*		Max_Phi		0.009	0.943
max_sum	q50_events*	Q_10_events*	sumq10_events	Max_Phi		0.008	0.95

	Duration
	Magnitude
	Frequency

Definition of terms

Max sum	scale of heighest flow in the previous summer (Apr-Sept)
Max prev	scale of heighest flow in the previous year
Max exposure	Longest period in previous year where flows were < = Q95
Previous minimum	lowest flow in previous year
Q10_events	No. of periods where flows were > = Q10 in previous year
sumQ10_events	No. of periods where flows were > = Q10 in previous summer
Q50_events	No of periods where flows were > = to Q50 in previous year
Sum_Q50_days	No of periods where flows were > = Q50 in previous summer
Csum_Q50_days	No. of days when flows were > = Q50 in current summer
Q95 events	No of periods where flows were < = Q95
Med Ph	Median Phi score of substrate
Max Phi	Max Phi score of substrate

Table 2: Model components selected from probability scoring, showing confidence that components influence responses observed

Ground beetles			Small rove beetles			Large rove beetles	
max sum	0.96		q95 events	0.91		Q50days	0.65
max prev	0.31		max exposure	0.64		q50events	0.70
Q10_events	0.25		previous min	0.91		sum_q50days	0.67
sumQ10 events	0.29		q50 events	0.02		max_prev	0.25
med phi	0.21		sum q50 events	0.02		q10events	0.28
max phi	0.27		csum_q50 days	0.05		sum_q10events	0.11
			med_phi	0.39		Med_phi	0.23
			max_phi	0.02		Max_phi	0.06

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Appendix A3:

EXPLANATION OF OBSERVED ASSEMBLAGE STRUCTURE WITHIN SEVERN/WYE CATCHMENTS

Introduction

Natural floodplains are complex landscapes at multiple levels of succession, utilised by highly diverse plant and animal assemblages they are inherently tied to the structuring flows of adjacent rivers. Increasing land pressures, channel modifications and flow alterations are irrevocably altering the ecosystems of floodplains globally, threatening a rich store of biodiversity and associated services (Ward et al., 1999). These gravel floodplain systems are often characterised by a scarcity of nutrients, extremes of temperature and humidity, and subject to habitat restructuring by regular erosive inundations (Gurnell et al., 2009). The resulting gravel and sand deposits are abundant in both unconstrained braided river systems (Petts et al., 2000) and unmodified high altitude headwater streams (Benda et al., 2005). England and Wales do not possess many river systems at these scales and most are subjected to some form of modification. The ERS component of riparian geomorphology follows a trend common to natural river systems, where patchy habitat distribution enhances overall biodiversity (Jackson and Pringle, 2010). However, its vulnerability to anthropogenic pressures, has led to a widespread reduction in its extent in many catchments (Bravard, 2010, Brewer et al., 2000). This has caused a concurrent contraction in the distribution of stenotopic invertebrate species, many of which have designated rarity status (Gunther and Assmann, 2005, Niemeier et al., 1997).

Terrestrial invertebrates inhabiting floodplains have been studied widely in Europe (Gerisch et al., 2012, Lambeets et al., 2009, Paetzold and Tockner, 2005), Scandinavia (Andersen, 2006), the United States (McCluney and Sabo, 2012, Ulyshen and Horn, 2010) and New Zealand (Greenwood and McIntosh, 2008). Despite their rarity, most of the research has concentrated on the hydrological controls on these invertebrates (Sadler et al., 2004), or on their role as a vector for intercepting and processing stream-originating nutrients (Hering and Plachter, 1997, Paetzold et al., 2005, Paetzold and Tockner, 2005). More recently, trait-based functional responses have been investigated (Gerisch et al., 2012) and their importance in maintaining diverse assemblages demonstrated (Lambeets et al., 2009). However, little is known of the wider landscape controls on this group, and as such it is not possible to assess the value of existing resources, other than by exhaustive surveying.

Unvegetated sediment bars occur along a patchy, linear gradient, occurring either as in-stream or riparian units (Petts et al., 2000). Any individual bar is at risk from flooding during high flows which in turn may cause erosion and downstream transportation of component sediments. Under natural, or near-natural flow regimes, total habitat available within the catchment tends towards constancy, with new bars forming as others erode or stabilise (van der Nat et al., 2003). Invertebrates inhabiting this transient habitat are equally subject to inundation pressures, and permanently resident species must utilise dispersal both to avoid inundation and to recolonise new areas of habitat (Bates et al., 2009, Desender, 1989, Hering et al., 2004, Plachter and Reich, 1998). Dispersal ability determines at what scale patchily distributed habitat becomes disconnected for colonising individuals. Weak dispersal enforces a reliance on high habitat density and low flows, which may increase the likelihood of local extinction events under high flows (Stelter et al., 1997).

Stenotopic riparian specialist species typically possess phenological and morphological adaptations that enable them to survive the demands of this environment (Adis and Junk, 2002, Bates et al., 2009). These may maximise their response to immediate inundation threats (e.g. macroptery) (Desender, 2000), or enhance seasonal avoidance (inland quiescence/diapause during flooding seasons) (Andersen, 2006). Highly adapted species actively utilise available environmental cues, such as rising water, to prompt inter-patch movement (Bates et al., 2006). Changes in day length and light angle initiate movement to flood-free overwintering positions (Andersen, 1989, Andersen, 2006) and rising water levels initiate a shift to higher ground, away from the wetted edge (Bates et

al., 2009). However, within the suite of species associated with this disturbed habitat, there are differences in the strength of these adaptations, particularly in observed dispersal rates (Lambeets et al., 2008). Local assemblages also appear to show structuring microspatially (Bates et al., 2007) and according to microclimate (Andersen, 1988, Henshall et al., 2011) and it may be that those species with weaker dispersal abilities position themselves away from the stream edge, reducing inundation exposure.

In the absence of autecological information on many of the species found in this habitat, increasing use has been made of trait-based assessments, especially for understanding susceptibility to flooding pressures and the functional diversity of such assemblages (Gerisch et al., 2012, Lambeets et al., 2009). Assessments of morphological or behavioural traits allow environmental cues and invertebrate responses to be linked (Violle et al., 2007), and by layering multiple traits, can help to investigate the complexity of community interactions (Mouchet et al., 2010). However, a key research gap remains in understanding existing distributions of species beyond the local, patch-scale level. As many species appear vulnerable to local loss (Lambeets et al., 2010, Stelter et al., 1997), understanding their distributions within catchments, and the level of habitat connectivity they require represent vital conservation considerations for this important, but easily overlooked invertebrate assemblage (Sadler et al., 2004).

Aim & objectives

The aim of this study is to investigate the importance of habitat connectivity to Coleoptera with high affinity to disturbed riparian habitat, hypothesising that traits directly linked to dispersal ability will dictate necessary levels of habitat availability and complexity.

To achieve this the study will:

- 1) measure morphological characteristics associated with flight and locomotion from riparian species;
- 2) categorise species into functional groups using measured traits characterising dispersal potential and observed co-existence within individual patches;
- 3) model functional group responses to connectivity and stream position parameters.

Methods

Study area and sampling

Twenty two sites were sampled from five Welsh (UK) rivers rising in the Cambrian mountains; Afon Banwy, River Severn, Afon Tanat, Afon Vyrnwy and River Wye (Figure 1). The rivers incorporated both regulated and unregulated flows, although all demonstrated 'flashy' flow regimes which maintain bare gravel/sand bars and associated with surface-fed, fast-draining catchments (Gurnell et al., 2009). This habitat was most abundant in headwater reaches of the rivers, decreasing in frequency with distance downstream. Sample points were identified from aerial photographs prior to ground-truthing and final selection.

Sampling of Coleoptera occurred between 15 May – 21 August 2009. At each site six pitfall traps (0.3l capacity, containing a 50:50 ethylene glycol:water mix) were placed in a grid at 1m and 3m from the stream edge. Traps were emptied fortnightly and reset. Flooding caused the loss of data at all sites throughout the study period and seasonal data were therefore derived from the remaining pooled samples, a standard procedure when sampling this dynamic environment (Lambeets et al., 2009). Although non-exhaustive and with a probable under-representation of cryptic/fossorial species, the method is a standard one for sampling invertebrate populations in this

habitat (Andersen, 1995, Baars, 1979, Bell and Sadler, 2003). Samples were identified to species level, adhering to current nomenclature (Duff, 2012) and classified according to their level of affinity to the ERS habitat (Lott, 2009, Luff, 2007, Sadler and Bell, 2002). Species with no known affinity were excluded from the analysis.

On each river parameters capturing the connectivity of the habitat were identified by measuring distance from nearest habitat patch (up and down stream), area of habitat within 1Km, and number of habitat patches within 1km of the sample sites, using digital data derived from Edina Digimap. These measurements represent each bar's relative isolation and the complexity of the matrix in which it was positioned. Distance of the patch from the river's headwaters was also included to establish the role of longitudinal assemblage structuring.

Trait measurements

To assess the dispersal potential of individual species, six individuals from each of 14 species common to both the Wye and Severn catchments (Table 1) were taken at random from the samples and measurements taken of wing, leg and body (front of pronotum to tip of abdomen) lengths, an adaptation of the technique described by Ribera et al (2001). Measurements were then Ln transformed to allow comparison between differently sized species and ratios of wing:body and leg:body derived as indicators of flight and running potential.

Statistical analyses

Trait groupings were derived by running analysis of variance (ANOVA) on morphological measurements, with a post hoc Scheffe test applied (as the most conservative available test) (Fowler et al., 1998). Species with related traits were then placed into one of three groups. To incorporate between-catchment and longitudinal influences on assemblage distributions, the likelihood of species being found together was investigated using Spearman's rank coefficients (enabling further subdivision of the specialist ground beetle grouping). The influence of habitat connectivity on these groupings was then investigated using Generalised Additive Mixed Modelling (GAMM) (Wood, 2006). To allow for over dispersion and spatial correlation (Lin and Zhang, 1999) within the data, site nested within river was used as a random factor with a Poisson distribution (O'Hara and Kotze, 2010, Pinheiro and Bates, 2000). Initial data exploration occurred to establish the validity of the observed values, checking for normality of distribution, the presence and importance of outlying data and heterogeneity of variance (Zuur et al., 2010). As data from one site (number 7, on the River Severn) were only collected once during the study values were not included in the final analysis to prevent over dispersion in final models (resulting from sampling protocol rather than ecological factors) (Hilbe, 2007).

Strongest models were identified from a suite of all possible models using Akaike's Information Criteria (AIC) (Burnham and Anderson, 2002). AIC was defined as: $AIC = 2L + 2K$, where L is the maximum log-likelihood of the model and K is the number of parameters in the model (Akaike, 1974). In addition all models then ranked according to their AIC values and their Akaike weights, w , calculated using the following formula

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{j=1}^R \exp\left(-\frac{1}{2}\Delta_j\right)},$$

where Δ_i is the difference between the AIC for model i and the model with the lowest AIC and the sum is over the other alternative models in the analysis set $j = 1$. These Akaike weights allowed the identification of a 95% confidence set of models by progressively summing the weights of highest ranking models until a value greater than 0.95 was achieved.

Finally, following ranking and addition, all components lying within the 95% confidence intervals were given a probability scoring, based on the cumulative value of their weights (w_i) from the individual models found within the 95% confidence intervals (Burnham and Anderson, 2002), and those components with the highest probabilities (above 0.5) were selected for graphic visualization.

Results

14,879 beetles were collected and identified, of these 12,883 were classified as having some level of affinity with the ERS habitat (86.6%).

Morphological grouping

Following analysis of morphological measurements of abundant species, three distinct groupings were identified. Between species variation in leg: body length ratio was significant at the <0.001 level ($F: 50.172$ on 11 df), as was wing and body length ($F: 33.508$ on 11 df). Post hoc testing split the species into two distinct groups when leg: body length were compared; group 1: *Bembidion* sp., *Paranchus albipes*; whereas in group 2: *Nagustrius sabulicollis*, *Aloconota cambrica*, *Deleaster dichrous*, *Neobisnius prolixus*, *Zoroachros minimus*, *Fleuxiautellus maritimus* and *Perileptus areolatus* there was no significant variation from other species.

Post hoc testing of wing:body length ratios defined the groups differently, placing *Bembidion tetracolum* and *P. albipes* with all the click and rove beetle species, and the remaining ground beetles in another, distinct group. From these two analyses, species were split into three nominal functional groups:

- (i) specialist ground beetles: *B. atrocaeruleum*, *B. decorum*, *B. prasinum*, *B. punctulatum*, *B. tibiale*, *P. areolatus*;
- (ii) low affinity ground beetles: *B. tetracolum*, *P. albipes*;
- (iii) specialist non-ground beetles: *F. maritimus*, *N. sabulicollis*, *Z. minimus*, *A. cambrica*, *D. dichrous*, *N. prolixus*.

Analyses of variance of these groups maintain significant differences in leg and wing ratios to body length at the <0.001 level ($F: 82.038$ on 2df and 102.619 on 2df respectively). Post hoc testing showed the difference to lie between wing: body ratios of specialist ground beetles and low affinity ground beetles ($p < 0.001$) and non-ground beetle specialists ($p < 0.001$). Leg:body variation was shown to be significant ($p < 0.001$) between all ground beetles and specialist non-ground beetles. Figure 2a –b shows box plots (with 95% confidence intervals) of the variation between morphological groups.

Member species of these morphological groupings showed strong likelihood of coexistence when count data was correlated, with further subdivision of the specialist ground beetle grouping identified, placing *P. aureolatus*, *B. atrocaeruleum*, *B. decorum* and *B. tibiale* in one group, and *B. prasinum* and *B. punctulatum* in another. Table 1 provides a summary of species matched using this method, with UK conservation status (where appropriate). These groupings were then used to model the importance of connectivity parameters on distributions.

Generalised Additive Modelling

For each grouping a total of 63 models were run, featuring every combination of connectivity variables (presented in Table 2a) prior to scoring and ranking. The optimum models presented are presented below (and in Table 2b). In all groups (except 3) probability scoring indicated that components of optimum models were also the most probable contributors to the observed assemblage structures. Group 3's probability scores were the lowest (caused by high numbers of possible models within the 95% confidence interval, and distance to nearest downstream patch (0.449) was marginally more probable than distance from headwaters (0.442).

Group 1a: Headwater ground beetles

The optimum model (with an AIC score 67.16) was a single factor model including 'distance of sampling point from headwaters'. However, the next model, also single factor, including 'number of habitat units within 1km' had such a similar AIC score (67.33) as to indicate equal validity. Both models are significant, and have probability scores (based on weightings from all models within the 95% confidence interval) of 0.537 and 0.631 respectively. Visualisation of the responses (figure 3) shows a strong decline in abundance with increasing distance from headwaters, and increasing abundance with habitat density.

Group 1b: Lowland ground beetles

The optimum model (AIC 59.34) included a significant contribution from 'the distance of sampling point from headwaters' and a non-significant element of 'number of habitat units within 1km'. However, when probability scoring was conducted, only the distance component received a high ranking (0.839), with number of units scoring (0.469). This relationship is the inverse of that shown by group 1a, with abundance increasing with distance from headwaters (figure 4)

Group 2: Low affinity ground beetles

The optimum model (AIC 64.46) contained two significant components, 'distance to nearest upstream habitat patch' and 'distance of sampling point from headwaters', and following probability scoring, both gave a figure of 0.961. There is a non-linear response to distance from headwaters, with highest abundances predicted at mid sections of the river, abundance increases strongly with increasing distance from the nearest upstream habitat unit (figure 5).

Group 3: high affinity non-ground beetles.

The least robust group for modeling; although the two most parsimonious models contained significant contributions from 'distance of sampling from headwaters' (AICs of 23.14 and 23.63), probability scoring gave low scores for all components, reducing the trustworthiness of the models. Based on these rankings, the contributions of distance (0.442), number of habitat units (0.452 and distance to nearest downstream habitat (0.449) are similarly, but weakly contributing to observed distributions. A trend for decreasing abundance with distance from headwaters and increasing abundance with number of habitat patches is indicated, along with a increasing abundance with distance to nearest downstream habitat patch (figure 6).

Discussion

This new approach of combining trait-based categorisation with landscape scale modelling opens new avenues in the area of floodplain invertebrate ecology. Research on assemblage responses to major inundation events has highlighted the discrepancies in recovery that exists between species after a local extinction event (Gerisch, 2011, Hering et al., 2004) and changes to functional capacity (Gerisch et al., 2012). By relating traits to their function, in this case the potential they provide for escape and recolonisation, it is possible to not only suggest reasons underpinning these discrepancies and changes, but also posit these as a possible explanation of observed distributions and levels of rarity.

Dispersal potential v habitat affinity

The strong dispersal potential measured in specialist ground beetles (groups 1a and 1b) clearly sets this functional group apart from other species studied, including other species within the study having high levels of affinity to the habitat (Sadler and Bell, 2002). That there is a difference in macroptery between high and low affinity ground beetles (group 2) argues that this is a genuine

disturbance-favouring trait, and not purely a familial trait. However, its absence from species in group 3, which also have high affinity to the habitat indicates that affinity does not automatically bestow high dispersal potential. This reduced trait-strength is not unexpected for generalist species with low levels of affinity (e.g. *B. tetracolum*), but is counter-intuitive for those species in group 3 such as *D. dichrous* and *A. cambrica*. Their life cycles are tied to this specific habitat and so the data are perhaps indicative of their reliance on local refugia as a primary mechanism for reducing inundation pressures, before resorting to energetically expensive flight. This group contains the most species with UK conservation status, which may also be indicative of their reliance on a well connected habitat matrix, which has strong geographical constraints.

Downstream changes in assemblage composition

Use of correlation analysis to identify the occurrence of spatially distinct assemblages, indicated a division of the 1st grouping of high-affinity ground beetles into two groups possessing similar morphological characteristics but found in different abundances at different sites. It has been shown that riparian assemblages have different functional impacts according to stream order (Hering and Plachter, 1997, Paetzold et al., 2005), this spatial separation indicates the possibility that this is (in part) species as well as resource driven.

Following model selection, different responses to connectivity parameters are evident between groupings. Groups 1a and 1b have opposite responses to distance from headwaters. Observed patch-scale spatial patterning of species (Bates et al., 2007) becomes emphasised and reinforced along downstream gradients; although able to co-exist, downstream changes in habitat benefit species from these two groups differently. Other physical traits such as flattened bodies (Andersen, 1988, Desender, 1989) or preferred micro-spatial positioning (Henshall et al., 2011) may better suit some species under (for instance) changing sediment calibres or hydrological regimes. Both groups are characterised by strong dispersal potential, having longer wings and legs. In headwater habitat with an increased flashiness due to surface water contributions, dispersal potential favours flood avoidance and colonisation of newly deposited habitat patches; in lowland habitat, where distances between habitat patches are typically much greater (over 1km), and flooding events are of a higher magnitude, strong dispersal abilities are essential to maintain the integrity of the regional population (Adis and Junk, 2002). For these two similar groupings it appears that changes in hydrology and habitat availability occurring on a longitudinal gradient impose differing levels of resource pressure, which in turn dictate the effectiveness of traits and influence regional assemblage structure.

Space for generalists

Low affinity ground beetles (group 2) were studied as, although common within the disturbed floodplain habitat, they are more akin to true generalists, being found in a variety of wet and damp environments (Luff, 2007). Their reduced flight ability is indicative of a lack of adaptation for rapid escape behaviour, but the modelling of distributions shows a non-linear association with isolated habitat patches, increasing in abundance downstream before a final drop off in abundance (figure 5). Reduced flight ability may explain a preference for more hydrologically stable lowland habitat, where although floods are of a higher magnitude, rapid changes in flow are buffered by groundwater storage (Laize and Hannah, 2010). Despite observations that macroptery increases in *B. tetracolum* with proximity to water (Adis and Junk, 2002), it appears that this shift, if present, does not achieve parity with permanently resident species (groups 1a and 1b). This grouping also contains the largest species in the study, *P. albipes* (~6.5mm-) , and increased relative size has been suggested as indicative of low disturbance tolerance in carabids (Kotze and O'Hara, 2003). Reasons for the preference for more isolated habitat are unclear, and present a potential area for further

investigation, but it may be the case that they are unable to compete with highly adapted species in their optimum habitat (explaining the highest abundances at intermediate distances downstream).

Reduced dispersal abilities and habitat density

Group 3 is the most diverse grouping and perhaps consequentially has the weakest models. However the indicated preference for dense distributions of headwater habitat patches is intuitive for species with weak dispersal traits, suggesting a need for multiple refugia within close proximity. However, the indication of an isolation measure in the probability ratings of variables, with abundance increasing with distance to next habitat unit downstream, is less obvious. This response may be agglomerative, isolation reducing emigration events. There is evidence of insects using visual based assessment of habitat quality to decide flight direction (Conradt and Roper, 2006), and this may provide an explanation for this observation (although further testing is required). This final group features a broad range of species from multiple families, with different functional roles (e.g. predator and detritivore), although nutrient processing is beyond the scope of this study. Based purely on their dispersal potential, they are the least capable of all species in the study, with relatively reduced flight and locomotion. It has been shown that some member species (e.g. *F. maritimus*) are more likely to be found higher up an individual habitat patch (Bates et al., 2007), by removing themselves from the wetted edge, they reduce the need for inundation escape, but are potentially less able to survive extreme local events or move to new habitat after such an event (Stelter et al., 1997). The density of habitat patches generally reduces downstream, although tributaries and underlying geology can create local increases in sediment supply and subsequent deposition (Benda et al., 2004, Knighton, 1980); it may be that these larger distances prevent colonisation of patches by downstream migration.

Conclusion

The research hypothesis was that traits relating to dispersal ability would indicate the requirement for high patch density by functional groups.

By focussing on traits which relate to dispersal and the wider structure of the landscape, this study does not examine the finer habitat filters which may control between patch selection. Factors such as vegetative cover, habitat heterogeneity and sediment calibre have all been suggested as environmental controls on assemblage composition (Sadler et al., 2004). But by broadening the scope of the question, we are able to provide a relatively simple explanation of observed community composition that provides essential information for enhancing the protection of rare and vulnerable species. The abundance and complexity of the habitat form with which they are associated is greatest in high altitude, near-natural rivers, and its distribution has been mapped across all river systems in England and Wales (O'Callaghan, 2011). Given the requirement by the rarest species for headwater, high patch density habitat, any practices that will impact on the habitat provision or degrade existing resource in these areas should be approached with caution. Similarly, the variation of habitat connectivity observed between functional groupings, is reflective of the need to view floodplain habitats at a catchment scale in order to maintain the longitudinal structure of associated ecosystems and their assemblages.

Tables

Table 1: Species groupings, defined by morphological comparison, with further subdivision derived from correlated co-existence within individual habitat patches. UK conservation status indicated where relevant.

Group 1a	Group 1b	Group 2	Group 3
Headwater ground beetle	Lowland ground beetle	Low affinity ground beetle	High affinity non-ground beetle
<i>B. decorum</i> <i>B. tibiale</i> <i>P. areolatus</i> (Na) <i>B. atrocaeruleum</i>	<i>B. prasinum</i> <i>B. punctulatum</i>	<i>B. tetracolum</i> <i>P. albipes</i>	<i>N. sabulicollis</i> (RDBK2) <i>A. cambrica</i> <i>D. dichrous</i> (Nb) <i>N. prolixus</i> (RDBK)
<i>Long wings & legs</i>	Long wings & legs	Long legs/short wings	<i>Short wings & legs</i>

Table 2a: List of all explanatory variables included in initial modelling process, with descriptions.

Variable	Description
<i>River type</i>	Ordinal classification of headwater midpoint and lowland flowplains
<i>Area</i>	area in m ² of sampled habitat patch
<i>Distance to nearest downstream habitat patch</i>	distance in m to nearest ERS downstream
<i>Distance to nearest upstream habitat patch</i>	distance in m to nearest ERS upstream
<i>Area of habitat within 1km</i>	area in m ² , measured 500m up and downstream from centre of sampled habitat patch
<i>No of habitat patches within 1km</i>	count data of patches measured 500m up and downstream from centre of sampled habitat patch
<i>Impoundment in headwaters</i>	presence of artificial impoundment in headwaters of named river*
<i>Large scale water abstraction in headwater</i>	presence of artificial abstraction in headwaters of named river*
<i>Naturalness</i>	Presence/absence of abstraction and impoundment*
<i>Distance from headwaters</i>	measured in km from OS designated headwaters

*based on catchment information from NRFA

Table 2b: Optimum models derived for each group, with AIC score and significant components highlighted (2 models give for group 1a due to similarity of AIC scores).

Group	Components	AIC	model weight	component probability score	p-value
1a	i) distance to next downstream patch	67.16	0.068	0.537	0.012
	ii) number of habitat patches within 1km	67.32	0.063	0.631	0.013
1b	distance from headwaters + number of habit patches within 1km	59.34	0.094	0.839 0.469	0.011
2	distance to nearest upstream patch + distance from headwaters	64.46	0.152	0.961 0.961	0.003
3	distance from headwaters + number of habit patches within 1km	23.14	0.061	0.443 0.452	0.038

Figures

Figure 1: Sampling points on rivers Tanat, Banwy, Vyrnwy, Wye and Severn, each representing a single gravel bar, where repeat sampling, via lethal pitfall trapping, took place.

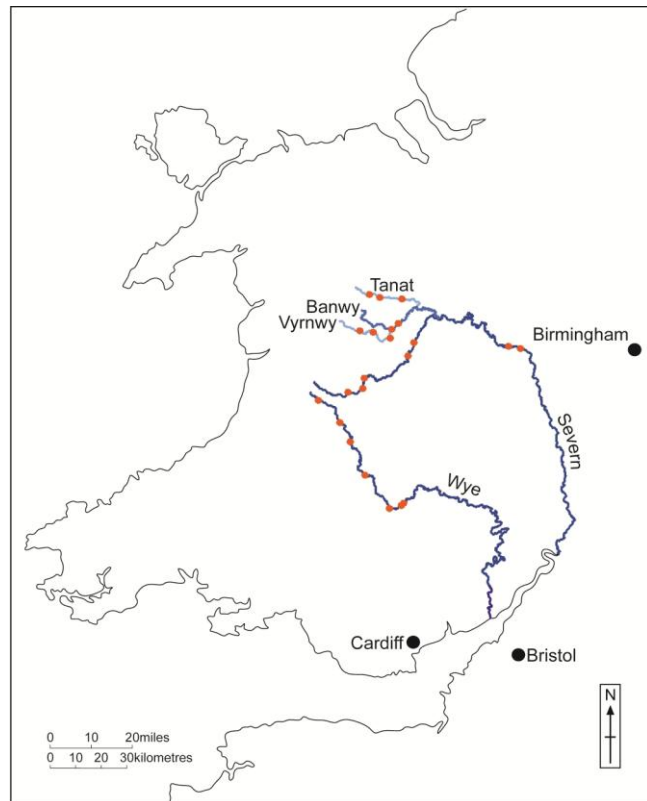
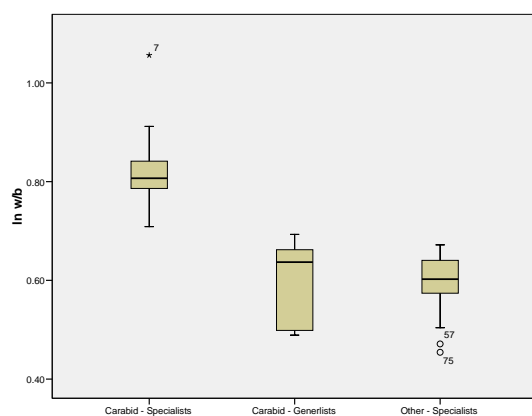


Figure 2: Box plots showing variations in morphological measurements from identified, characteristic species, a) shows variation in body: wing length ratio, b) shows variation in body: leg length ratio

2a



2b

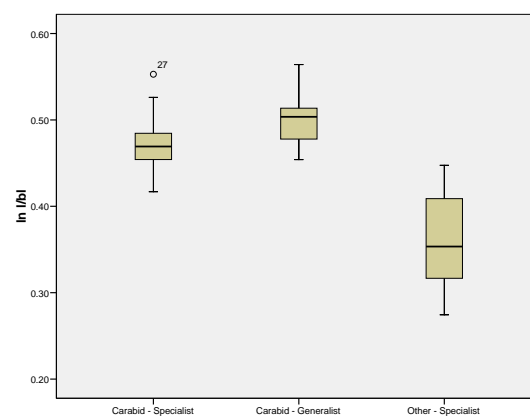


Figure 3

Visualized responses of specialist, headwater ground beetle abundances to a) sampling distance from headwaters, and b) the number of habitat units occurring within 1km (sample site at the centre of the km).

Figure 3

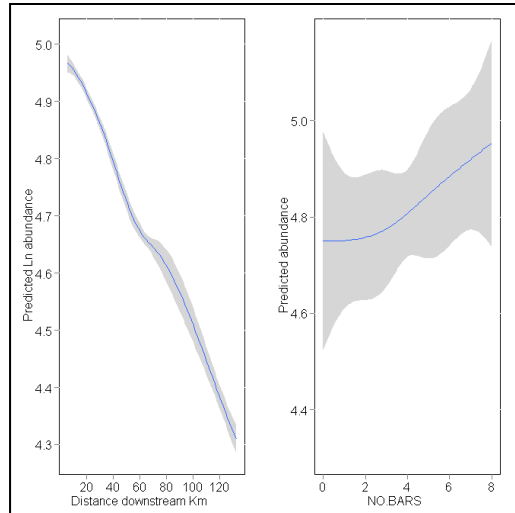


Figure 4

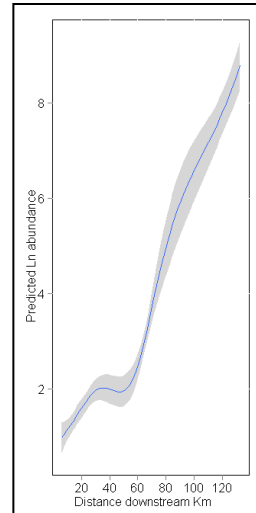


Figure 4

Visualized responses of specialist, lowland ground beetle abundances to a) sampling distance from headwaters, showing strong positive association with increasing distance.

Figure 5

Visualized responses of low-affinity ground beetle abundances (Ln transformed) to a) sampling distance from headwaters, and b) the distance to the nearest upstream habitat unit.

Figure 5

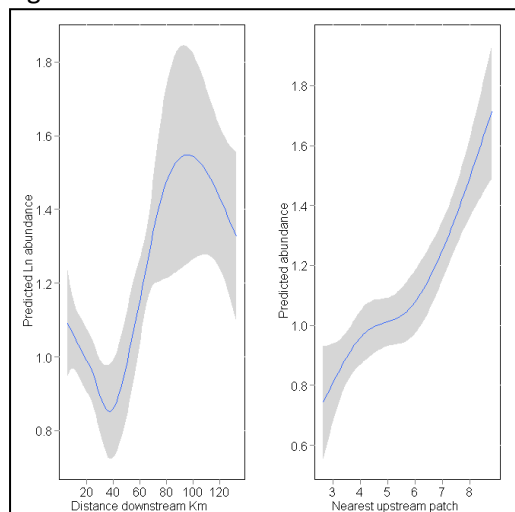


Figure 6

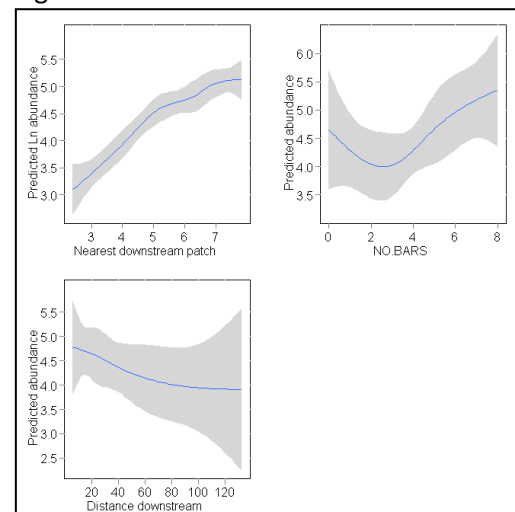


Figure 6

Visualized responses of high-affinity non-ground beetle abundances (Ln transformed) to a) the distance to the nearest downstream habitat unit, b) the number of habitat units occurring within 1km (sample site at the centre of the km) and c) sampling distance from headwaters.

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Appendix A4:

FOOD WEB DEVELOPMENT AND FUNCTIONAL ROLE OF SPECIALISTS

Introduction

Riverine landscapes and their associated floodplains are dynamic environments characterised by high levels of physical habitat heterogeneity and turnover (Bates et al., 2009). Longitudinal and lateral structuring of these habitats is controlled fundamentally by the river flow regime (Poff et al., 1997) and geomorphology, notably sediment supply (Gurnell et al., 2009). Levels of connectivity between the channel and wider landscape are variable (Ward et al., 2002) with often strong flows of nutrients and food resources (Nakano and Murakami, 2001, Baxter et al., 2005, Jardine et al., 2008, Richardson et al., 2010). Floodplains are vulnerable to direct and indirect anthropogenic disturbance, becoming increasingly degraded by pressures of urbanisation, pollution, dam impoundment, abstraction (Tockner and Stanford, 2002) and climate change (Easterling et al., 2000). As a result, more dynamic channel planforms (such as wandering channels and braided floodplain systems) have declined dramatically to a point where they are regarded as one of the World's most endangered freshwater systems (Tockner et al., 2006). The complex interconnectedness of in-channel, riparian and floodplain zones have been demonstrated hydrologically, geomorphologically (Klaar et al., 2009), biogeochemically (Burt and Pinay, 2005) and ecologically (van der Nat et al., 2002, van der Nat et al., 2003, Ward et al., 2002, McCluney and Sabo, 2012). This ecological dynamic is responsible for the conservation significance of floodplains (Eyre et al., 2002, Lambeets et al., 2008a, Sadler and Bates, 2008, Sadler et al., 2004, Anderson and Hanssen, 2005) with flooding (inundation) as a structuring force for the communities (Lambeets et al., 2008b), leading to clear functional variability in life forms and traits, especially in the numerically abundant invertebrate fauna (Lambeets et al., 2009).

Coleoptera associated with riparian margins are dominant and highly adapted invertebrates (Adis and Junk, 2002, Lambeets et al., 2008b). The apparent similarity of the species found in riparian coleopteran communities has been hypothesised as a rare example of a lack of 'intrageneric isolation' (Thiele, 1977), that is multiple species occupying the same niche within individual microhabitats, indicating the utilisation of mechanisms to reduce competitive interactions. Common to all riparian specialists are mechanisms (behavioural and/or morphological) which are adapted to the environmental pressures of inundation, potentially high sediment temperatures and low moisture. In 'adverse' environments, stronger adaptive measures may be required (Lytle et al., 2008, Parmesan et al., 2000), with poorly-adapted species being 'filtered out' (Cornwell et al., 2006) from continued habitat and associated resource use. Characteristic coleopteran traits include high reflectivity (Desender, 1989), flattened bodies (Andersen, 1985), avoidance behaviour (Hammond, 1998), spatial positioning (Andersen, 1988, Bates et al., 2007b) and seasonal changes in habitat choice (Andersen, 2006, Kocarek, 2001, Lundgren et al., 2009). Many of these mechanisms enable species to tolerate the high levels of inundation-driven disturbance (Lambeets et al., 2008b, Paetzold et al., 2008). The strong seasonal element of increased winter flood inundation pressure may be overcome by the common strategy of overwintering at distance from the river (Andersen, 1968), but year-round, episodic high flows e.g. associated with summer convective rainfall (Lavers et al., 2010) are also possible, subjecting adult communities active in riparian habitats to strong selective pressures. Specific adaptations to flood inundation pressure serve to spatially delineate community composition along longitudinal and lateral gradients (Lambeets et al., 2008b); changes to the flooding frequency or magnitude can further alter this composition (Paetzold et al., 2008), and cause short to medium term variability in abundance and assemblage composition (Gerisch, 2011, Hering et al., 2004). When traits are matched to local habitat and environmental conditions, the match allows dominance and maximises resource use (Greenwood and McIntosh, 2008). The high level of riparian habitat reworking excludes many other species, allowing species with specific adaptive traits to fully utilise available prey. However, the presence of multiple traits within an assemblage (Lambeets et al., 2009) and microhabitats existing within the matrix of local habitat (Sadler and Bates, 2008, Henshall et al., 2011), also suggests multiple strategies for minimising inundation

pressures. We seek to address a critical research gap in this article by testing the hypothesis that the traits that enable species to inhabit disturbed floodplains also drive prey choice under differing environmental conditions.

Understanding how complex assemblages utilise the resource and react to environmental pressures is essential for understanding the ecological functioning of floodplains. The extent of the aquatic subsidy to predatory Coleoptera is known to vary longitudinally, rising from 40% in headwater streams to 80% in higher order, lowland rivers (Hering and Plachter, 1997, Paetzold et al., 2005), which is at least partly due to increased downstream productivity as well as prey availability. Other invertebrate studies of the riparian zone have used stable isotope analysis (SIA) to examine the strength of aquatic subsidies to Aranea (Briers et al., 2005, Collier et al., 2002), Orthoptera (Bastow et al., 2002), Formicidae and Coleoptera (Paetzold et al., 2005). These SIA studies have not distinguished between the functional traits of the species present in this important ecotone environment. The level of uptake of aquatic resources by riparian consumers has been observed to vary spatially and seasonally between taxa (Hering and Plachter, 1997, Briers et al., 2005, Paetzold et al., 2006). Invertebrates, which have a lifecycle at least partially dependent on bare and exposed sediments situated in the active floodplain, are likely to have a stronger dependence on aquatic prey items than itinerant species that utilise short-term influxes. There is some evidence that specialist predator abundances are linked to emergence levels of aquatic insects (Paetzold et al., 2006), although it is unclear whether this abundance is enabled by the subsidy, or whether the two groups have a level of life-cycle synchronicity, predator emergence coinciding with maximum prey abundances. Within-species spatial variation in subsidy level (Hering et al., 2004, Paetzold and Tockner, 2005) indicates that dietary plasticity is an important strategy for riparian predators, a concept however, which remains untested. As the hydrology of rivers basins becomes more buffered with increasing distance from headwaters (Laize and Hannah, 2010), we hypothesise that the 'value' of different traits will vary, favouring different functional groups and altering the stakes of the risk : subsidy trade off for riparian consumers.

Although there is an increasing amount of work on riparian invertebrate community dynamics there is limited knowledge about their functional response to hydrological (and habitat) variability and how functional groupings change under different inundation conditions (Gerisch, 2011, Lambeets et al., 2009). In the light of on-going anthropogenic impacts, global threats to floodplain integrity and changing hydrological regimes envisaged under present climate change scenarios (Easterling et al., 2000), the ecological function of this important group needs to be better understood.

We aimed to investigate functional processes in riparian Coleoptera, using stable isotope analysis to identify environmentally, spatially and temporally driven variation in dietary composition occurring amongst functional groups. We achieved this through addressing a series of three linked objectives to: (i) define hypothetical functional groups, using dispersal related traits, (ii) examine variations in dietary composition between these groups along a lateral gradient away from the river's edge and longitudinally downstream, and over three seasons (iii) investigate the role of different inundation pressures on prey choice by the different functional groups.

We achieved our aims and objectives and in the Discussion we assess the contributions the study has made to floodplain ecology research. We also highlight some of the methodological issues with the work in relation to the temporal and spatial scales of the study and the role of detritivores and phytophagous species in nutrient processing.

Results

Invertebrate data and functional groups

The samples were derived from 1,695 terrestrial Coleoptera, 973 potential aquatic prey and 260 potential terrestrial prey. Some samples (Collembola and aphids) comprised multiple individuals (3-5) due to the small size of organisms. Isotopic values were obtained for 50 terrestrial prey samples, 262 aquatic prey samples (reduced to 130; see methods) and 366 predatory terrestrial coleopteran samples. Consumers were assigned to 5 functional groups defined by on morphological and behavioural characteristics (Table 1).

Measured morphological variation analysed via ANOVA showed significant difference between the leg : body length ratios of all ground beetles, specialist click and rove beetles ($p < 0.001$: F. 82.04 on 2df), all ground beetles had significantly longer legs. Between wing: body length ratio of specialist ground beetles and all other beetles (including species of non-specialist ground beetles) also differed significantly ($p < 0.001$: F 102.62 on 2df), the specialist ground beetles had longer wings.

Generalised Linear Modelling further refined these groups. The specialist ground beetles were subdivided, into a distinct headwater grouping, including *Bembidion atrocaeruleum* (Stephens, 1828) and *Bembidion decorum* (Zanker in Panzer, 1800) (AIC 82.61, $p < 0.005$: d 8.17, 19df) and a lowland associated grouping, including *Bembidion punctulatum* (Drapaiz, 1821) and *Bembidion tibiale* (Duftschmid, 1812) (AIC 77.77, $p < 0.05$: d 27.99, df 19). Specialist click and rove beetles which lack both the longer legs and wings of ground beetles also exhibited a high affinity with headwater habitat (AIC 93.49, $p < 0.005$: d 21.07, df 19). The resulting five groups, defined by morphological and modelling of distribution, comprised; headwater specialist ground beetles, lowland specialist ground beetles, low affinity ground beetles, no affinity ground beetles and specialist non-ground beetles.

Environmental and Habitat Variation

Digital elevation models (DEM), river level and flow (discharge) data were used to identify three inundation classes for analysis of patch scale processes (Table 2; and methods for details). Five bars experienced low inundation pressure (<50% loss of habitat), 6 bars experienced moderate pressure (51-90% loss) and 9 bars experienced high pressure (>90%), examples of inundation extent are shown in Figure 1. River depth (level) was higher consistently during autumn and winter associated with higher rainfall. The spring-summer maximum depth of 143.3 cm was exceeded seven times between October and March, the peak event being 176.2 cm, which inundated all patches (1.23m, above the depth measured in April 2009 when the d-GPS surveys were conducted). Figure 2 shows the daily river depth during the period of peak invertebrate activity in the study (April – October 2009), six bars experienced total inundation during this period, whilst the five least affected bars lost less than 50% of available area under the highest flows in September 2009 (1.4m above April 2009). The depth data also shows that the duration of inundation events varied between bars, from several weeks in July for shallow profile bars, to hours for steeper profile bars in short-lived pulse events in July, September and October. The extent, or presence of habitat availability, was compromised for prolonged periods on the lower bars, requiring greater use of refugia by resident fauna; more elevated bars retain the shingle habitat under all but autumn-winter flows.

Correlation analysis of environmental and inundation variables conducted to establish covariance that might influence invertebrate behaviour indicated the presence of significant relationships between inundation and extent of vegetation cover (negative), also bar area and length of wetted edge (positive) (Table 3). Which of the correlating variables had the strongest environmental effect was assessed and inundation and bar area were selected for exploration in isotopic modelling.

Isotope data

Exploration of the potential prey within the SIAR (Stable Isotopes in R) (Parnell et al., 2008) mixing model indicated that four invertebrate groups formed the majority of all prey selected: simuliids, Plecoptera, Collembola and aphids. Simulid larvae showed greater abundance in comparison to similarly sized Chironomidae, whilst Plecoptera typically emerge directly onto the riparian zone, rather than from the river surface, or from vegetation (e.g. caddis and mayflies). These potential prey exhibited a clear separation of isotopic values, with aquatic sources (simuliids and Plecoptera) relatively enriched in $\delta^{15}\text{N}$ compared to terrestrial sources (Collembola and aphids), with values between 4.07-12.63 $\delta^{15}\text{N}$ for the former and 1.44-8.26 $\delta^{15}\text{N}$ for the latter. Coleopteran values consistently lay between those of terrestrial and aquatic sources, indicating contributions from both prey groups (Figure 3).

Isotopic niche positioning

Estimation of isotopic niche area for member species from predefined coleopteran functional groups indicates differing levels of aquatic prey utilisation (Figure 4). *Stenus* spp. and *Coccinella 5-punctata* (Linnaeus, 1758) (Group 4) and non-specialist ground beetles (Group 5) showed low levels of $\delta^{15}\text{N}$ enrichment, indicative of a terrestrially sourced diet. Conversely, two specialist ground beetles with different preferred positions, stream edge and whole patch (*B. atrocaeruleum* and *B. punctulatum* respectively) exhibited the highest levels of $\delta^{15}\text{N}$ enrichment, indicating greater use of aquatic prey. Overlapping the basal and top positions a weak specialist, *Bembidion tetracolum* (Say, 1823) exhibited medial levels of $\delta^{15}\text{N}$ enrichment.

Physical habitat variability

Exploration of influence of habitat variables in SIAR identified two controls of prey choice, but only for *B. tetracolum* which has a weak affinity to the floodplain habitat (Figure 5). In coarser substrates (Phi class -5 to -6) the terrestrial component of diet increased from 50% to 72%. Terrestrial prey subsidy ranged from 50-70% as the levels of habitat heterogeneity on the bars increased. Bar area, which was highlighted as a potential influence in the environmental correlations showed no influence on prey selection in any group.

Effect of lateral sampling position

Different dietary composition was detected for all groups according to the sampling distance from the stream edge. *B. atrocaeruleum* (Group 1), known to be mobile within the habitat and associated with headwaters, showed the strongest variation in diet (Figure 6a). Medial (most probable) values revealed a 60% aquatic and 40% terrestrial contributions at the wetted edge, compared to a 30%:70% split further inland. *B. punctulatum* (Group 2), known to have a preference for the wetted edge area of the disturbed riparian habitat, showed a similar but smaller decrease in aquatic contributions inland from 62% to 55% (Figure 6b). *Stenus* spp. and *C. 5-punctata* (Group 5) and non-specialised ground beetles (Group 4) showed no change according to sampling position, at 70% terrestrial prey for ground beetles for no affinity and >95% terrestrial for specialist non-ground beetles. *B. tetracolum* (Group 3) showed a stable dietary composition, at 30% aquatic derived prey, regardless of sampling position.

Seasonal variation

Specialist riparian ground beetles exhibited a strong seasonal variation in dietary composition, with the importance of aquatic prey declining sharply in spring samples. *B. atrocaeruleum* exhibited 50%

aquatic prey, 50% terrestrial prey in summer and autumn, changing to 32% aquatic, 68% terrestrial in the spring (Figure 7a). *B. punctulatum* exhibited consistent 60:40% aquatic: terrestrial split for summer/autumn changing to 35:65% in the spring (Figure 7b).

Inundation and resource acquisition

The three numerically dominant species *B. atrocaeruleum* (headwater), *B. punctulatum* (lowland) and *B. tetracolum* (low habitat affinity) are all from the same genus, and are similar sizes (~5mm). Median values of dietary proportions indicated differing responses to inundation pressures. *B. atrocaeruleum* and *B. punctulatum* show values indicative of their preferred micro-spatial positioning, which converge under high inundation levels, as available habitat is reduced and encounters with alternative prey increase, stream-edge *B. punctulatum* reduces its intake of aquatic prey under higher levels of inundation pressure, whilst the mobile *B. atrocaeruleum* reduces its intake of terrestrial prey under the same conditions. *B. tetracolum* appears to switch rapidly to a terrestrially based diet under moderate inundation risk, which may be indicative of flood aversion behaviour. On bars with low inundation pressures, *B. atrocaeruleum* showed values of 35% aquatic and 65% terrestrial dietary composition, which changed to 42% aquatic and 58% terrestrial under moderate inundation pressures and 45% aquatic, 55% terrestrial under high inundation pressures (Figure 8a). Under low to moderate pressures, the values of *B. punctulatum* show a dominance of aquatic subsidy (60%), declining to 35% under high pressure (Figure 8b). *B. tetracolum* has both aquatic and terrestrial sources at ~50% under low pressure, with the aquatic subsidy declining to 30% at moderate levels and 15% under high pressure (Figure 8c).

The longitudinal patterns of variation across the additional 15 sites revealed strong trends downstream, especially for *B. punctulatum* (Figure 9a), which had a 55 % aquatic signal from samples taken in the headwaters to a maximum of 80% at the site 170km downstream. Conversely, *B. atrocaeruleum* (Figure 9b) maintained a terrestrially dominated diet from the headwaters (70%) to the most downstream sampling location (60%), albeit with an increase in aquatic subsidy for mid-catchment sampling points. Finally, *B. tetracolum* exhibited a switch from 65% terrestrial diet at its highest sampling point to a consistent 55% aquatic diet at the two sampling areas furthest downstream.

Discussion

The results demonstrate the presence of strong variations in the choice of prey by riparian Coleoptera across multiple gradients. The evidence indicates that these choices are in part driven by behavioural and morphological traits that determine the resilience of representative species to inundation pressures. Dietary composition shows that under the highest levels of disturbance (autumn-winter flooding), all species employ avoidance strategies until inundation pressure becomes reduced in spring. These data also suggest that the beetles do not undergo total quiescence during the winter and maintain at least some level of activity away from the active floodplain. Finally, our results show evidence of exaggerated relative source contributions with increasing distance from the headwaters, with the species which preferentially inhabit the stream edge markedly increasing uptake of aquatic prey at downstream sites. We discuss each element in turn.

Trait possession and influence on prey selection

Trait groupings were defined by behavioural and morphological characteristics (Ribera et al., 2001), and these groupings became clearly functionally delineated when relative isotopic niche positions were investigated. An increasing utilization of aquatic subsidies was present when adaptations that reduced the risks associated with high flows. Previous investigations have tended to class functionality by taxa; ant raiding parties (Hering, 1995) web building spiders (Burdon and Harding, 2008), predatory beetles (Anderson and Hanssen, 2005, Sadler et al., 2004, Van Looy et al., 2005), but there has been little or no success in establishing how species with life-cycles tied to the floodplain may differ functionally from generalist, opportunistic species. Our evidence confirms, to our knowledge, for the first time that not only do invertebrates make different prey selection choices (as observed by Hering and Plachter, 1997, Paetzold et al., 2006) but, that there is also a gradation of trait-driven specialisms, which dictate functional responses to the high-flow events characteristic of the habitat. Species may possess a total affinity to the habitat (e.g. *C. 5-punctata*), but lack the traits which allow full utilisation of the subsidies available. Conversely, a combination of beneficial traits (e.g. mobility, positioning preference) which provide advantages during disturbance (Desender, 1989) allows flexible, and therefore broader utilisation of available subsidies. Whilst micro-spatial positioning has been demonstrated (Andersen, 1988, Bates et al., 2007b, Henshall et al., 2011) as evidence of resource partitioning amongst specialist invertebrates, we believe that this is the first time resource partitioning has been shown to extend to prey selection.

Influence of habitat variability on prey selection

Although micro-spatial positioning of species is believed to be controlled by various physical components of the landscape, including sediment calibre, vegetation levels, and humidity (e.g. Henshall et al., 2011), the only species where any of these induced a prey selection response was *B. tetracolum*, which has a low affinity to the habitat. Its response to sediment calibre showed a reduction in aquatic prey both for larger substrates, and highest levels of aquatic prey at the lowest level of habitat heterogeneity. However, both of these variables are tied inherently to inundation: coarser sediments associated with greater inundation (Paetzold et al., 2008) and increased heterogeneity symptomatic of terrestrialsation of the riparian habitat (Sadler et al., 2004) and reduced permeability for aquatic prey (Petersen et al., 2004). As hydrological variation is the primary driver of habitat formation/removal in floodplains (Gurnell et al., 2009), it is ecologically meaningful to suggest that these results are a reflection of the role of inundation in ordering calibre and the suppressed productivity of low heterogeneous habitat.

Lateral influence of aquatic prey subsidies

Variation in the strength of aquatic influence on the isotopic signal of differently adapted consumers illustrates strong functional differences in elements of the riparian fauna. As the biomass of emerging and stranded aquatic invertebrates drops off rapidly within a few metres of stream edge (Briers et al., 2005), species which are highly dependent on the subsidy must necessarily place themselves at great 'risk' of inundation by staying close to their prey. The other alternative is to employ dietary plasticity, so that under adverse conditions, alternative prey are selected. Some species do exhibit a strong preference for stream edge positioning (e.g. *B. punctulatum*, *B. decorum*) and use greater proportion of aquatic prey. Similar species with equally high dispersal potential (e.g. *B. atrocaeruleum*) exhibit different behaviour, with individuals typically showing greater within patch mobility (Bates et al., 2007b). Whilst the majority of the individuals of the *B. punctulatum*/*B. decorum* will be found close to the stream edge, *B. atrocaeruleum* is less densely clustered. The former strategy allows for a greater, more reliable uptake of the aquatic subsidy but potentially places an entire local population at risk from inundation events; the latter strategy reduces access to the aquatic subsidy, but in the event of flooding, a larger proportion of the local population avoids the disturbance. When we tested whether these positioning choices influenced prey preference, all of the *Bembidion* species in this study (regardless of grouping) demonstrated levels of dietary plasticity between stream edge individuals and those sampled further inland, with increasing levels of terrestrial subsidy at inland sampling points. Given the relative impermeability of the riparian zone to the aquatic subsidy, this increase in prey sourcing is to be expected, as terrestrial items become more abundant than aquatic, but it also supports the hypothesis that prey-switching is an important trait in these species, allowing them to make best use of available resources.

Seasonal variation in prey choice

The strength of this capacity for dietary plasticity is best demonstrated by data on seasonal variations in isotopic signals of consumers. This seasonal element has been observed before (Paetzold et al., 2005, Kato et al., 2004), although this was within the context of shifting levels of subsidy tied to emergence rates from the river. Our study, based on data collected over 12 months, appears to substantiate the behavioural observations made of European and Fennoscandian riparian communities (Andersen, 1968, Andersen, 2006), where the default overwintering strategy is to move inland, away from the active channel and thereby removing the population from higher winter flows with potential to rework the floodplain habitat. We hypothesised that as this movement begins in early autumn, it might be possible to detect an obligative shift in diet by riparian consumers, driven both by reduced prey and habitat availability. Our findings indicate that this is the case for all functional groups, even for those with the stream-edge preference. In addition, the strength of this switch toward terrestrial indicates, we suggest, that the overwintering sites are not characterized by total quiescence, but levels of activity that allow enough prey consumption as to alter the isotopic signal of the community. This appears to be the first time that such a shift has been demonstrated in species usually described as having total affinity to the disturbed riparian habitat.

Inundation pressure as a driver of prey selection

By analysing a geographically proximate population, where environmental variables rather than phenotypic variation are most likely to drive observed variation between bars, we could first test that inundation is the demonstrable factor influencing prey selection (after eliminating habitat characteristics associated with within-patch distributions). Tellingly, those species with limited adaptations to the disturbance regime were absent from highly inundated patches, as such our data covers only the two highly adapted groups and the mildly adapted group, which were all species of

Bembidion. At low levels of inundation pressure, there is evidence of resource partitioning between the two highly adapted species, with the stream edge species dominated by aquatic and the mobile species by terrestrial isotopic signals. The convergence of these dietary contributions under heightened inundation pressures is indicative of reduced foraging area. As water levels rise, stream edge species migrate up the floodplain (Tockner et al., 2006), encountering more terrestrial prey; whilst mobile species have a greater likelihood of entering the stream edge zone and encountering aquatic prey items. Both responses indicate an opportunistic plasticity in diet that is only mildly affected by flooding pressures. Their mutual dispersal abilities allow them to persist within the habitat and exploit its resources with reduced risk of mortality. The observed, extreme change in prey selection by the weakly adapted *B. tetracolum* is indicative of its lack of specialism. *B. tetracolum* is able to opportunistically take aquatic prey items under low risk conditions, but forced by a lack of useful traits to abandon the habitat and its subsidy under higher inundation conditions. Species-specific variations in population recovery have been found following major flood events (Hering et al., 2004, Lambeets et al., 2008b); our data seem to indicate that alongside flood survival mechanisms, continued ability to utilise resources may play a part in these species-specific variations.

Downstream changes in prey selection

The increasing contribution of aquatic prey to *B. punctulatum* downstream is in accord with studies of higher order rivers (Hering et al., 2004, Paetzold et al., 2005), but the trend is less strong in *B. atrocaeruleum* and *B. tetracolum*. Elsewhere, we mention that *B. atrocaeruleum* is associated with headwater habitats (Luff, 2007), although it persists for considerable distances downstream (>150km). The within-patch mobility is appropriate for habitat vulnerable to the unpredictable high flow events characteristic of high altitude streams. It ensures that a proportion of the local population has reduced exposure to sudden rises in flow. However, there is a trade off, as it also reduces the local population's total access to aquatic subsidies. Habitat further downstream has a less flashy hydrological response and greater area of floodplain. Consequently stream-edge positioning incurs less sudden inundation risk. Under these conditions, traits which favour stream-edge positioning have optimum value, as the whole local population can benefit from the increased stability to utilise the subsidy. The exclusion of *B. atrocaeruleum* may indicate a reduction in the efficiency of its traits under lowland, downstream conditions, the temporary rise in subsidies perhaps indicative of a convergence of trait value at mid-points in the river.

Conclusions and significance

Although easily overlooked, the invertebrate fauna of floodplains represent a component of floodplain biodiversity. This study demonstrates that hydrologically driven pressures of the stream:riparian ecotone require the possession of specific traits. Without these traits, species are either unable to process the aquatic subsidy, enhancing its movement onto the floodplain, or may only do so under the low flow conditions.

Subtle changes in behaviour and the strength of physical adaptation dictate the optimum positioning of different beetle species, altering their functional contribution to the riparian zone. High affinity species, with relatively weak dispersal traits, have to forego the potential subsidy available from the adjacent stream by positioning themselves above the zone at greatest risk of flooding. However, this positions them to utilise available terrestrial prey, suggesting that they possess traits that fit them for the specific demands of this micro-habitat. Strong dispersal traits better fit species to utilise the aquatic subsidy, but a second trait filter acts upon able dispersers that favours different strategies under the different hydrological regimes occurring downstream.

Observed abundances of riparian Coleoptera in floodplain habitats have been explained as a functional response to the specific pressures of the habitat: high disturbance, low productivity and relatively strong external subsidies from adjacent terrestrial ecosystems (Paetzold et al., 2005, Sadler et al., 2004, Bonn et al., 2002). With high levels of rarity, the assemblages represent a valuable component of floodplain biodiversity, and as consumers of emerging invertebrates, a major vector for transporting aquatically derived nutrients into the floodplain. This study has explored some of the complexities inherent in these assemblages, for instance, why dispersal ability and proclivity varies so much between specialist floodplain invertebrates. Variation in feeding strategies and uptake efficiency in an apparently homogenous grouping, extends laterally and longitudinally, partitioning habitat and prey resources. The complexity of floodplain invertebrate communities has been well described, but we are now able to suggest how that complexity translates into important invertebrate functional roles within the floodplain. With an increasing interest in reconnecting floodplains and rivers (Palmer et al., 2005), these invertebrates represent a key functional element in ensuring that such reconnections have demonstrable ecological value.

Material and Methods

Ethics Statement

The landowners gave permission for access to the sites. Permits were not required specifically for the collection of invertebrates at the survey sites. The sampling was based around hand searching thus was of a relatively low intensity and unlikely to have impacts on local populations.

Study System

The sampling was nested to include: (i) a detailed study of 20 sampling points on a 5km stretch of the upper River Severn in mid-Wales (52.5°N, -3.4°E), which contains extensive areas of gravel and sand bars, and (ii) 15 further sampling points along a 150km stretch of the River Severn, incorporating similar habitat, from the headwaters at Llandilo, down to Ironbridge Gorge in the English Midlands (Figure 9). Care was taken to avoid sampling bars where livestock had access due to the potential for nutrient enrichment and invertebrate community alteration (Bates et al., 2007a).

Despite impoundment further upstream, the river flow regime retains high variability, sustaining the river's wandering gravel bed (*sensu* Church, 1983) form within its floodplain, this ensures a high turnover of riparian habitat, utilised by characteristic specialist arthropods. The stretch of the river immediately downstream of Llandinam has been studied extensively for over a decade and is known to contain a diverse and abundant assemblage of specialist invertebrates (Bates et al., 2006, Henshall et al., 2011, Sadler et al., 2004) including dominant ground beetle species (*B. atrocaeruleum*, *B. punctulatum* and *B. tetracolum*) which persist along the 150km gradient.

Environmental Variables

A suite of environmental variables were measured on each of the 35 patches (gravel bars). Incline (1 – gentle; 2 – moderate; 3 – steep), area (m²), length of wetted edge (m) were measured in situ. Habitat heterogeneity (1 – low; 2 – moderate; 3 – high), vegetation structure (1- bare; 2 – annual/biannual; 3- perennial) and substrate calibre/size measured in Phi classes (1 – coarse gravel; 2 - very coarse gravel) were derived from previous survey data (Bates and Sadler, 2005). Inundation susceptibility was assessed by surveying each bar during a period of low flow (April 2009) using a Leica Geosystems 1200 d-GPS for 20 gravel bars in the upper reach of the river. The surveying was done by first walking the outline of each bar, then collecting point data using a 5 x 5 metre grid, and finally targeting all breaks in slope (Brasington et al., 2000). These surveys were used to produce a digital elevation model (DEM) of each habitat patch in a GIS (ArcGIS 9.2, ESRI Redlands, USA). Detailed contour maps were produced using splining within ArcGIS Spatial Analyst at 20cm resolution. The GIS layer was tilted to replicate the water slope through the river reach (Paetzold et al., 2008) and related to stage data (river depth) provided by a permanently installed pressure transducer, which recorded data at fifteen minutes intervals throughout the study period (April 2009–April 2010). The GIS and flow data were used to model the area and percentage of habitat submerged under differing river depths, allowing each patch to be assigned an inundation susceptibility value of low (<50% loss of habitat), moderate (51-90% loss) or high (>90% loss) at a river depth 1m above the April 2009 flow (Figure 2). The validity of the inundation maps was ground-truthed by direct observation across the range of flow events during the sampling period.

Invertebrate Sampling and Trait Groups

Samples of dominant terrestrial Coleoptera (Carabidae, Staphylinidae and Coccinellidae) and their potential prey (aquatic and terrestrial) were collected three times during the study (June 2009,

September 2009 and April 2010). Potential terrestrial prey (Collembola and aphids) were collected by hand from the substrate and host plants, taking 10 aphids, and 20-30 collembola from each gravel bar. Potential aquatic prey were collected using a standard three minute kick sample with a 500µm net (Winterbourn, 1985), repeated three times at four positions within the sample reaches to incorporate major channel forms (e.g. pools, riffles, glides). All major families of invertebrates were sorted from the samples, with late instar individuals selected for analysis, as they are isotopically closest to adults (Paetzold et al., 2005). Individuals represented Diptera (including Chironomidae, Simuliidae and Tipulidae), Ephemeroptera, Plecoptera and Trichoptera. For the SIA analyses, orders were separated into families to account for different feeding strategies (e.g. predator/herbivore).

In an adaptation of the methodology used by Ribera et al. (2001) six specimens of each of twelve dominant sampled Coleoptera had wing, leg and body measurements taken, these were then Ln transformed. These morphological data provided ratios of wing: body and leg: body which were analysed using ANOVA with a post-hoc Tukey test to identify statistically-significantly/ similar different groups. Species were grouped according to morphological similarity. To examine the ecological validity of these groupings data from a larger regional study (O'Callaghan, 2011) were used to derive Spearman's rank coefficients of species' co-existence based on presence and abundance and significant correlations grouped (Fowler et al., 1998). Regional variations in assemblage were modelled using generalised linear modelling (McCullagh and Nelder, 1983) to further explain longitudinal changes in species' distribution. This process suggested groupings (Table 1), based on measured traits, modelled distributions and known behaviour (Bates et al., 2007b, Henshall et al., 2011, Luff, 2007), and identified target *Bembidion* species for SIA analysis.

Stable Isotope Analysis

After collection the samples were returned to the laboratory and frozen, prior to identification to species (for Coleoptera) and family (for potential prey) levels. All samples had gut contents removed, were rinsed and dried. Individual samples were split, with one half undergoing lipid extraction prior to analysis for $\delta^{13}\text{C}$ and the other retained for $\delta^{15}\text{N}$. Lipid extraction was chosen over post-analytical correction methods to reduce the strength of between sample and season variability (Post et al., 2007). A 2:1 mix of ethanol: methanol was added to samples for a minimum of 30 minutes before centrifuging and disposal of the solvent. This process was repeated three times before the remaining sample was dried for 24 hours at 60°C (Folch et al., 1957). Individual samples were then weighed (Carbon: 0.2mg \pm 0.05mg; Nitrogen: 0.6mg \pm 0.06mg) into tin cups prior to combustion. Stable isotope composition was measured by continuous flow mass spectrometry at the SILLA Laboratory, University of Birmingham using an Isoprime™ IRMS connected to an Elementar PYRO cube®. Precision was ensured by reference to calibrated standards CH3 and N1 from IAE. The two techniques were analysed on separate sub-samples avoiding observed influences of the lipid extraction process on $\delta^{15}\text{N}$ (Soreide et al., 2006) and precision was better than 0.7‰. The ratios of $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ are presented as relative difference per mil (‰) using the equation:

$$\delta X = [R_{\text{sample}}/R_{\text{standard}} - 1] \times 1000$$

where X = ^{13}C or ^{15}N , and R = $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. ^{13}C : ^{12}C is expressed relative to PDB (Pee Dee Belemnite), where $R_{\text{standard}} = 1.1237$ atom % ^{13}C (Craig, 1957). ^{15}N : ^{14}N is expressed relative to atmospheric N_2 , where $R_{\text{standard}} = 0.3663$ atom % ^{15}N (Mariotti, 1983).

Data Analysis

Species data were analysed separately and by the functional groupings shown in Table 1. Sample sizes were large enough to allow species-specific analysis of three ground beetles with an affinity to

the habitat, *B. atrocaeruleum*, *B. punctulatum* and *B. tetracolum*. This study did not attempt to characterise responses of phytophagous specialist species present in the habitat and which sit in the same morphological groupings as predatory *Stenus* spp and *C. 5-punctata*, e.g. *Zoroachros minimus* (Boisduval and Lacordaire, 1835) or *Fleutiauxellus maritimus* (Curtis, 1840). Neither did we seek to analyse the fossorial Staphylinids, e.g. *Hydrosmecta* spp. associated with the habitat, due to their small size. These remain areas for potential further exploration but were beyond the scope of the current study.

Analyses were conducted to determine how dietary composition was influenced by habitat variables: inundation susceptibility (Inundation), sampling position (wetted edge or vegetated inland), patch area (Area), sediment calibre (Phi), gradient (incline), vegetation type (Vegetation), wetted perimeter length (Edge) and patch heterogeneity (Heterogeneity), and season and longitudinal position along the catchment. The inundation analysis excluded specialist non-ground beetles (group 4) and generalist ground beetles (group 5) due to the small sample numbers retrieved from highly inundated (> 90%) patches. This analysis was conducted only on samples collected in autumn 2009, as these represented individuals exposed to known inundation pressures. Correlation between environmental variables and inundation susceptibility was assessed using a Spearman's rank coefficients (Table 3). Where significant correlations occurred, these were assessed for ecological relevance (i.e. which was the stronger driver in the relationship) and individually were run in SIAR to determine their influence upon consumer isotopic signals.

Isotope Analyses

SIA provides a mechanism for assessing variation in dietary composition both spatially and within assemblages. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are naturally occurring isotopic forms which are fractionated by all organisms during metabolism and excretion (Hood-Nowotny and Knols, 2007) allowing for studies of trophic positioning within food webs (Layman et al., 2007, Peterson and Fry, 1987). Stable Isotope analysis was conducted using a Bayesian mixing model, SIAR (version 4), available as an open source package (Parnell et al., 2010) within R (R Development Core Team, 2010). Isotopic position was assigned using a Bayesian probability framework to evaluate most likely distributions of isotopic values by functional group, data were plotted to provide a visual estimation of trophic positioning via isotopic niche (Jackson et al., 2011). A refinement of the 'total area' concept was used to assess the spatial extent of a food web (Layman et al., 2007). Dietary proportions were determined in SIAR in a model fitted via a Markov Chain Monte Carlo (MCMC) method, which provides probability density function distributions of the feasible (total range) and most probable (median) proportions of the organisms' diet. The model captures errors associated with input variables including trophic enrichment factors and source variability, as well as an overall residual error term (Parnell et al., 2010). We utilised data from previous gut content and isotopic studies (Davies, 1953, Hering and Plachter, 1997, Paetzold et al., 2005) to inform *a priori* selection of potential prey items producing a final two-source model of aquatic and terrestrial energy sources to riparian invertebrate production. Trophic enrichment occurs in all consumers, although rates vary between organisms, individuals and tissues (Bennett and Hobson, 2009, Post et al., 2007, Vander Zanden and Rasmussen, 2001). For invertebrates a standard trophic enrichment rate has been established at $2.3\text{‰} \pm 0.15$ for $\delta^{15}\text{N}$ and $0.5\text{‰} \pm 0.13$ $\delta^{13}\text{C}$ (McCutchan et al., 2003), which we included in the mixing models.

Tables

Table 1: Functional groups of predatory terrestrial Coleoptera sampled from ERS on the upper River Severn, giving example member species, geographical and micro-spatial preferences, and morphological characteristics.

Functional group	Micro-spatial preference	Morphology	Example member species
Group1 Specialist ground beetles	Headwaters Mobile within patch	Long legs & wings	<i>B. atrocaeruleum</i> <i>B. tibiale</i>
Group 2 Specialist ground beetles	Lowland wetted edge	Long legs & wings	<i>B. punctulatum</i> <i>B. decorum</i>
Group 3 Weakly adapted ground beetles	Damp ground	Long legs	<i>B. tetracolum</i> <i>P. albipes</i>
Group 4 Ground beetles - no ERS association	In land	Long legs	<i>Pterostichus</i> <i>madidus</i>
Group 5 Specialist non- ground beetles	raised ERS Headwaters	Shorter legs & wings	<i>Stenus</i> spp <i>Coccinella</i> 5- <i>punctata</i>

Table 2: Inundation classes of studied habitat patches (bars), with percentage habitat lost with a 1m increase above base flow measurements (summer maxima), or for patches lower than 1m, at the point at which they were submerged

Patch	% of habitat submerged with 1m increase over base flow	Inundation susceptibility
1	100	high
2	86	moderate
3	89	moderate
4	58	moderate
5	53	moderate
6	100	high
7	100	high
8	100	high
9	100	high
10	28	low
11	51	moderate
12	39	low
13	13	low
14	39	low
15	100	high
16	96	high
17	93	high
18	40	low
19	92	high
20	62	moderate

Table 3: Significance values of Spearman's rank correlation coefficients for environmental variables. . Main relationships are driven by inundation levels (vegetation cover) or size (area, and edge length).

	Heterogeneity	Vegetation	Area	Substrate Phi	Edge length	Inundation
Heterogeneity	-	0.173	0.203	0.774	0.075	0.165
Vegetation	0.308	-	0.553	0.297	0.881	0.026*
Area	0.946	0.941	-	0.413	0.019*	0.422
Substrate Phi	0.599	0.935	0.584	-	0.669	0.835
Edge length	0.96	0.93	0.021	0.446	-	0.515
Inundation	0.145	0.027*	0.456	0.888	0.974	-

* significant at > 0.05

Figures

Figure 1: Digital Elevation Models showing the different extent of habitat loss under low, medium and high flows for representative gravel bars with (a) elevated profile and (b) shallow profile. Figure 1a shows patch 10, a large area, complex habitat patch, of which only 28% is submerged when levels are 1m above base flows; Figure 1b shows patch 15, a low elevation habitat patch, of which 100% is submerged under the same conditions.

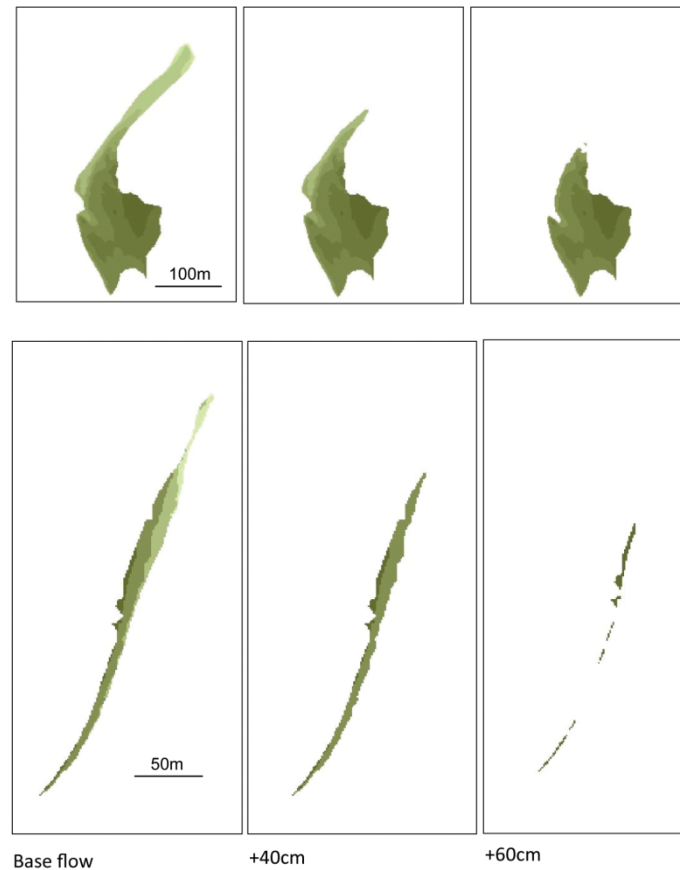


Figure 2: Daily depth readings for the River Severn at Llandinam Gravels between April-October 2009 showing variations around the baseline depth of 54cm on April 4th, the date on which gravel bars were surveyed.

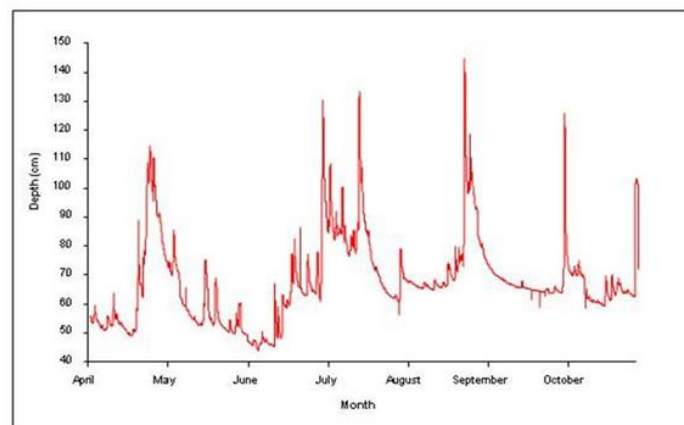


Figure 3: Biplot of principle identified prey sources and consumer data. Aquatic invertebrates (blackflies and stoneflies show greatest $\delta^{15}\text{N}$, relative to terrestrial invertebrates (springtails and aphids). The majority of consumer data lies within observed prey values, indicative of dietary contributions from both aquatic and terrestrial prey. Mean isotopic values for prey items are shown \pm SD, individual consumer values are shown.

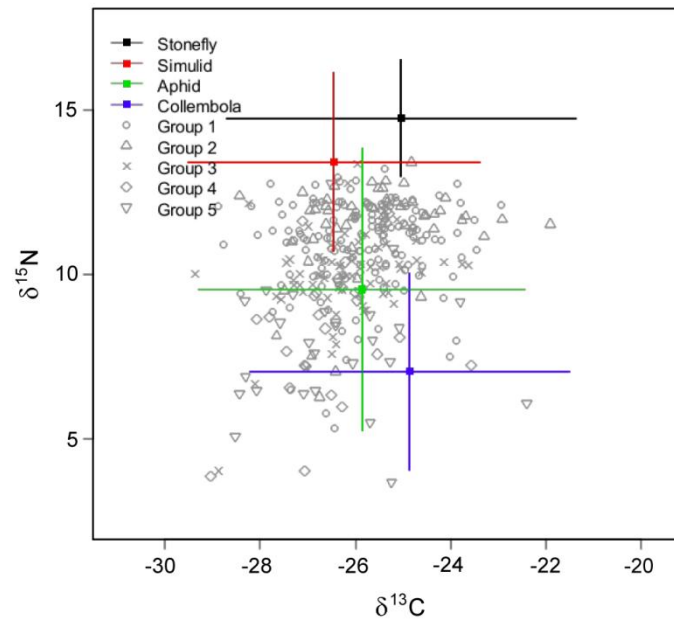


Figure 4: The isotopic niche areas for hypothesized functional groups (1 is headwater specialist ground beetles, 2 is lowland specialist ground beetles, 3, weak affinity ground beetles, 4, ground beetles with no habitat affinity; 5, specialist non-ground beetles associated with headwaters). Dotted lines indicate the convex hull for each group, the extent of all individuals' plotted isotopic values; ellipses represent the probable area in which the population's plotted values are likely to be found. Greater levels of $\delta^{15}\text{N}$ are indicative of greater contributions from aquatic prey items.

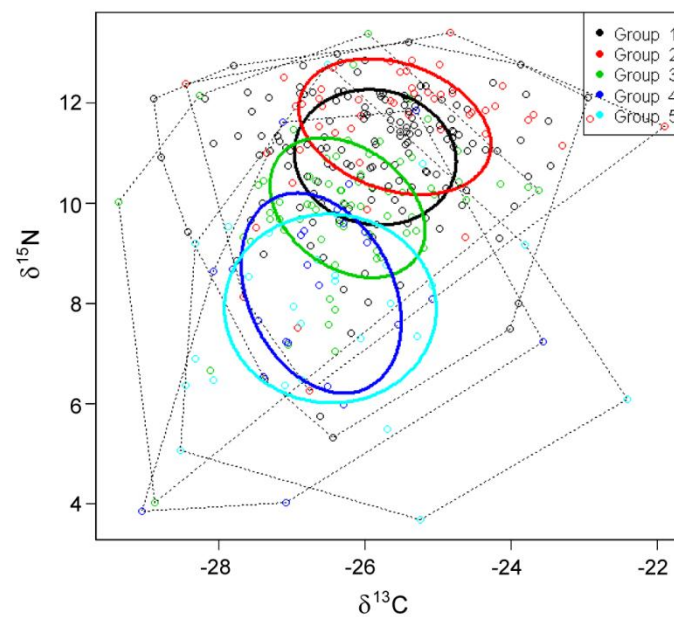


Figure 5: Probability density function of role of substrate calibre (a) and habitat heterogeneity on *B. tetracolum*. The mid-line represents the mean with 25%, 75% and 95% credible intervals shown. Terrestrial prey increases in very coarse gravels, and with increasing habitat heterogeneity.

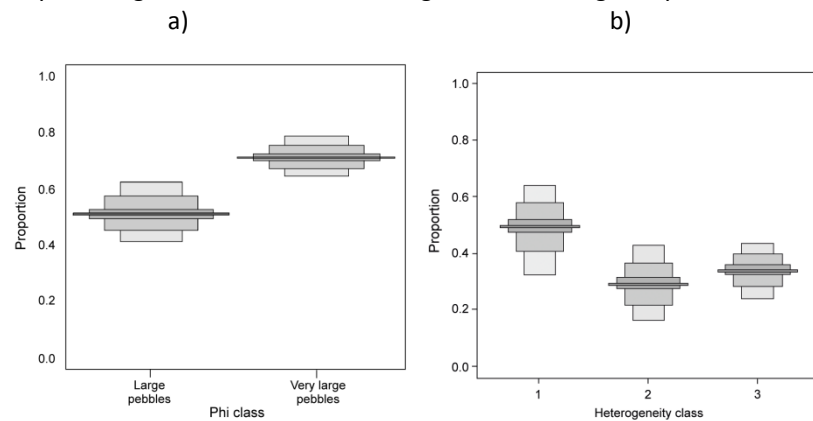


Figure 6: Probability density function of dietary proportions of two species of specialist ground beetles, *B. atrocaeruleum* (a) and *B. punctulatum* (b) illustrating the relative dietary contributions made by aquatic and terrestrial prey according to whether samples were collected from the wetted edge of the habitat patch, or inland, at the point of permanent vegetation. The mid-line represents their mean with 25%, 75% and 95% credibility intervals.

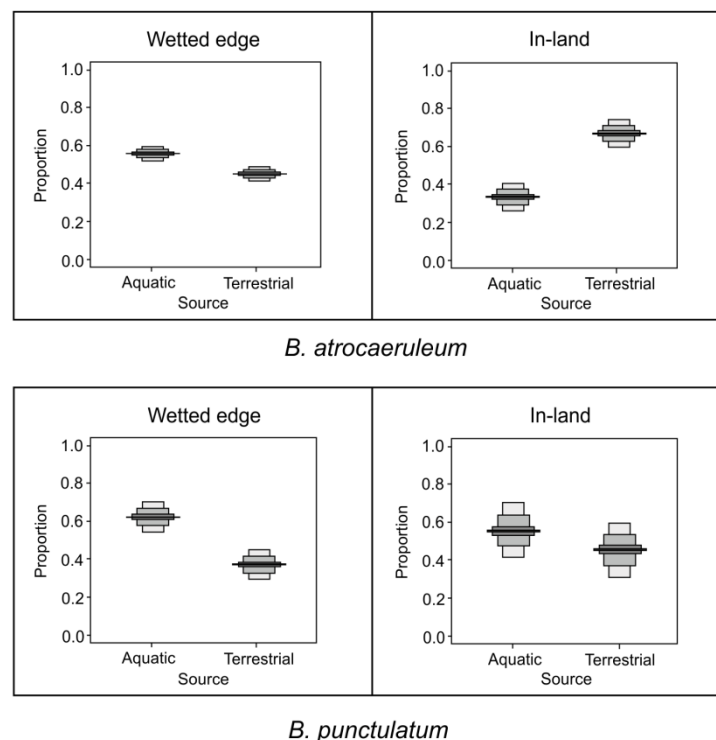


Figure 7: Probability density function of seasonal change in dietary composition in *B. atrocaeruleum* and *B. punctulatum* showing summer (A) 2009, autumn (B) 2009 and spring (C) 2010. The mid-line represents the mean with 25%, 75% and 95% credible intervals shown.

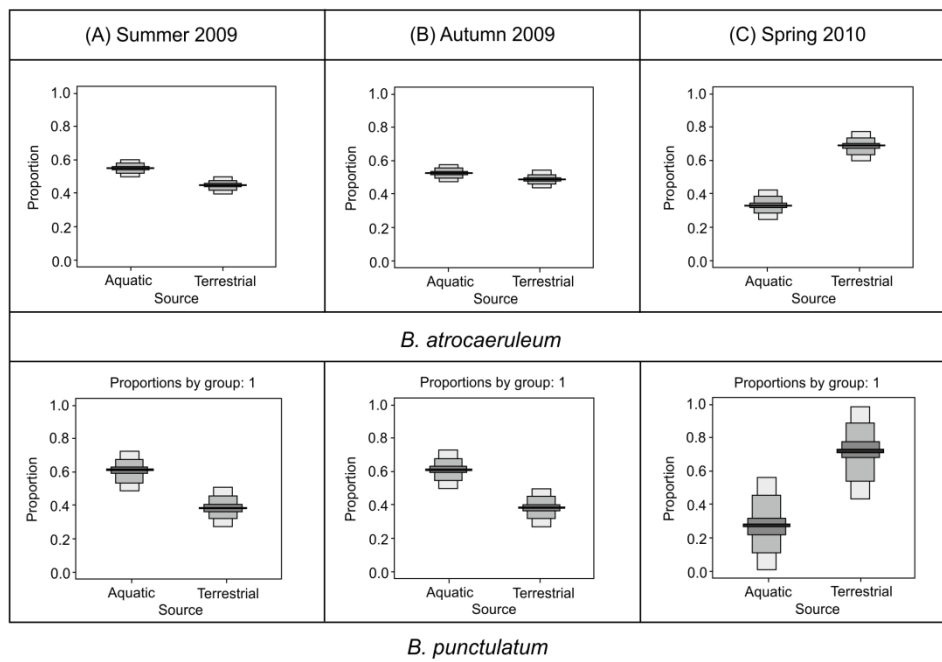


Figure 8: Probability density functions of ground beetle species from each of the groups with a level of association with the disturbed floodplain habitat, (A) *B. atrocaeruleum*, (B) *B. punctulatum* and (C) *B. tetracolum*, showing variation in dietary composition grouped by inundation levels (Low, Moderate, High; see Table 1 for descriptions of levels). The mid-line represents the mean with 25%, 75% and 95% credible intervals shown.

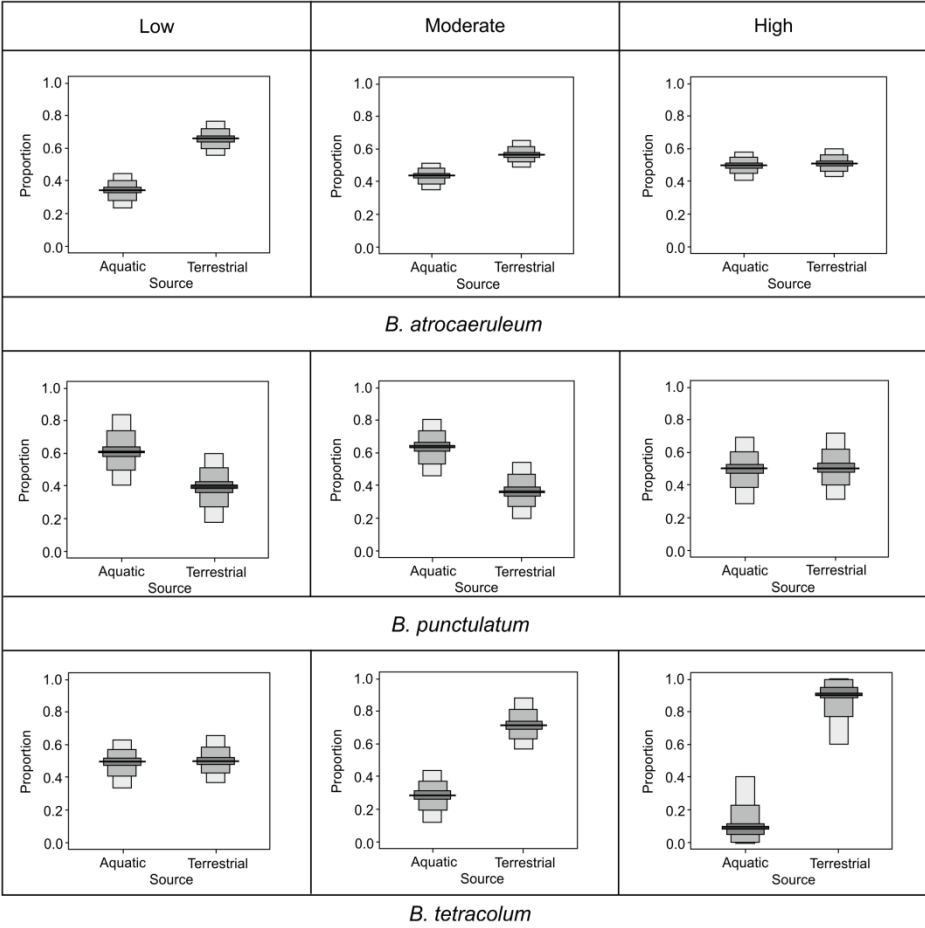
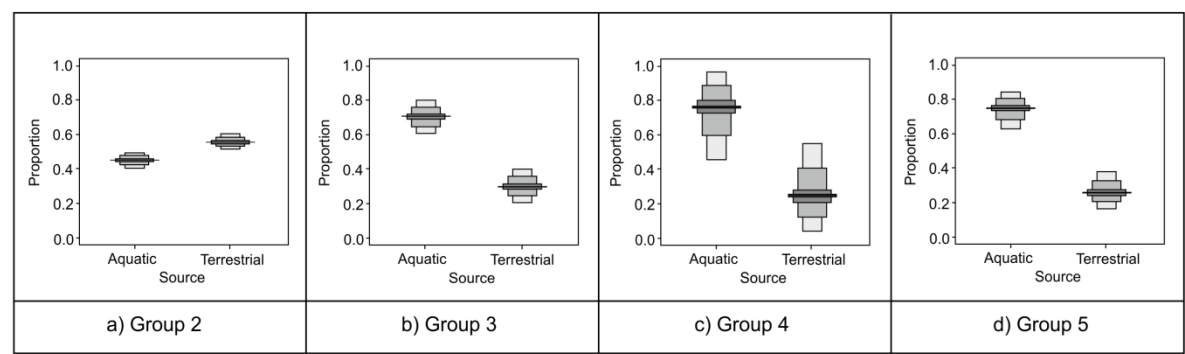
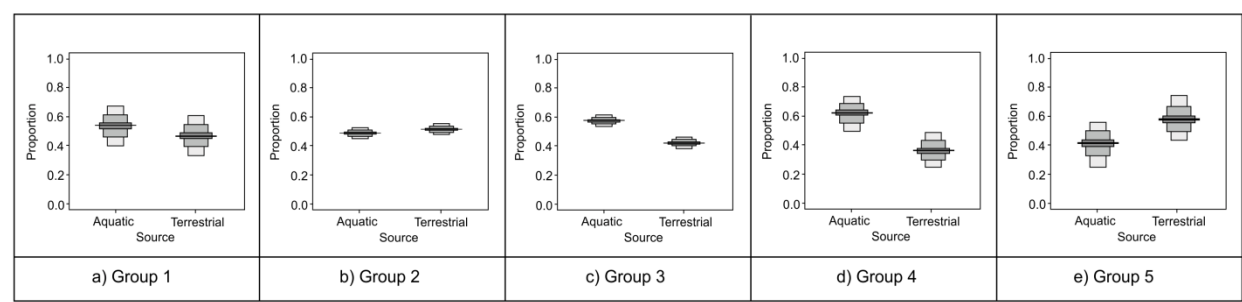


Figure 9: Probability density functions of longitudinal variation in prey source for the two specialist species, *B. atrocaeruleum* (a) and *B. punctulatum* (b), along a headwater to lowland floodplain gradient (five grouped sample areas, see Figure 10). The mid-line represent their median and the shaded boxes representing the 50%, 75% and 95% credible intervals from dark to light grey. Groups represent clustered sample points along the gradient (1 highest reaches above Llanidloes – 5, lowland reaches – Sheinton to Ironbridge)

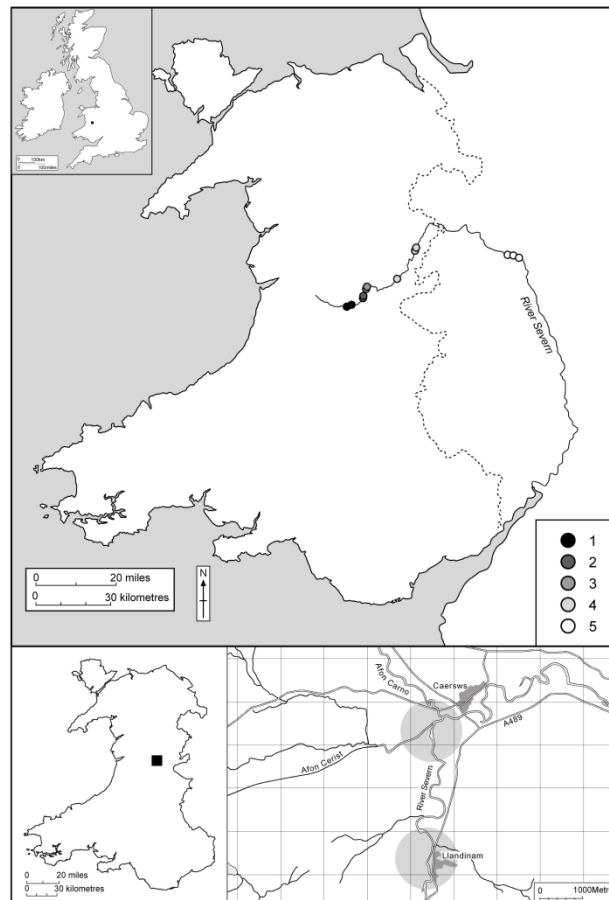


B. punctulatum



B. atrocaeruleum

Figure 10: Sample sites on the River Severn, UK, indicating headwater study area containing 20 bars used for inundation data, and the five reaches sampled (15 sites in total) for longitudinal data.



Appendix A5:

OVERVIEW OF GENETIC PROOF OF CONCEPT STUDY

Bembidion atrocaeruleum, Carabidae, Coleoptera (Stephens, 1828) is a widespread, but highly specialised ground beetle exclusively associated with coarse riparian sediments, having a largely montane distribution across Europe (Luff, 1998). It is associated with patchy habitat subject to frequent flood disturbance. This habitat type supports a high number of specialist species, many of which are rare, and in some cases endemic (Anderson and Hanssen, 2005, Eyre et al., 2000, Sadler and Bates, 2008). The habitat is vulnerable to anthropogenic degradation, through alteration of hydrology (Petts and Gurnell, 2005) or river channel (Florsheim et al., 2008), and the ability of specialist species to colonise alternative habitat patches between rivers and catchments is poorly understood. *B. atrocaeruleum* uses environmental cues to instigate short (maximum 200m) flights between habitat patches (Bates et al., 2006), but data on dispersal potential across greater distances is lacking. Microsatellite loci have been identified in other carabids (e.g. Contreras-Diaz et al., 2006, Keller and Largiader, 2003), but this represents the first attempt to identify them within the *Bembidion* genus that we are aware of.

Tissue samples from ten individuals collected from a single centrally located site on the River Severn, UK were used by Genetic Identification Services (GIS, www.genetic-id-services.com) to construct four microsatellite-enriched libraries with the magnetic bead-based enrichment procedure described by Jones et al. (2002). Libraries were prepared in parallel using Biotin-CA (15), Biotin-GA(15), Biotin-AAC(12) and Biotin-ATG(12) as capture oligonucleotides. Sequencing of randomly selected recombinant clones and primer design followed Jones et al. (2002). Primers for 24 microsatellite loci of high quality and with suitable flanking regions were tested and screened for polymorphism on seven individuals from the central Severn population using a single optimal amplification reaction mixture consisting of 1x Biolase © Buffer (from 10x stock solution supplied by the manufacturer), 2mM MgCl₂, 0.2 mM dNTPs, 6µM each primer, 0.025 U/µl Biolase DNA Polymerase (Bioline US, Taunton, MA, USA) and 0.2ng/µl clonal template DNA in 50 µl final reaction volume. Polymerase chain reaction (PCR) consisted of an initial three-minute denaturation at 94°C, followed by 35 cycles of denaturation (94°C, 40 seconds), annealing (55°C, 40 seconds), and extension (72°C, 30 seconds), with final extension time of 4 minutes at 72°C. PCR products were separated on a 3.5% agarose gel stained with ethidium bromide, and this approach revealed polymorphism in 13 of the 24 screened loci.

To assess the potential for detecting population structure both among local habitats along the River Severn and between the River Severn and adjacent River Wye, we initially attempted to amplify all 13 polymorphic loci across five populations (central Severn, three Severn tributaries, and one Wye population; N=29-32 each). Forward primers were tagged with dyes obtained from Applied Biosystems (Foster City, California; Table 1), PCR mixtures and program were as above, products were run on a 3730 automated sequencer (Applied Biosystems), and genotyping was performed on GENEMAPPER v 4.0 (Applied Biosystems). Only seven of the 13 loci amplified consistently across all populations, and we report on these seven polymorphic loci here.

Number of alleles per locus ranged from 4-12 (Table 1), and overall $F_{ST} = 0.025$ ($P < 0.01$), as calculated via AMOVA with an infinite allele model in Arlequin version 3.5.1.2 (Excoffier and Lischer, 2010). Six of ten pairwise F_{ST} values were significant ($p < 0.05$, Table 2). Arlequin analysis revealed no evidence for linkage disequilibrium between any loci, either across the full sample extent or within individual populations. We also used Arlequin to perform exact tests of Hardy-Weinberg equilibrium (HWE) for each locus in each population. Observed and expected heterozygosities did not differ significantly at any locus except D101, which showed a significant homozygosity excess in all five populations (Table 1 for central Severn population), probably due to null alleles. Therefore, we re-ran AMOVA including only the six loci that consistently demonstrated HWE. Excluding D101, overall $F_{ST} = 0.005$ ($P = 0.04$), and 3/10 pairwise F_{ST} values were significant (Table 2).

The population dynamics of patchily distributed riparian invertebrates, their responses to disturbance events and the potential for recolonisation routes after these events are important questions in floodplain conservation biology, particularly given the globally threatened status of natural floodplain systems (Tockner and Stanford, 2002). The ability of these microsatellite loci to detect significant structure among *B. atroceruleum* populations across a minimal spatial extent suggests their strong potential for their use in addressing these questions.

Table 1: Details of 7 microsatellite loci isolated from *Bembidion atrocaeruleum*. All anneal temperatures were 55°C.

Locus	Primer sequence 5' – 3'	Dye	Repeat Motif	N _A	Size range	H _e [*]	H _o [*]	P
Ba-A108	F: AACGCACTTTCGACTTCGATA R: ATCGGCCCATACCATAAATC	NED	di-	9	110-141	0.72	0.56	0.19
Ba-C1	F: ACCGCCCTCAATGATGAC R: TTCCTCTGCCTCGTCCAC	6FAM	tri-	10	93-138	0.78	0.81	0.57
Ba-C2	F: ATATGCAGTCCAAACCAAGAC R: GCTGAGGATAATGTTGAGAATG	HEX	tri-	12	129-165	0.78	0.94	0.64
Ba-C102	F: AGCCCAACACGATAAAACG R: CAACCATCATCCAGTTCGA	HEX	tri-	4	186-195	0.48	0.44	0.72
Ba-C103	F: CCTGCTGCATGATATTTGG R: AGCCAGGTACGTGCAAAC	6FAM	tri-	7	262-282	0.23	0.25	0.26
Ba-C104	F: TCCGTTTCTTCACTGACC R: CCATCATCCGTTACACCAC	NED	tri-	9	198-220	0.78	0.74	1.0
Ba-D101	F: ACCAATACGTGCTTCTCGTGT R: GCTGTTGTTGTTGCTGTTGAG	NED	tri-	10	244-263	0.66	0.16	<0.001**
Notes: N _A = number of alleles per locus, H _o = observed heterozygosity, H _e = expected heterozygosity, P = exact test P-value * Heterozygosities calculated for the central population on the River Severn, main channel (N=32) ["Severn" in Table 2] ** statistically significant								

Table 2: Pairwise F_{ST} (above diagonal, *P<0.05), first value including and second value excluding locus D101; and Euclidean distance (km, below diagonal) between five populations of *B. atrocaeruleum* (from two catchments, Severn (S) and Wye (W)).

River	Banwy (S)	Severn (S)	Tanat (S)	Vyrnwy (S)	Wye (W)
Banwy		0.01*/0.009	<0.001/<0.001	0.03*/0.003	0.01/0.001
Severn	21.5		0.03*/0.003	0.05*/0.01*	0.01/0.01*
Tanat	14.8	36.3		0.02*/0.01*	0.04*/<0.001
Vyrnwy	13.2	24.8	17		0.06*/0.004
Wye	33.5	15.8	48.7	39.7	

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