Controls on the distribution of specialist invertebrates inhabiting exposed riverine sediments in England and Wales

Matthew John O'Callaghan

A thesis submitted to
the University of Birmingham
for the degree of
Doctor of Philosophy

School of Geography, Earth and Environmental Sciences
College of Life and Environmental Sciences
University of Birmingham
June 2011

Abstract

Occupying a disjointed and vulnerable habitat, specialist Coleoptera associated with Exposed Riverine Sediments (ERS) are shown to exhibit high levels of adaptation. An assessment of the English and Welsh habitat resource confirms the presence of strong geographical and physical restraints on its distribution which partially explain the rarity of some of the associated Coleoptera. Assemblage studies reveal the presence of multiple adaptive strategies that enable specialists to utilise the resource in spite of perceived environmental pressures, and the strength of these morphological and behavioural adaptations can be used to predict abundance and distribution at alpha, beta and gamma levels. Furthermore, adaptations enforce varying nutrient acquisition strategies which spatially define communities. This study demonstrates the need specialist invertebrates have for a complex and highly connected ERS habitat with English and Welsh rivers, that exhibits structural variation along a longitudinal gradient. Reliant on riverine processes and subsidies the habitat and its associated invertebrates are symptomatic of a healthy and naturally structured lotic system operating laterally and across reach scales.

Acknowledgements

The support, advice and guidance of the following people have been invaluable in the completion of this research: my supervisors Jon Sadler, David Hannah and Mike Williams; Ian Boomer, for his extensive work in processing the stable isotope samples. Adam Bates, James Hale, Sarah Henshall and Megan Klaar for their advice and support in the field, laboratory and in data analysis; Richard Johnson and Mel Bickerton for their laboratory and technical support, and Kevin Burkhill for his assistance with the production of figures. I would also like to thank the many land owners who granted me permission to access sites, particularly Montgomeryshire Wildlife Trust for allowing the use of Llandinam Gravels.

The financial support of the Environment Agency made the entire project possible.

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Exposed Riverine Sediments, the role and value of the resource in English and Welsh rivers

1.1 Introduction

The occurrence of exposed riverine sediments (ERS) as an integral morphological unit of natural rivers has, in recent decades, become an historical observation for many lotic environments as anthropogenic demands have reduced and removed the habitat (Brewer et al., 2000, Gilvear, 1993, Petts and Gurnell, 2005). This loss has been observed within the UK and across Europe (e.g. Hohensinner et al., 2004), but our understanding of the impacts of this on associated invertebrate ecosystems has until recently largely been overlooked as the requirements of flood planning, charismatic higher fauna, and power and water needs took priority. More recently this knowledge gap has attracted more attention (e.g. Lambeets et al., 2008, Paetzold et al., 2008). The realisation that river systems must be viewed as complex multi-dimensional structures has included habitats such as ERS into recent conservation and restoration thinking (Jahnig et al., 2009). This inclusion has highlighted a need to understand better the ecology, function and vulnerabilities of the invertebrates whose lifecycles are inherently tied to the resource (Anderson and Hanssen, 2005).

The characterisation of a constrained invertebrate ERS fauna (particularly Coleoptera) was first undertaken in Fennoscandia (Andersen, 1968, Andersen, 1969) with knowledge of European and UK assemblages following much later (Bonn and Kleinwachter, 1999, Desender, 1989, Eyre and Luff, 2002, Eyre et al., 2002, Hering and Plachter, 1997, Sadler and Bell, 2002). This more recent research was broadened by the inclusion of research on other invertebrates including spiders (Framenau et al., 1996, Greenwood and McIntosh, 2008, Lambeets et al., 2006), grasshoppers (Bastow et al., 2002, Stelter et al., 1997) and flies (Drake et al., 2007). Alongside this knowledge sits an ever growing understanding of the controls of sediment transport and deposition, including the formation and dynamics of ERS (Petts et al., 2000, Kondolf et al., 2002, Caruso, 2006, Ward et al., 1999a).

The ERS resource within England and Wales has been acknowledged as a habitat of specific conservation concern (Environment Agency, 2002), as has its rarest Coleopteran fauna (including the endemic species *Thinobius newberyi* (Scheerpeltz) and *Meotica anglica* (Benick)), which have been targeted with a Biodiversity Action Plan (Anon, 1999). Many of the species found within the resource exhibit a high level of fidelity to the habitat (Bates and Sadler, 2005) and these species frequently possess some level of conservation status within the UK (Eyre et al., 2001b, Sadler et al., 2004a) and Europe (Anderson and Hanssen, 2005, Plachter and Reich, 1998, Van Looy et al., 2005). Contractions in populations have been observed (based on historical data) but only recently has it been demonstrated that anthropogenic pressures are responsible via loss of habitat (Graf, 2006), changes in flow regime (Paetzold et al., 2008) and habitat degradation (Bates et al., 2007). Although distributions of English and Welsh species are reasonably well understood (Bates and Sadler, 2004, Eyre et al., 2001a, Eyre et al., 2001b, Sadler and Bell, 2002), there has been a lack of knowledge on the landscape controls that can predict the distribution and structure of assemblages and which are valuable in protecting against future population contractions, or for informing habitat restoration requirements. As such this study presents an opportunity to explore the sensitivities of specialist assemblages and understand how they utilise their environment. By increasing the understanding of community ecology, the relative strength of potential threats can be assessed.

The ERS resource should be viewed within the larger context of the riverine landscape, where the river itself acts as a dynamic force that controls much of the geomorphic and biotic structure of the adjacent flood plains (Ward et al., 1999b). The extent and diversity of the ERS are dictated by the scale and influence of the river, which may produce the complex high volume forms associated with braided rivers (van der Nat et al., 2003) (Figure 1.1) or more laterally constrained distributions found in single channel rivers (Church, 1992), more typical of English and Welsh rivers (Figure 1.2).

Figure 1.1: Savage Creek, Denali National Park, Alaska, exhibiting multiple channels of differing depths and widths, across a wide floodplain.

Figure 1.2: Single channel ERS deposits in the headwaters of the River Severn, Llandinam, Wales. Extensive deposits are confined to one side of the channel with small island deposits immediately downstream of within-channel coarse woody debris. The bank immediately opposite is comprised of seasonally inundated Willow Carr.

Common to both morphological forms is the occurrence of flows that restructure the habitat to such an extent that primary succession is suppressed (Sadler and Bates, 2008), thereby removing within-habitat nutrient production and exacerbating biotic extremes (Henshall et al., in press, Desender, 1989). The conditions imposed on organisms utilising the resource enforce high levels of adaptation which allow them to survive abiotic pressures such as inundation or wide thermal thermal variability (Andersen, 1968) and maximise resource acquisition (Hering and Plachter, 1997, Paetzold and Tockner, 2005). Under less disturbed conditions these adaptations disadvantage species (Sadler et al., 2004b) and exclude them from potential refugia if the ERS habitat is permanently removed.

1.2 Study aims and objectives

The aim of this research is to understand landscape factors that control current ERS specialist distributions, and the effects that these have on community structure at local and regional scales, thereby allowing an assessment on the vulnerability of assemblages to threats posed by hypothetical future environmental changes. This aim is met through five objectives which evaluate landscape processes at several scales. They are:

- Evaluate the extent and distribution of the current English and Welsh ERS resource, and categorise the landscape forms (hydrological and geographical) with which it is associated.

- Model the distribution of ERS specialists according to habitat characteristics at a regional scale and across rivers, assessing which elements can be used to predict species' presence and assemblage structure at a local scale.

- Use long-term data sets to assess the role variations in inundation pressures have in structuring local assemblages.

- Investigate how different specialists utilise available prey resources at a local scale according to inundation pressures.

- Assess whether a change in nutrient pathways occurs along a longitudinal gradient by examining dietary proportions of distinct sample groups from headwaters to low altitude floodplains.

1.3 Thesis structure

This thesis is written in the form of extended papers, and as such may feature some repeated elements, particularly in analytical or statistical methodologies.

Chapter 2 begins the thesis by assessing the current extent of the ERS resource in England and Wales by presenting a database of extensive habitat patches identified via aerial photographs and maps. Using a subset of these data, commonalities in the river profiles (magnitude, flow profiles, geology and morphology) are characterised and used as tools to model the complexity and extent of the resource within a river.

Chapter 3 uses field collected data on ERS Coleopteran assemblages from 22 sites on five rivers to create models predicting the landscape controls on the distribution of species and functional groups. The importance of anthropogenic impacts, habitat complexity and connectivity and longitudinal positioning are assessed to determine which factors most constrain local populations.

Chapter 4 assesses the impact on local assemblages of long-term flow regime patterns by combining river discharge data for the Upper River Severn with seven years of Coleoptera assemblage data. Generalised Additive Models are used to examine long-term trends in abundance. Generalised Linear Models are used to assess the importance of key elements of flow regime such the timing and duration of high and low flows in driving familial abundance across six habitat patches on the River Severn at Llandinam, mid-Wales.

Chapters 5 and 6 concentrate on resource acquisition by ERS Coleoptera at a local and regional scale using stable isotope analysis to quantify aquatic and terrestrial prey ratios. Chapter 5 examines how different functional groups' prey selection is driven by morphological and behavioural characteristics; which also dictate their responses to inundation pressures. Chapter 6 looks at the same functional groups, but across a 150km longitudinal gradient to examine how resource acquisition changes within and between groups according to sampling position.

Chapter 7 summarises the research conclusions, using them to suggest strategies to maintain and enhance current assemblage distributions in England and Wales, and suggests future avenues of research that will benefit management and conservation of the ERS habitat and its associated fauna.

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2

Exposed Riverine Sediments in England and Wales: investigating controls on the abundance and complexity of the habitat

Exposed riverine sediments (ERS) are an ecologically valuable, but poorly understood habitat associated with the riparian zone of natural and semi-natural rivers. Found globally, they are formed by erosive and depositional processes occurring under fluctuating flow regimes and, as such, are susceptible to changes in the availability of sediments and alterations in flow patterns. Although identified in England and Wales as a habitat of conservation value, little is known regarding their current extent and distribution, the river systems with which they are associated, or the strongest natural and anthropogenic controls on abundance or complexity. This study addresses this knowledge gap by developing and analysing an extensive database of extant ERS habitat (as of 2009) and uses a subset of these data to characterise the rivers with which is it associated. The magnitude (size) and shape (form) of river flow regime are coupled with physical, geological and anthropogenic variables to produce multiple linear regression models predicting habitat area (m^2/km^{-1}) and density (number of bars/km^{-1}). The frequency of excess Q_{10} flow events is shown to influence area positively, whilst abstraction has a negative impact. The slope of the river (descent in metres/km) positively influences ERS density, but impoundment has a negative impact. Natural variables are the strongest influence on habitat provision on the rivers studied, but anthropogenic impacts reduce the complexity and cohesion of the ERS mosaic.

2.1 Introduction

At its broadest, ERS 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 bankfull and the typical base flow of the river"* (Bates and Sadler, 2005, p.5). 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 size with downstream transportation (Brookes, 1994, Surian, 2002), notwithstanding variations resulting from tributary inputs (Benda et al., 2004, 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, Church, 2002), their formation being a product of the interaction between discharge, slope and sediment supply, identified by geomorphologists as the principle components in the structuring of river morphology (e.g. Vandenberg, 1995). Within channel sediments are eroded, transported and deposited according to sediment calibre and supply, and variations in the river's energy, which is derived from a combination of river flow (characterised by discharge or water depth) and the power with which it is flowing (largely related to channel gradient) (Carling, 1992, Bettess, 1994). This river energy will vary spatially (geomorphologically) and temporally (with flow variability), and these variations dictate the form of the river and the occurrence of ERS (Gurnell et al., 2009). These interactions have been visualised (Figure 2.1) to provide a predictor of river channel form (Church, 2002, Gurnell et al., 2009).

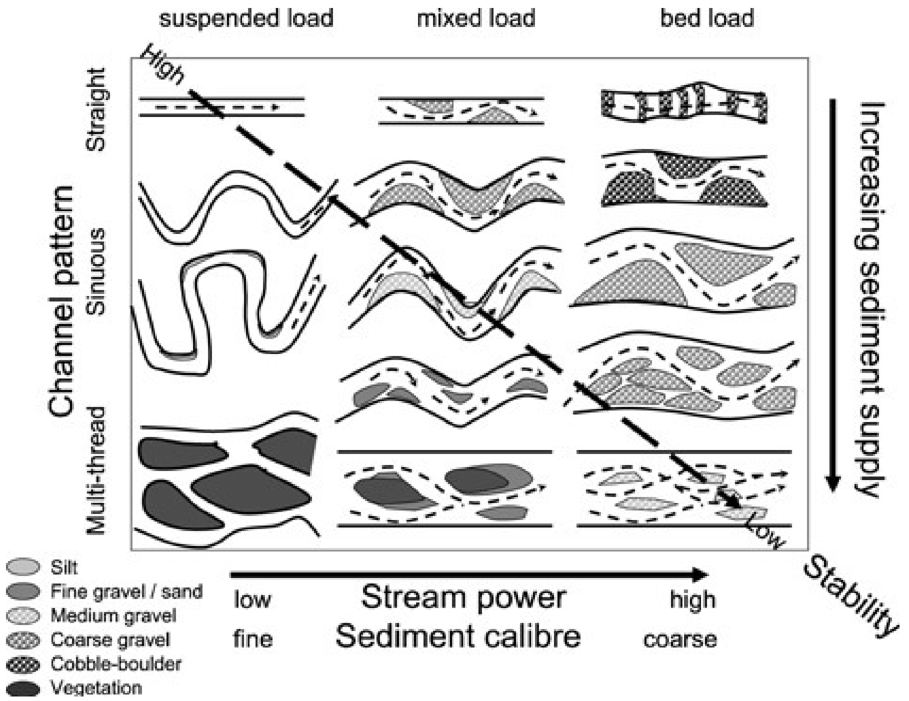


Figure 2.1: Classification of channel morphological types, showing ERS likelihood according to form, sediment supply and size and stream power (reproduced from Gurnell et al., 2009).

Even in highly unstable channels, sediment mobilisation occurs infrequently, under only the highest flows, when large-scale movements occur followed by rapid redeposition as stream power reduces to normal levels. The duration of the high flow events and the size of the sediments dictate the distances transported, although for larger sediments this is seldom more than tens of metres (Bridge, 2003). These processes also serve to mobilise sediments from the adjacent floodplain, particularly where the channel is laterally mobile, which can account for the majority of local, within-channel sediments (Surian and Cisotto, 2007). Within the context of the wider floodplain, channel instability produces a complex, but coherent, landscape with the turnover rates of channel, riparian habitats (such as ERS) and the wider floodplain tending towards equilibrium, described as a ‘shifting mosaic steady state’ (van der Nat et al., 2003). Turnover rates themselves vary according to position and local morphology, constrained headwaters showing reduced turnover in comparison to braided headwaters (Ward et al., 2002a) and high altitude areas exhibiting greater turnover rates than lowland reaches nearing the estuary (Arscott et al., 2002). ERS are dependent on high turnover rates and reduced stability, a main characteristic being the lack of permanent vegetative cover. Where inundation and habitat restructuring are infrequent, successional processes stabilise recently exposed sediments and return them to a terrestrial, vegetated form (Asaeda et al., 2010, Gurnell et al., 2001).

This complex interaction of flow, power, sediment and turnover explains the vulnerability of ERS to anthropogenic impacts. Impoundment, sediment mining, water abstraction and channel alterations disrupt the natural processes which maintain the fluctuating mosaic of habitat forms. Impoundments have several effects; capturing upstream sediments and preventing replenishment by downstream erosion (Petts and Gurnell, 2005), whilst controlled releases of captured sediments can bury existing habitat and alter its structure (Sakamoto et al., 2010). Impoundment also alters the flow regime, reducing the variation between minimum and maximum flows both daily and annually (Arrigoni et al., 2010) and, as such, the magnitude of restructuring processes (Brandt, 2000), resulting in reduced channel complexity and increased stability (Petts et al., 1993). Substrate extraction (as resource exploitation or for flood amelioration) has marked impacts on channel structure, typically reducing complexity and degrading habitat diversity, the transportation and supply equilibrium being broken (Gaillot and Piegay, 1999, Kondolf et al., 2002). Land-use change (via afforestation) has also reduced sediment inputs in areas where agriculture has reduced (Bravard et al., 1997, Liebault and Piegay, 2002), having the same impact as substrate removal. These two impacts (impoundment and sediment removal) have been suggested as the principle causes in the change of many of Europe's large rivers from braided to single channel regimes (Bravard, 2010, Hohensinner et al., 2004). Water abstraction and channel modification have similar impacts, reducing the frequency and magnitude of high flow events and allowing vegetative stabilisation of the riparian zone (Brunke, 2002), whilst channel modifications increase local stream power and enhance sediment mobilisation (Brookes, 1985), removing substrates faster than replenishment, particularly where bank erosion is prevented (Florsheim et al., 2008). These increases are often concurrent with a natural reduction in habitat turnover rates (Arscott et al., 2002), occurring largely in developed or urbanised, often lowland areas (Paul and Meyer, 2001, Surian and Rinaldi, 2003, Fotherby, 2009). With turnover also adversely affected by system modification (Ward et al., 2002b), urban pressures exaggerate the reduction in habitat rejuvenation in low altitude rivers.

ERS are seen as important as they are indicative of a natural river system in landscape equilibrium, and play a part in the ecosystem services provided by such systems (Paetzold et al., 2005, Petts et al., 2000). Their role as a habitat resource for specialist and often rare invertebrates is also now established (Anderson and Hanssen, 2005, Drake et al., 2007, Sadler and Bates, 2008). The English and Welsh resource was targeted in a specific habitat action plan (Environment Agency, 2002), yet understanding of the distribution of the resource remains limited. This study will address this knowledge gap and aims (1) to create a new database of ERS areas in England and Wales and (2) to analyse emergent ERS patterns in relation to the nature of the flow regimes, environmental factors and anthropogenic influences that are hypothesised to affect the extant resource.

2.2 Methodology

Initial identification of ERS sites was made by cross-referencing aerial photography with detailed Ordnance Survey Maps (accessed via Digimap). The English and Welsh database includes coordinates of areas of extensive ERS (either single patches or complex areas) visible in photographs or marked as shingle, gravel or sand on maps. Coordinates were then imported to a Microsoft Access database allowing for archiving, future enhancement and categorisation. A subset of 20 rivers with abundant ERS was chosen to represent the three main geographic distributions of the resource in the south west and north of England and Wales (Figure 2.3) and (again using aerial photography and map information) their ERS resource was measured at higher resolution to assess area (m^2/km^{-1}), density of habitat units (number of patches/km^{-1}) and slope (m/km^{-1}) for each river.

Classification of flow regimes of the rivers in the subset was calculated using data supplied from the National River Flow Archive (NRFA) by the Centre for Ecology and Hydrology. Data were obtained from stations with a complete (or minimum 90%) record of data from 1988-2008 (Figure 2.2). These long-term datasets allowed hydrologically similar rivers to be identified using regime classifications (Hannah et al., 2000, Harris et al., 2000). This technique groups rivers based on magnitude and shape attributes, which in turn can be combined to provide descriptive classes. Data were converted from discharge records (m^3s^{-1}) into runoff (mm $month^{-1}$), to standardise for differences in catchment area and thereby allowing between-catchment comparison. Additional information on catchment geology and anthropogenic modifications were derived from the NRFA. Rivers were grouped by magnitude based on four indices: mean, maximum, minimum and standard deviation of monthly values, regardless of their timing (Harris et al., 2000, Monk et al., 2006). Standardisation of data using z-scores (mean = 0, standard deviation = 1) allowed comparison of regime 'shapes', identifying variations in seasonal patterns of high and low flows, (Hannah et al., 2000). Both magnitude and shape groups were defined using hierarchical cluster analysis (Ward's method) with dendrograms and agglomeration schedules (scree plots) used to identify robustly the number of clusters to retain and gauging stations that showed similarity (Griffith and Amrhein, 1997).

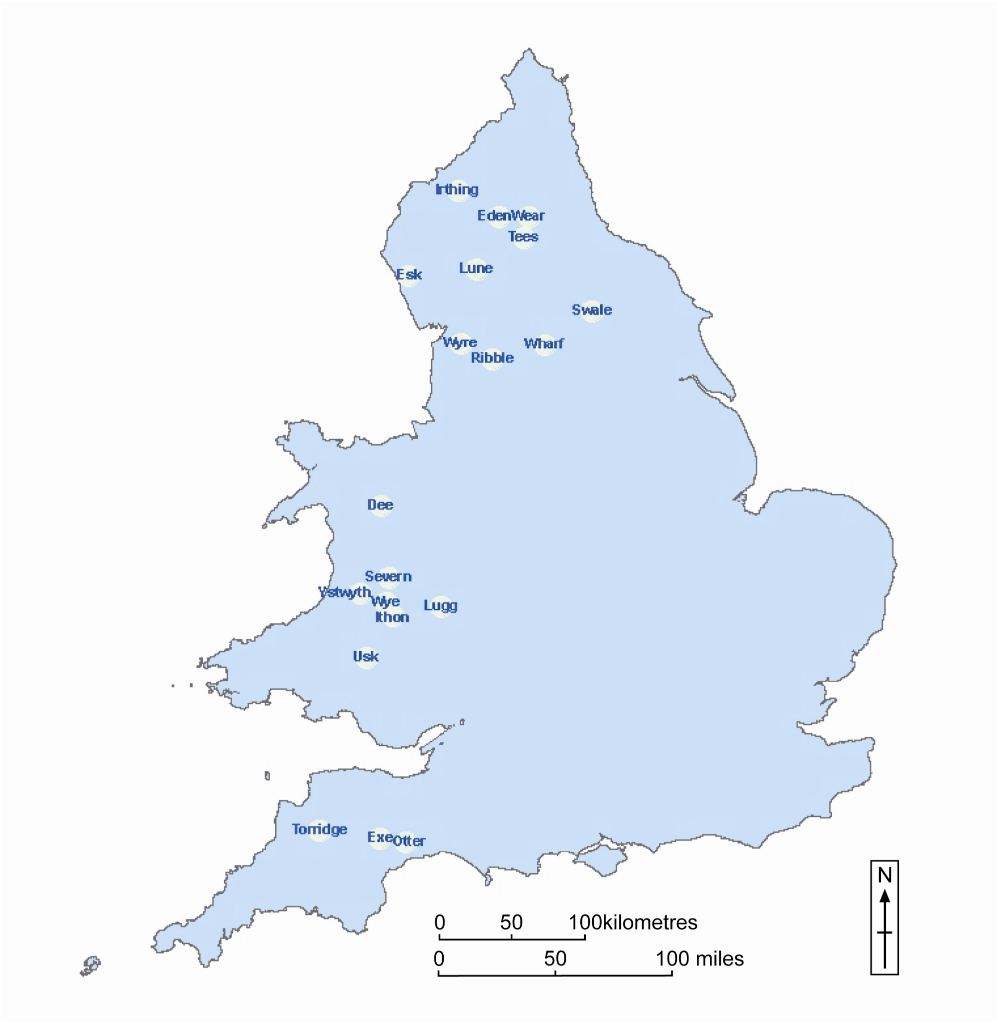


Figure 2.2: Distribution of gauging stations across the south west and north of England, and Wales, used to source run-off data for classification of regime shape and magnitude characteristics, labelled by river.

Prior to analysis the data were explored to identify outliers in explanatory variables, co- linearity between the explanatory variables and variables requiring transformation (Zuur et al., 2010). These variables were initially analysed using Spearman correlation to identify those with strong relationships (> 0.4) to habitat metrics, as data were non-parametrically distributed.

Multiple Linear Regression models were run for habitat abundance and complexity, and flow characteristics, river slope, anthropogenic modifications and geology as explanatory variables. The most important explanatory variables were identified using a drop 1 selection process, which presented the most probable, significant combinations (Zuur et al., 2007). Visual model validation occurred, whereby plots of standardised residuals against fitted values were used to assess homogeneity, histograms of residuals were used to test normality and plots of residuals against explanatory variables established independence (after Zuur et al., 2010). No patterns were visible in any of the plots.

An information-theoretic approach to model selection was taken whereby the most parsimonious model was selected from a suite of possible models using Akaike's Information Criterion (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, 1973). The models were 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 $j = 1$. Using the Akaike weights, a 95% confidence set of models was identified starting with the models with highest Akaike weight and repeatedly adding the model with the next highest weight until the cumulative weight was greater than 0.95.

2.3 Results

2.3.1 English and Welsh ERS resource

The majority of the ERS resource are confined to the North of England (on rivers rising along the Pennine spine), Wales and the South West of England (Figure 2.3). The resource is absent from rivers associated with major groundwater aquifers found in much of south and east England, as well as from heavily engineered rivers in populace areas such as the West Midlands. The full dataset is included on a supplementary CD.

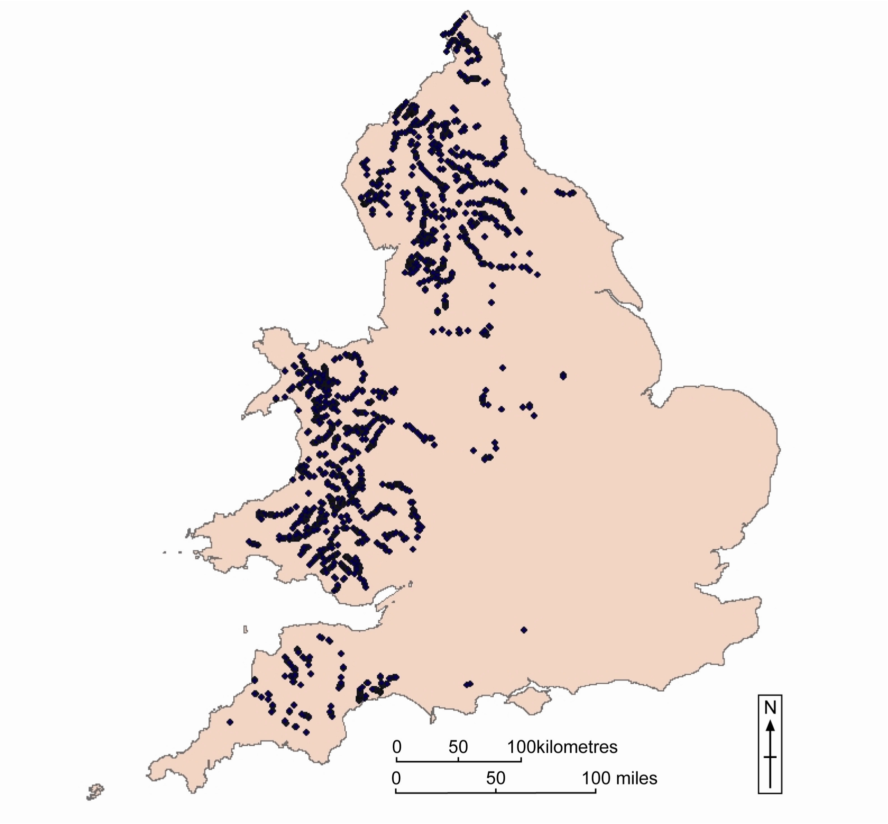


Figure 2.3: Distribution of all major areas of ERS identified within England and Wales, showing highest densities in the south west and north of England and Wales. Each point represents the grid reference for a site of ERS, ranging from single patches, to complex areas of multiple patches.

2.3.2 Flow regime classifications of river subset.

Regime shape and magnitude were derived using long-term (1988-2008) mean monthly runoff data from 20 stations. Following inspection of cluster dendrogram and agglomerative analysis (scree plot) indicating levels of similarity between gauging stations, four distinct groups were identified for both flow regime magnitude (Table 2.1) and shape (Table 2.2). Four magnitude classes were identified from minimum, maximum, mean flows and their standard deviations (Figure 2.4):

Class 1:	High flows, with highest values in all indices, including catchment size (8 rivers).
Class 2:	Second highest flows, consistent across all indices except Standard Deviation, where its range has the highest value (2 rivers).
Class 3:	Intermediate flows, which although having lowest mean flows, has higher maximum flows than Class 4 (5 rivers).
Class 4:	Lowest magnitude, with higher mean flows than Class 3, but with lower mean and maximum flows (4 rivers).

Table 2.1: Summary statistics of magnitude classes (mm month^{-1})

	Class 1	Class 2	Class 3	Class 4
Mean (mm month $^{-1}$)	151.56	124.43	76.51	53.43
Min (mm month $^{-1}$)	76.51	49.61	31.3	23.66
Max (mm month $^{-1}$)	238.8	221.71	139.86	102.82
Std Dec (mm month $^{-1}$)	59.73	64.3	39.47	27.09
Mean Catchment area (km^2)	404.42	165.9	353.61	105.25
No. of rivers	2	4	8	5

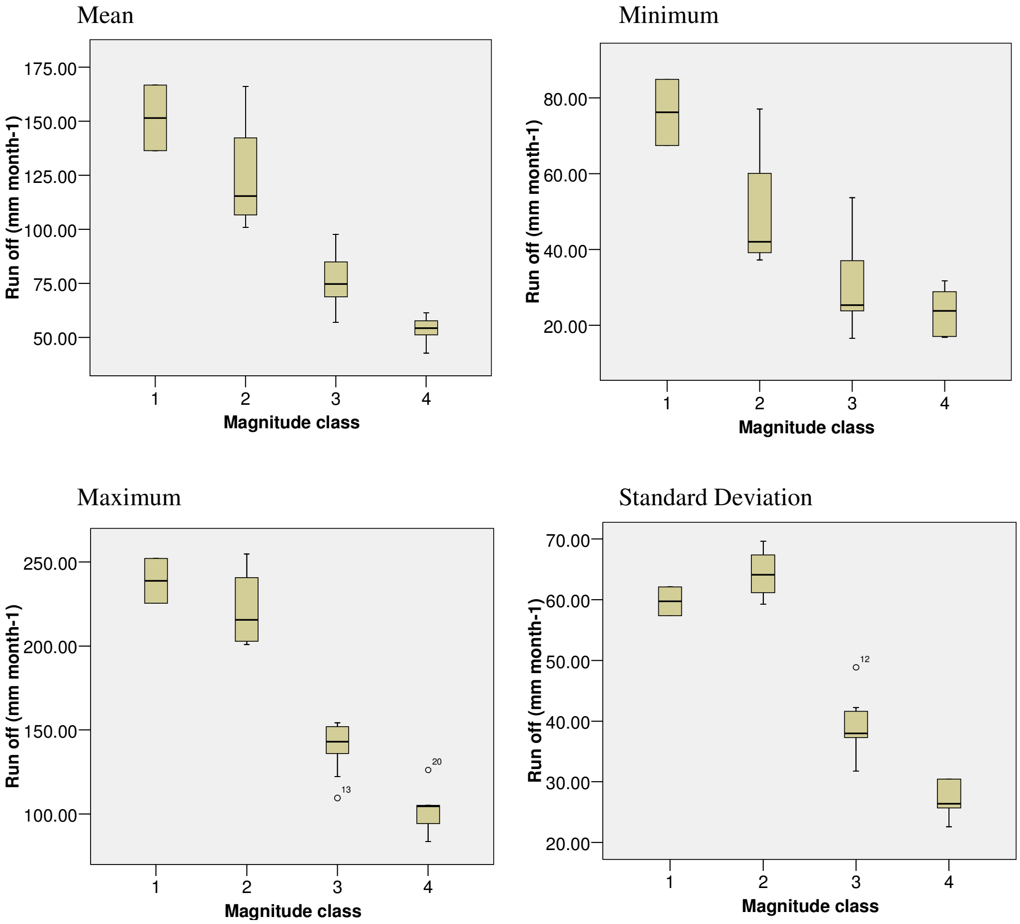


Figure 2.4: Box plots of monthly mean, minimum, maximum and standard deviation runoff within the four flow magnitude classes (1-4). Box length represents interquartile range, whiskers show the extent of minimum and maximum values (outliers plotted individually) and median values are shown by the horizontal line in each box.

Regime shape is described from plotted z-scores of standardised discharge data (Figure 2.5).

Class A: January peak flow, with the autumnal rise to maximum showing a period of stability in October and November, and a steady spring decline.

Class B: Prolonged December-February maximum flow, with level of autumnal stable period higher and less distinct that Class A and an erratic spring, decline.

Class C: Two peak flow periods in autumn and winter.

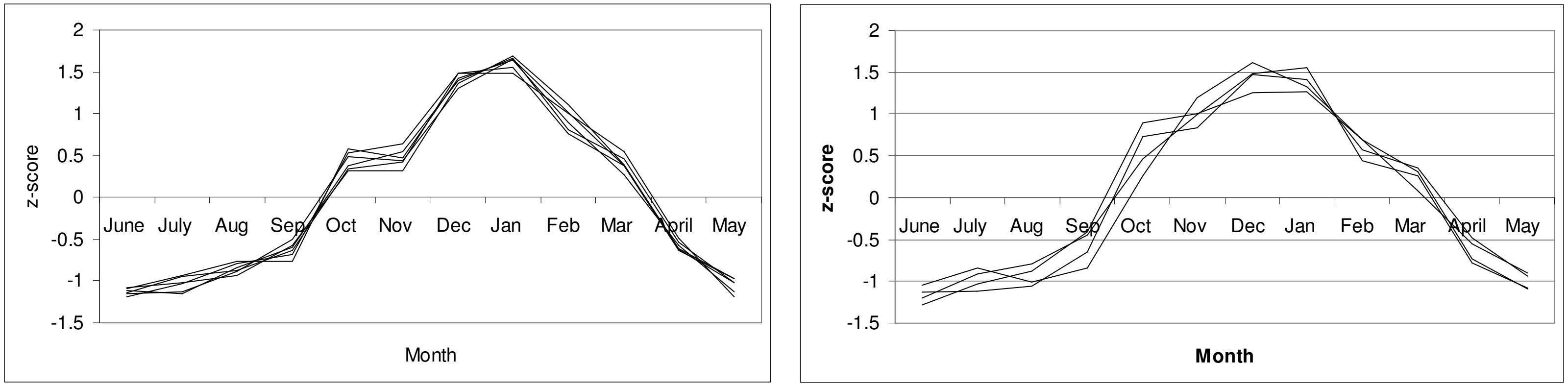
Class D: Maximum peak is in January, with a reduced late summer flow.

Regime shape and magnitude classifications were then combined to identify hydrologically similar gauging stations, the underlying geology and level of anthropogenic influence on each station was also determined (Table 2.2) and the distribution of these classifications mapped (Figure 2.6), magnitude classifications show no discernible patter of distribution, regime shapes A and C dominate in the north west of England, whilst shape B has a westerly distribution.

Table 2.2: Combined magnitude and regime shape classes given by river, along with geographical region, underlying geology and anthropogenic impacts within catchment.

River	Class	Region	Geology	Abstraction	Impoundment
Dee	1B	N Wales	Igneous/Limestone	Y	Y
Esk	1C	NW	Lava.tuff.granite	N	N
Eden	2A	NW	Boulder clay/sandstone	N	N
Lune	2A	NW	Boulder clay	N	N
Wye	2B	Mid Wales	Sediments	Y	N
Ystwyth	2B	Mid Wales	Shales	N	N
Ribble	3A	NW	Boulder clay	N	N
Severn	3A	Mid Wales	Boulder clay	Y	Y
Tees	3A	NE	Boulder clay	N	Y
Wharfe	3A	NE	Boulder clay	Y	Y
Torridge	3B	SW	Shale/Sandstone	Y	Y
Wyre	3C	NW	Millstone grit/glacial	Y	N
Exe	3D	SW	Sandstone	Y	Y
Ithon	3D	Mid Wales	Shales	N	N
Irthing	4A	NW	Boulder clay	Y	Y
Lugg	4D	W	Alluvial	Y	N
Otter	4D	SW	Alluvial	Y	N
Swale	4D	NE	Glacial	N	N
Usk	4D	S Wales	Alluvial/boulder clay	N	Y
Wear	4D	NE	Alluvial/boulder clay	N	Y

Class A Class B



Class C Class D

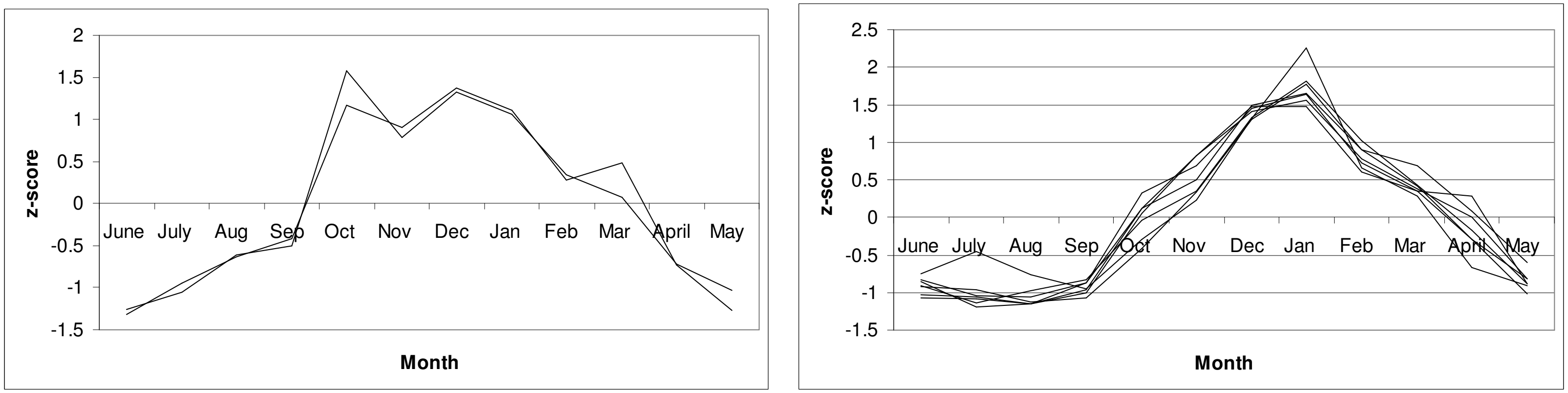
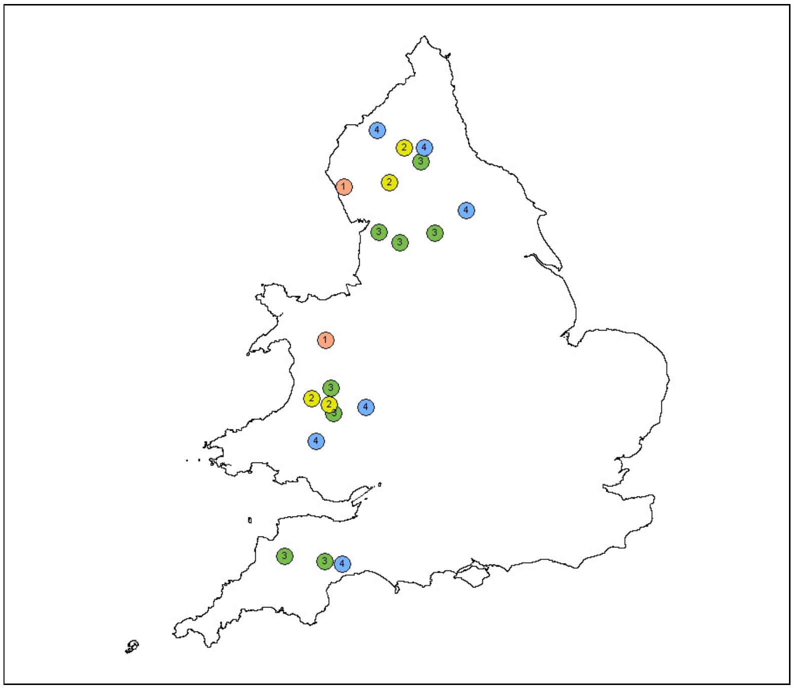
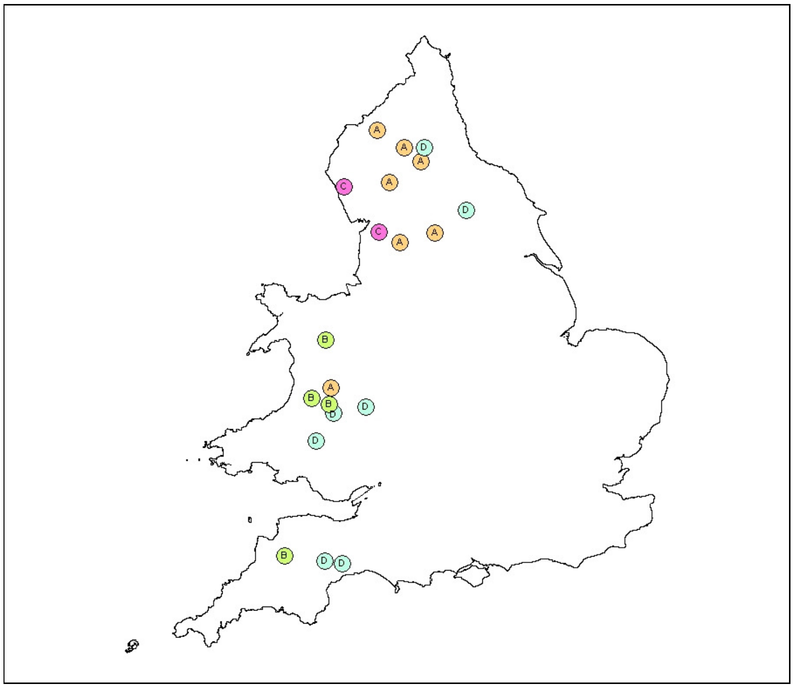


Figure 2.5: Classification and grouping of rivers using standardised average monthly runoff (mm month^{-1} converted into z-scores), showing variation in timing and characteristics of high and low flows; lines represent flows of constituent rivers within each classification.



a) magnitude



b) regime shape

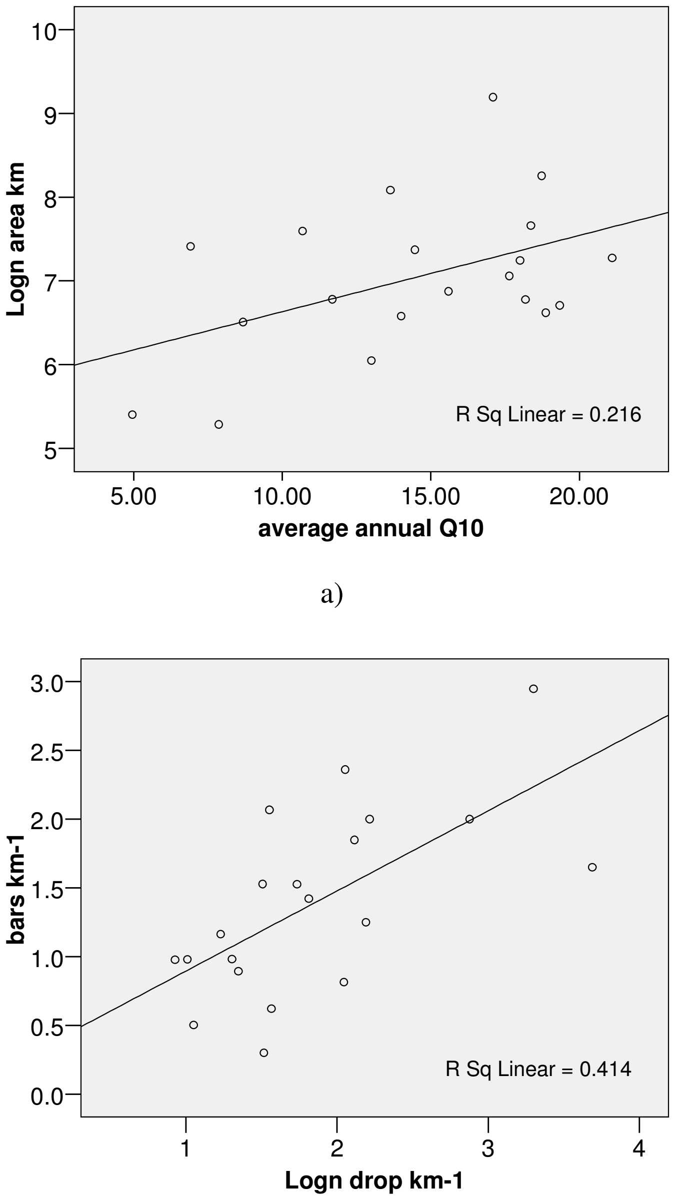
Figure 2.6: Geographical distribution of gauging stations according to a) magnitude and b) regime shape class as defined in Table 2.2.

2.3.3 Multiple Linear Regression

Regression models lying within a 95% confidence interval were derived for mean m^2/km^{-1} of river (area) and number of bars/km of river (density) using a drop 1 selection procedure validated by AIC scores and ranking by weights (Appendix 1). The area of ERS/km^{-1} model included average annual number of Q_{10} events (the highest discharge rates occurring ten per cent or less of the time) and water abstraction, with increased Q_{10} events positively affecting area, and abstraction negatively, the adjusted $r^2 = 0.216$, significant at the <0.05 level (Table 2.3). The density model (number of ERS patches/km^{-1}) indicated slope (as drop in metres/km^{-1}) and impoundment as the strongest significant parameters (adjusted $r^2 = 0.407$), density increasing with slope but reduced in impounded streams, significant at the < 0.005 level (Table 2.3). Visualisation (Figure 2.7) demonstrated that area is positively associated with Q_{10} events and density positively associated with slope.

Table 2.3: Multiple linear regression models with best fit for ERS area and density using hydrological and landscape variables.

Model	adjusted r^2	F	dF	Variables	p-value
Area	0.216	4.57	17	Av. Annual Q_{10} events Abstraction	**<0.05**
Bars/km	0.407	7.46	17	Slope Impoundment	**<0.005**



a)

b)

2.7a) ERS area: Q_{10} events 2.7b) Patch density:slope

Figure 2.7: Scatter plots of significant positive model elements a) increasing habitat area with higher monthly average of Q_{10} events b) increasing patch density with steeper stream slope.

2.4 Discussion

This study is the first geographical overview of the extent and distribution of the English and Welsh ERS resource, and characterises the rivers and landscapes with which it associated. Complex river systems are known to be degraded and morphologically simplified by anthropogenic modifications and developmental pressures (Brewer et al., 2000, Gurnell et al., 2009, Petts, 1984), with subsequent ecological ramifications (Ward and Stanford, 1995). Loss of habitat and changes in flow regimes are also known to impact riparian arthropod community cohesion and function (Bonn et al., 2002, Greenwood and McIntosh, 2010, Hering, 1995, Lambeets et al., 2008). By understanding the controls on the existing ERS resource in England and Wales (within a context of historical degradation) the long-term maintenance of current resource levels may be secured, aiding the conservation of specialist invertebrates.

A visual evaluation of the distribution of the current ERS resource (Figure 2.3) confirms the regional distribution suggested in earlier estimates (Eyre and Lott, 1997), with densities greatest in Wales, south western and northern England. Its absence from the remaining rivers may have several causes, including anthropogenic induced losses due to channel and flow alterations (Brunke, 2002, Gaeuman et al., 2005) and natural reductions of habitat turnover in lower altitude rivers (Arscott et al., 2002). The underlying importance of sediment supply and mobilisation potential should not be overlooked, and enforces much of the geographical restriction of the resource, dependent as these are on the characteristics of headwaters and flow regimes (Gurnell et al., 2009). Each of the rivers selected for analysis descend steeply from high altitude sources; are not associated with major aquifers but are more responsive, surface water dominated and their catchments are typically characterised by glacial or alluvial deposits with relatively low permeability. Stream slope dictates the potential power available for sediment mobilisation and subsequent deposition (Church, 1992), and coupled with the timing and magnitude of flow events dictates the morphology of channel and floodplain. Surface water dominated regimes in England and Wales exhibit wide variations in flow over short time frames, with the variance most pronounced in steep catchments providing rapid runoff of surface waters. This flashy hydrology is a key element in maintaining high levels of habitat turnover (and ERS) by resetting the successional clock. By comparison ground water dominated rivers have buffered flow variations (e.g. Wood et al., 2001), applying fewer turnover pressures on colonising riparian vegetation (Naiman and Decamps, 1997, Nilsson and Svedmark, 2002), thereby eliminating the potential for ERS establishment.

The best fitted models of factors predicting ERS area and density demonstrate that the habitat persists due to hydrogeomorphological processes and landscape factors; the river drives the form of terrestrial floodplain. The available area of habitat is positively influenced by the number of individual Q_{10}, high flow events, exceeded $\leq$ 10% of the time over the 20 year discharge record (a parameter that occurs in four of the possible seven models). These refer to the episodic, resetting events that have the potential to prevent succession or induce habitat turnover. Q_{10} events necessarily occur only $\leq$ 10% of the time, but their distribution through the hydrological year will dictate the level of habitat restructuring. A more stable regime will exhibit fewer Q_{10}

events, and therefore riparian areas will have longer stabilisation periods between them, allowing the development of more complex vegetation.

ERS density is positively influenced by increased stream slope (a parameter consistent across all possible models), which dictates stream power through the supply of kinetic energy. Steeper slopes increase stream power, resulting in greater sediment mobilisation potential, moderated by sediment calibre and erodibility (Howard et al., 1994). Local hydrogeomorphology dictates where mobilised sediments are deposited and the distances they are transported. Erosion, mobilisation and deposition occur very locally, within ≤ tens of metres (Bridge, 2003). ERS density increases with slope as raised power increases sediment processing, but the distances involved remain low. The absence of regime shape in the model outputs indicates that timing is not a factor in structuring ERS, although there are indications that magnitude may be (according to weaker models), a reflection of sediment transport potential (Gurnell et al., 2009).

Whilst natural characteristics of river systems are shown to predict the extent and distribution of ERS habitat, anthropogenic alterations reduce ERS provision and densities (again supporting observations of historical losses). The reduced ERS area modelled for rivers where water abstraction occurs supports long-term observations of changes in channel form. Abstraction is associated with a reduction in the area of habitat, a consequence of stabilised and lowered long-term flows imposing fewer pressures on riparian vegetation. Consequently, the permanently vegetated zone encroaches onto existing ERS, stabilising the sediments and further reducing restructuring potential under high flows. A gradual process, its effects have been observed on wandering and braided rivers globally (Petts, 1996, Whiting, 2002). The shape of the daily regime may not change, Q_{10} events may still occur to rework non-stabilised sediments, but reduced flows enhance floodplain stability and therefore limit the sediment supply for mobilisation. ERS density models indicate a negative response to impoundment. Impoundment has a dual effect of interrupting downstream sediment transportation and stabilising downstream flows (reducing the habitat-restructuring flashy events). This has been shown to decrease rapidly within-channel sediments post completion (Ligon et al., 1995, Petts and Gurnell, 2005, Graf, 2006, Greenwood et al., 1999). The data included here indicate that the reduction is sustained (the most recent impoundment in the dataset occurred in 1981), with the resource reaching a new, reduced equilibrium, relative to rivers where the regime is unaltered.

2.4.1 Conclusions

Past degradations of English and Welsh ERS largely occurred as a result of intensive management schemes in the latter half of the 20th Century (Brewer et al., 2000). These resulted in reductions or the entire removal of the ERS resource from many rivers. The current distribution (as identified for the first time in the ERS inventory created herein) is found in both near-natural rivers and, to a lesser extent, anthropogenically altered systems. Interruptions to the continuity of sediment transportation and urban pressures have largely removed the resource from many low altitude rivers. Three natural influences enforce a natural geographic limitation on the distribution of ERS, with steep stream slope, flashy flow regimes and supplies of erodible sediments maintaining the resource's abundance and complexity. The current distribution represents a relict level of the resource, which remains vulnerable to anthropogenic disturbance, but it is not clear whether a new equilibrium has been reached following the completion of major engineering and impoundment projects.

In the short-term, the priority for the resource is to maintain and protect current distributions of ERS, and to establish whether they are stable, declining or increasing. The database of the resource will act as an essential reference tool in this process. The negative impacts of impoundment and abstraction are well known for both aquatic and riparian ecosystems, and the models of ERS distributions further emphasise the care that should be employed when these are considered for natural systems.

River restoration projects indicate that complexity of channel morphology (with associated ERS) can be reintroduced longitudinally (Caruso, 2006, Jahnig et al., 2009, Jansson et al., 2007), although in a crowded landscape the multiple pressures on floodplains predicate against fully restored connectivity. But even partial restoration may serve to improve ERS distribution. Field observations of both the Severn and the Wye established that ERS persists downstream of low-impact ‘soft’ floodplain alterations (such as earth embankments), suggesting models for future application on degraded rivers. Whilst the resource has declined it exhibits an inherent resilience where some level of natural state persists and where environmental conditions are conducive.

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3

The role of habitat connectivity in maintaining complex riparian communities of specialist invertebrates

Sampling of specialist invertebrates (Coleoptera) from riparian gravel deposits found alongside five Welsh rivers was used to derive predictive models of community distribution based on predetermined connectivity parameters. Species were assigned to functional guilds based on morphological traits associated with dispersal ability. The influence of habitat complexity upon these guilds was tested using Generalised Linear Modelling. Of the three identified groups, that containing the rarest species showed strongest dependence on a highly connected and complex habitat mosaic (and possessed weak morphological adaptations). Specialist, but widely distributed species showed no dependence on a well connected habitat and possessed strong dispersal favouring adaptations, with apparent niche partitioning between morphologically similar species exhibited via a change in longitudinal composition of communities. Finally, ubiquitous generalist species showed a negative response to increased habitat complexity (with concurrent decreased morphological adaptations) but a positive response to patch isolation. Rarity appears to be a function of reduced physical adaptations (particularly reduced mobility) to the disturbance prone environment in some specialist species, which emphasises their need for a spatially complex and linked mosaic of undisturbed habitat.

3.1 Introduction

Terrestrial arthropods inhabiting dynamic riparian ecotones have been studied widely in Europe and Fennoscandia (Desender, 1989, Anderson and Hanssen, 2005, Paetzold et al., 2006, Sadler and Bates, 2008). The habitat with which they are associated is characteristically unstable, nutrient deficient, subject to extremes of temperature and frequently reworked by flood events (Sadler et al., 2004, Bates et al., 2009). Associated with continental scale braided river systems (Petts et al., 2000) as well as headwater upland stream systems (Benda et al., 2005), the habitat typically decreases in abundance with stream order, becoming finer and deposited within meanders, as a result of reduced sediment inputs, slower flows and decreased inclines (Bettess, 1994), these correspond to disequilibrium and equilibrium floodplains (Ward et al., 2002) The habitat is vulnerable to alterations to the natural river state (direct and indirect) and as such is associated with natural or scarcely modified streams (Bates et al., 2009). Limited distribution of the habitat necessarily constrains the distribution of associated stenotopic species, many of which have been classified as rare (Niemeier et al., 1997, Gunther and Assmann, 2005), and in the case of two UK species (*Thinobius newberyi* and *Meotica anglica*), endemic.

A problem for conservation practitioners is that no reliable assessment mechanism exists for predicting the quality of habitat, at either patch or matrix scale, except through physical sampling. Similarly there may be a temptation to focus on individual species which are of conservation concern. The conservation status of habitat mosaics is however better assessed by examining the health of resident communities (Kremen et al., 1993).

Exposed riverine sediments have a patchy and linear distribution. Any single patch may be at risk from stochastic flooding events which may also involve erosion and downstream deposition of some of the sediments, although in unmanaged systems the total amount of habitat will remain approximately constant, assuming the presence of flashy flows and fresh sediment inputs (Ward et al., 2002). Specialist arthropods can only persist by being able to survive or escape these major disturbance events and by being able to recolonise the habitat post inundation. In this context, a functioning riparian gravel bar resource is necessarily a well connected one, with susceptibility to isolation varying between taxa and functional guilds according to their life histories and dispersal capabilities (Tockner et al., 1998). Individual species may face increased pressures if the equilibrium state of habitat supply is altered. The grasshopper *Bryoderma tuberculata* (Fabricius) is found in metapopulations on riparian gravel bars in the European Northern Alps. Individual populations are subject to local extinction (as a result of habitat immersion or loss) and the metapopulation is reliant on the persistence of enough connected habitat to permit recolonisation. The metapopulation is therefore vulnerable to both catastrophic inundation events, eliminating multiple populations, and to reductions in flooding, producing a long-term reduction in habitat (as bare gravel is vegetatively colonised) (Reich, 1991, Stelter et al., 1997).

Typically, stenotopic species have phenological and morphological adaptations that enable them to survive the demands of their environment (Adis and Junk, 2002, Bates et al., 2009). These may increase their response to immediate inundation threats (presence or size of wings and wing muscles) (Desender, 2000), or enhance seasonal avoidance (inland quiescence/diapause during flooding season) (Andersen, 2006).

The older and more stable the environment that specialist species inhabit, the greater and more pronounced these traits, demonstrating that they have evolved to improve survival and fitness. There is also scope for within-species variation, according to the strength of environmental influences on individual populations – as shown by the increasing percentage of macropterous (large winged) *Bembidion tetracolum* (Say) with proximity to stream channel (Siepe, 1989), or wing muscle occurrence in Central Amazonian Cicindela (Coleoptera) decreasing with distance from and elevation above the river (Adis and Junk, 2002).

Successful species actively utilise the environmental cues (such as rising water) available in the habitat to prompt inter-patch movement, an adaptation symptomatic of both their specialisation and fitness for the environment which they occupy. These cues may prompt seasonal (e.g. light cues initiating movement to overwintering habitat (Andersen, 1989, Andersen, 2006)) or rapid, stochastic (Bates et al., 2009) movements, but both responses presuppose the physical ability to make the movement. An aquatic parallel can be seen in the Ferocious Water Bug (*Abedus herpeti,* (Hidalgo)). To avoid scouring during high flow events, individuals exit the stream channel and move inland following rainfall cues of fixed length and intensity (Lytle, 1999). Bates also argues that the open habitat associated with riparian gravels and shingles requires adaptation to avoid predation, either by avoidance (typically fossorial lifestyles) or escape, through rapid movement across the surface (Lindroth, 1974, Desender, 1989).

Species-specific studies have shown that there is variation in the strength of behavioural and morphological adaptations, however these studies are by no means exhaustive. The click beetle, *Fleutiauxellus maritimus* (Curtis) exhibited no between-patch movement, in contrast to the ground beetle *Bembidion atrocaeruleum* (Stephens) which moved between patches, up to several hundreds of metres, in the same study (Bates et al., 2005). The wolf spider *Pardosa agricola* (Thorell) exhibits a limited, short-range dispersal insufficient to allow cross-channel movement and therefore potentially isolating populations (Lambeets et al., 2010). It is therefore likely that the type and strength of adaptations impact upon a species' likelihood of surviving individual inundations. In a study of Carabidae (ground beetle) recovery following a 100 year flood on the River Isar in Germany, population recovery was related to the avoidance adaptations and to the timing of the lifecycle. Bembidion species were adults at the time of the flooding and able to escape, rapidly recolonise and reproduce in a competition free environment, their numbers rapidly exceeding previous records. In comparison *Nebria picicornis* (Fabricius) was in its pupal (and therefore vulnerable) stage at the time of flooding and showed no recovery during the study (Hering et al., 2004). Microspatial positioning has been shown to structure specialist communities (Bates et al., 2007a) with elevation above stream level acting as a strong predictor of species occurrence, an observation repeated in spatially distant populations (Desender, 1989).

Although the environmental requirements of a few species have been well studied, allowing limited predictions of distribution and presence/absence to be made, for the majority of species there is a paucity of autecological data. In the absence of such information, more generalised knowledge must be applied. A common approach when studying arthropod communities is to infer functionality from morphology i.e. make assumptions on a species' requirements and behaviour based on physical adaptations to the environment in which it is found (Adis and Junk, 2002, Ribera et al., 2001, Jelaska and Durbesic, 2009, Moretti and Legg, 2009). Vegetation structure, temperature regimes, topography and prey emergence or preference are likely to affect both the trophic and spatial positioning of any given species, whilst physical constraints (e.g. apterous or alate) and species-specific behaviour will inform dispersal propensity (Auclerc et al., 2009). In the context of a dynamic riparian habitat here studied, the ability of individuals to survive disturbance events will be a key determinant in a species' persistence. A strong argument can be made that survival probability will be predicted by functional traits such as size, trophic position, reproductive strategy and geographical distribution. The multiple and combined traits will act to increase or reduce a species' fitness within any local environment (Barbaro and van Halder, 2009, Pizzolotto, 2009). Due to the high levels of disturbance encountered with ERS, it is possible to hypothesise that the type and strength of adaptations employed to minimise the impact of this can predict distributions under differing regimes.

The paucity of species-specific knowledge inhibits our understanding of communities' susceptibility to isolation, and the importance of dispersal potential within this fragmented and patchy habitat, particularly if the matrix becomes degraded. Connectivity parameters, including responses to the extent, density or relative isolation of habitat patches, may well be the best assessment tool available for multiple species inhabiting this environment, allowing morphological adaptations to be matched to their perceived usefulness within the context of a dynamic and sometimes chaotic habitat.

3.2 Study aims, objectives and hypotheses

1. Assess the role of habitat complexity in predicting the distribution of specialist riparian Coleoptera.
2. Determine functional groups from morphological characteristics and test the accuracy of these defined groups by modelling their distributions from field data.
3. Assess the relationship between functional groups, habitat complexity and levels of specialisation.

Objectives

- Identify ERS habitat areas for sampling, and assign connectivity and disturbance parameters.
- Measure and analyse morphological characteristics of abundant species found within the habitat and areas of between-species variation.
- Investigate assemblage structure and assign species to functional groups using morphological data and abundance correlations.
- Model the role connectivity and disturbance parameters have in predicting patch scale assemblage structure.

Hypotheses

The hypotheses of this chapter are that morphological characteristics will be common to functional groups and that this commonality will be reflected in model outputs, with characteristics indicative of potential mobility and therefore distribution within the habitat patches studied.

3.3 Methodology

3.3.1 Study sites and sampling methods.

Twenty two sites were sampled from five rivers (Figure 3.1) rising in the mid-Welsh Cambrian mountains which are subject to a high annual and year- round precipitation (relative to the majority of the inland British Isles). The rivers included sites covering both natural and modified streams, all maintaining a level of flashiness needed for the persistence of exposed river sediments. Each of the five rivers contains characteristic areas of within channel and riparian gravel bars which decrease in frequency with increasing distance from the headwaters (Chapter 2). Intensive flood controls or channel alterations are absent until the rivers Vyrnwy, Severn and Wye reach the English borders in Shropshire and Herefordshire, and areas of more dense human habitation. The Tanat and Banwy are tributaries of the Vyrnwy, which in turn is a tributary of the Severn. The Wye has no physical connection with any of the other rivers in the study. Sampling points were identified from each of the rivers' headwaters until they merged with another larger river, or (for the Severn and Wye) to the point of the last accessible area of coarse gravel habitat. Aerial photographs were cross referenced with pre-existing River Habitat Surveys provided by the Environment Agency, to select the study sites prior to site visits, to assess accessibility and suitability. Site area and nearest patch of habitat up and downstream (from midpoint of site), along with the total area of habitat within 1km, and the number of habitat patches within 1km were measured using Ordnance Survey maps (accessed via Digimap). These parameters were intended to measure a site's relative isolation and the complexity of the matrix which it inhabits. Distance of site from headwater was also included to establish the strength of influence of longitudinal factors in altering community structure. Field observations established that all sites were characterised by an area of early successional annual or biannual vegetation emerging from bare gravel, typically *Polygonum persicaria* (Redshank), *Digitalis purpurea* (Foxglove) and the invasive *Impatiens glandulifera* (Himalayan Balsam) giving way to perennial woody vegetation with increasing distance from the stream. Adjacent land use was agricultural, with sheep grazing at higher altitudes and cattle at lower. Sampling was only conducted on habitat patches from which livestock has been excluded, to avoid potential degradation by trampling and nutrient enrichment (Bates et al., 2007b).

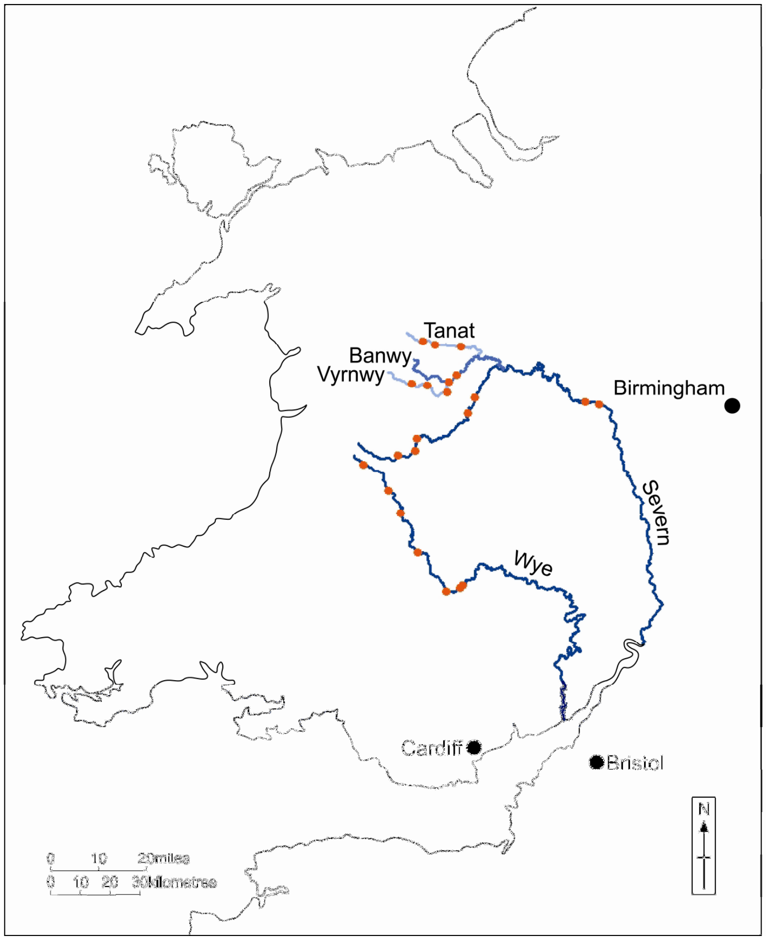


Figure 3.1: Distribution of sampling points (marked by red dots) on the rivers Banwy, Severn, Tanat, Vyrnwy and Wye, including a range of distance downstream, disturbance and connectivity levels,

Sampling took place fortnightly from 15 May – 21 August 2009 with six pitfall traps (0.3L capacity with a 50:50 ethylene glycol: water preservative solution) placed in a grid at 1m and 2m from the water's edge on each site (Lott and Eyre, 1996, Vanbergen et al., 2010, Boscaini et al., 2000). Flooding events caused the loss of some traps and therefore data at all sites randomly throughout the study period. Analysis was therefore conducted on pooled seasonal data, a standard procedure when sampling such a highly dynamic habitat (Lambeets et al., 2009). When traps had been lost by flooding (or by animal or human interference) they were reset. Although non-exhaustive (Andersen, 1995) and with a probable over representation of more mobile ground beetles and under-representation of cryptic/fossorial species (Baars, 1979, Bell, 1990) the methodology is a standard one to study ground-dwelling invertebrates. Further resolution could be obtained by combining pitfall trapping with a handsearching method (Andersen, 1995).

Upon collection, samples were stored in 70% ethylene glycol prior to identification to species level in the laboratory. Samples were pooled by site and date prior to identification using appropriate keys (Tottenham, 1954, Joy, 1976, Luff, 2007, Lott, 2009) Identification adhered to current nomenclature (Duff, 2008). Where identification was uncertain, colleagues within the University of Birmingham provided confirmation. Voucher specimens were carded and are retained at the University of Birmingham, whilst all samples were transferred to 70% IMS for storage. Following identification, specialist species with a known dependence on the habitat for at least part of their lifecycle were identified (Eyre and Lott, 1997, Sadler and Bell, 2002, Luff, 2007). Species with no known affinity to the habitat were excluded from the analyses.

3.3.2 Statistical analyses.

In an adaptation of the methodology used by Ribera et al. (2001), six specimens of each of 12 species, from the ground beetle (*Bembidion atrocaeruleum, B. decorum,* Zenker*), B. prasinum* (Duftschmid)*, B. punctulatum* (Drapiez)*, B. tetracolum, Paranchus albipes* (Fabricius)*, Perileptus areolatus* (Creutzer)), click beetle (*Fleutiaxellus maritimus, Negastrius sabulicola* (Boheman)*, Zorochrus minimus* (Boisduval and Lacordaire)) and rove beetle (Staphylinidae) (*Aloconta cambrica* (Wollaston)*, Deleaster dichrous* (Gravenhorst)) families were selected and their wing, leg and body (front of pronotum to tip of abdomen) measured to provide morphological data of leg: body and wing: body ratios. Measurements were Log_n transformed prior to exploration and analyses via ANOVA, with a post hoc Scheffe test applied (selected as the most conservative available) (Fowler et al., 1998). Species were then grouped according to morphological similarity. To test the validity of these groupings, Spearman's rank coefficients (as the data were non-parametrically distributed) were derived for their presence and abundance, confirming the probability of the associations; the morphological groups were expanded by applying Spearman's coefficients for all specialist species within the samples.

Data exploration was initially conducted 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., 2009). As a result of these preliminary analyses, data from site seven were rejected from the final analysis as they formed unrepresentative outliers in the dataset due to low retrieval rate. Rejection was justified to prevent over-dispersion in the modelling process (Hilbe, 2007).

The impact of predefined connectivity parameters on functional groups' abundance and distribution was examined by Generalised Linear Modelling (Quinn and Keough, 2002) once spatial influences (i.e. that proximate communities show similar abundances) had been ruled out by applying a Mantel test (Legendre and Legendre, 1998) to the data (F: 0.143; df: 1; p 0.71). GLM were run as the most appropriate method for count data, ensuring ecological valid whole values in the final outputs. Similarly, negative values were not ecologically valid in final models, so Poisson rather than Gaussian distribution was applied (Zuur et al., 2007).

The most important explanatory variables were selected using a drop 1 selection process to select the most probable, significant combination of variables (Zuur et al., 2007). Model validation was performed visually using plots of standardised residuals against fitted values to assess homogeneity, histograms of the residuals to verify normality, plots of residuals against each explanatory variable to establish independence. No patterns were visible in any of the plots.

Akaike's Information Criterion (AIC) (Burnham and Anderson, 2002) was used to validate and select possible models via weighting. The process (see Chapter 2) allows identification of models lying within 95% confidence intervals, as well as a single optimum model.

3.4 Results

Of the 14,879 Coleoptera sampled, 12,883 were classified as wholly or partly specialist species associated with the habitat (86.6%).

3.4.1 Morphological grouping

The Log_n transformed morphological measurements of wing, leg and body length were used to derive ratios as indications of the strength of mobility.

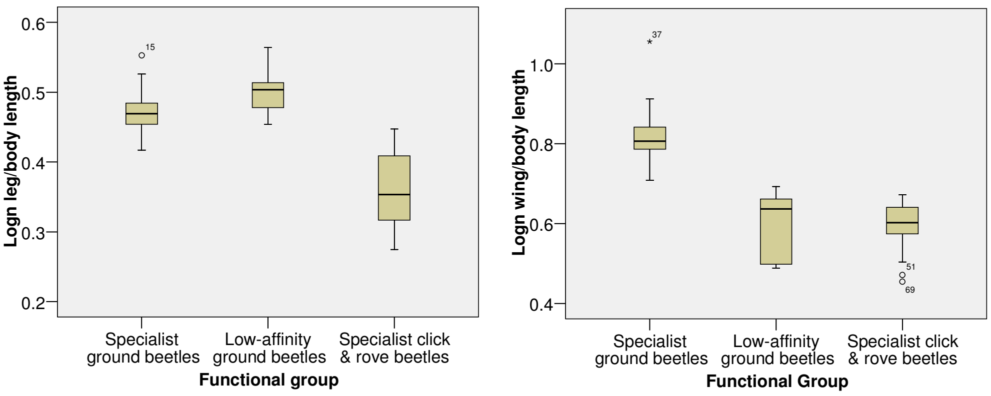
One-way Analysis of Variance showed that between species variation in leg-body length rations were significant at the < 0.001 level (F:50.172; df: 11), as were those between wing and body length (F:33.508; df: 11). Post-hoc testing split the species into two distinct groups when leg:body length ratios were compared:

Group 1: Five *Bembidion sp.*, *P. albipes*

Group 2: *F. maritimus*, *N. sabulicola*, *A. cambrica*, *D. dichrous*

(Z. minimus and *P. areolatus* showed an overlap between the two groups)

When the same post hoc testing was applied to wing: body length two slightly different groups were derived. The first contained *P.albipes, B. tetracolum*, *A. cambrica*, *D. dichrous* and the three click beetle species. The second contained the remaining ground beetle species. The two analyses of variance allowed separation of the 12 species into three nominal functional groups – (i) specialist ground beetles (*B. atrocaeruleum*, *B. decorum*, *B. prasinum*, *B. punctulatum* and *P.areolatus*), with known high levels of affinity to the habitat. (ii) low affinity ground beetles (*B. tetracolum* and *P.albipes*), associated with damp habitats, but not exclusively ERS, and (iii) click and rove beetle specialists (*A. cambrica*, *D. dichrous*, *F. maritimus*, *N. sabulicolis* and *Z. minimus*), also with known high levels of affinity to the habitat. When the data from these three groups was pooled, further analysis of variance indicated both leg and wing ratios to body length were significantly different at the $p < 0.001$ level (F: 82.04; df: 2 and F: 102.62; df 2, respectively). Post-hoc testing showed significant differences between the wing: body ratio of specialist ground beetles and low-affinity ground beetles ($p < 0.001$) and click and rove beetle specialists ($p < 0.001$). There was no significant difference between low-affinity ground beetles and click and rove beetle specialists. When variance was analysed for leg:body length ratio, significant difference was detected between all ground beetles and click and rove beetle specialists ($p < 0.001$). Visualisation reinforces these separations (Figure 3.2) indicating low levels of morphological overlap.



a) b)

Figure 3.2: Box plots (with 95% confidence intervals) of functional Coleopteran groups derived from Analysis of Variance of Log_n transformed morphological variations, a) variation in Leg: Body length ratio by nominal functional group, and b) variation in Wing: Body length ratio by nominal group. Outlying data points are included, labelled with their sample number.

Spearman Rank coefficients of the species were derived to act as verification for morphological separations. Significant correlations were observed within the morphologically grouped species (Table 3.1) and the process subdivided specialist ground beetles into two groupings, *B. atrocaeruleum*, *B. decorum* and *B. tibiale*, and *B. punctulatum* and *B. prasinum*.

The two processes, morphological comparisons of the 12 species, and Spearmans ranking of the larger dataset allowed species to be assigned to one of four groups (Table 3.1) which formed the datasets for inclusion in the modelling process. This process then allowed adaptations, habitat requirements and optimum position within the river corridor to be assigned to functional groups (Table 3.2).

Table 3.1: Functional groups (with conservation status) derived from morphology and Spearman's correlations.

Specialist ground beetles 1	Specialist ground beetles 2	Low-affinity ground beetles	Specialist click and rove beetles
Bembidion atrocaeruleum	*Agonum marginatum*	*Agonum emarginatum*	*Fleutiauxellus maritimus*
Bembidion decorum	*Bembidion prasinum*	*Bembidion tetracolum*	*Nagustrius sabulicola*
Bembidion tibiale	*Bembidion punctulatum*	*Paranchus albipes*	*Zorochrus minimus*
Perileptus areolatus			*Aloconota cambrica*
			Deleaster dichrous
			Hydrosmecta fragilis
			Hydrosmecta longula
			Neobisnius prolixus
			Philonthus rubripennis
			Stenus guttula

3.2.2 Generalised linear modelling

Four groups were modelled with Poisson distributions (with specialist ground beetles split according to their grouping by correlation coefficients). Best fitting models were selected following AIC scoring and Akaike weighting to derive all models lying within the 95% credibility interval (Appendix 2), summary outputs are presented in Table 3.3.

Specialist ground beetles 1: the best fitting model includes the distance from headwaters of the sampling point (AIC 82.61), with abundance decreasing downstream (d: 8.17: df: 19; $p < 0.005$). (Henceforward referred to as headwater ground beetles).

Specialist ground beetles 2: the best fitting model (AIC 77.77) gives a positive association with distance downstream of the headwaters (d:27.99; df 19; $p < 0.05$). (Henceforward referred to as floodplain ground beetles).

Specialist click and rove beetles: the best fitting model (AIC 93.49) predicts increased abundance with increased habitat complexity (measure by number of gravel bars within 1km) and decreasing abundance with distance from headwater (d: 21.07; df: 19; $p < 0.005$).

Low-affinity ground beetles: the best fitting model (AIC 70.35) shows abundance increase with distance to the nearest downstream habitat patch (d: 9.71; df: 19; $p < 0.005$).

Table 3.2: Summary of functional groups' morphology, habitat requirements and corridor positioning

Group	Location	Connectivity	leg:body	wing: body
Headwater ground beetles	Headwaters	Low	Long	Long
Floodplain ground beetles	Floodplains	Low	Long	Long
Low-affinity ground beetles	Ubiquitous	Isolated	Long	Short
Specialist click and rove beetles	Headwater	High	Short	Short

Table 3.3: Summary of GLM outputs for effects of connectivity parameters on functional groups.

	AIC	Deviance	d/df*	P
Headwater ground beetles	82.61	8.17	0.44	< 0.005
Floodplain ground beetles	77.77	27.99	1.47	< 0.05
Low-affinity ground beetles	93.49	21.07	1.05	< 0.005
Specialist click and rove beetles	70.35	9.71	0.51	< 0.005

*d/df provides measure of dispersion; a value <2 indicates acceptable levels of dispersion within data

3.5 Discussion

Predicting the environmental factors that govern the structure of arthropod communities would greatly aid their conservation, yet, as this chapter demonstrates, real-world interactions are complex and require multiple approaches when explored.

Viewing the species within the context of morphological groupings allows a corroborative pattern to emerge, confirming studies showing that functional form of species has a controlling role on their distribution within the habitat studied (Desender, 1989). The ratio of wing and leg to body length produces distinct groups with little overlap. It has been suggested that the leg:body length ratio is an indicator of feeding strategy (Davies, 1953), hence the actively predacious ground beetles possessing longer legs in relation to their body length than other species (*P. aureolatus* overlaps the groups, which may be a function of small body size (2.3-2.8mm) and a proportionally greater margin of error when measuring. When combined with separation by wing length versus body length, the groups identified here split along specialist rather than familial lines, with specialist ground beetles having longer wings that low-affinity species, which show no significant difference from specialist click and rove beetles.

Based on these identified traits, the initial observation is that distribution may be indicated by the level of morphological adaptation exhibited by a guild. Consequently, the specialist ground beetle species (headwater and floodplain) possess longer legs and larger wings and show a widespread (if local) distribution within the national habitat resource (Luff, 1998). They are the most adapted of the three groups identified, both for disturbance avoidance and for between patch movement. Isolation of individual populations is likely to be less of a threat for this group, due to their enhanced locomotive and apterous abilities. Although the low-affinity group possess the longer legs of all ground beetles, their wing length is not comparable to that of specialists, suggesting that they are less well adapted to escape the irregular, flashy flows found in headwater stream systems (where the most complex habitat is found). Despite the known increase in macroptery in riparian populations of *B. tetracolum (*Adis and Junk*, 2002)*, this apparently does not achieve parity with permanently resident specialist ground beetles This group also contains the largest species studied (*P. albipes* and *A. emarginatum,* 6.5-8.8mm and 7.5-9mm, respectively) and larger size has been suggested as an indicator of low disturbance tolerance (Ribera et al., 2001, Kotze and O'Hara, 2003). Coupled with the increased numbers of specialists within these connected patches, there is scope for further exploration of the role of competition in suppressing the numbers of generalist species.

The separation (by Spearman's Correlation) of the specialist ground beetles into two groups is explained when their distribution is modelled, with the second group (1b, containing *B. prasinum* and *B. punctulatum*) preferentially occupying a spatially removed habitat, downstream of those species associated with the headwater habitat (although never to the exclusion of the latter group). In the light of known morphological differences possessed by these two species (especially greater flattening of body (Luff, 2007)), they would have a competitive advantage in the finer sediments associated with the downstream habitats in comparison to their more robust relatives. Downstream patches within the study were also physically the most isolated, typically by kilometres rather than metres (Chapter 2), so a heightened level of mobility may also be inferred for these two species. Whilst both groups' optimum models include the distance downstream as an explanatory variable, the headwater specialist ground beetles (Table 3.3) exhibit a negative response, whilst the floodplain specialist ground beetles (Table 3.4) exhibit a positive response. The low-affinity ground beetles are ubiquitous across sites, but their distribution is the most confusing modelled (Table 3.5), showing a positive response according to the distance of the nearest habitat patch downstream (increasing with isolation). This can be an indication of a lack of reliance on well-connected habitat, and indicative of the species' casual affinity to the resource. Further data are required for this group to be able to describe controls on its distribution with any ecological certainty.

As well as being separated morphologically, specialist groups exhibit differing predictive environmental parameters in models. The click and rove beetle specialists possess significantly shorter legs and wings in relation to their body length, suggesting reduced fitness for rapid and sustained disturbance avoidance. Their fidelity with the habitat however is established, coupled with higher levels of rarity (taken from conservation status designations). It has been repeatedly demonstrated that there are species-specific levels of inundation tolerance within specialist invertebrates, and that this tolerance is largely a function of adaptation (Bonn et al., 2002, van Looy et al., 2007, Paetzold et al., 2008). The contention of this study is that there is a gradation of adaptation within specialist species that determines the probability of long-term population persistence in a compromised habitat. Those species with primarily behavioural adaptations (i.e. the click and rovef beetles which tend to occupy habitat elevated above frequently inundated sediments) become disadvantaged when physical adaptations are required for active avoidance. Although not included in the assemblage identified here, a strong comparison can be made with *Lionychus quadrillum* (Duftschmid) and *Elaphropus parvellus* (Dejean), both species associated with exposed riverine sediments, but found in sandy deposits on higher points within the habitat (Lambeets et al., 2009). Reduced physical adaptations will increase the dependency of the group upon a well-connected habitat (as indicated in their model, Table 3.4), minimizing the need for prolonged flight or in-channel movement. This form of ERS is associated with headwater reaches, which explains the negative response to distance downstream which is also included in the model. The more abundant and widely distributed specialist ground beetle species are therefore arguably the guild best adapted to the dynamic habitat, accounting for their success, a trait already identified by Lambeets et al. (2009) for *B. decorum*. Specialist ground beetles' increased dispersal potential reduces the requirement for a very complex habitat mosaic and increases the likelihood of the colonisation/recolonisation of any single habitat patch, post inundation or deposition.

This research suggests that connectivity plays an important role in predicting the Coleoptera assemblages present on the exposed riverine sediments in the system studied. Rarer species with strong affinities to the habitat appear most dependent on its least abundant form, the well-connected upland systems found only in the first few kilometres of the rivers studied. Behavioural rather than physical adaptations determine their specialisation, resulting in reduced dispersal ability and an absence from poorly connected habitat mosaics. Local populations within this group will be doubly vulnerable to stochastic inundation events due to extinction potential and reduced recolonisation likelihood. Other specialist species are however more successful at inter-patch movement and are consequently both more abundant and widely distributed, with further morphological variation creating subdivisions of specialisation and enhancing longitudinal changes in assemblage composition. Low-affinity species meanwhile exhibit an opportunistic utilisation of the resource, but the apparent suppression of their abundance in the optimum habitat suggests that they are at a competitive disadvantage in this environment, and that their presence within any patch is also likely to be a function of adjacent habitat suitability.

3.5.1 Conclusions

This preliminary study on the modelling potential for functional guilds demonstrates the potential of the methodology for gaining a greater understanding of the environmental requirements of arthropods. Even with a constrained database, clear trends can be demonstrated which allow functional guilds to be postulated and corroborated. For conservation purposes, the importance of a complex and spatially coherent habitat matrix is demonstrated for rarer species, an essential consideration in future stream restoration and management projects. Future research is also suggested; the need for a larger, contiguous dataset which would allow thorough testing of connectivity parameters and the role of morphology in defining functional guilds. Secondly, this study provides some indication that competitive exclusion (or suppression) may be occurring within the optimum habitat. Whether this is the case, or a correlation with a concurrent decrease in adjacent habitat quality can be studied, to identify how specialists are achieving better resource utilisation to the detriment of other species. Finally, variation in prey abundance may vary according to the area of habitat patch and the relative hostility encountered there. Microspatial studies have already shown variations in the positioning of Coleoptera within the habitat (Henshall et al., 2011), further work could be undertaken to examine how greater area may affect productivity and resource utilisation.

3.6 References

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4

The long-term value of high flow events in maintaining abundant and diverse riparian invertebrate communities

Using long-term datasets of Coleoptera assemblages found at Llandinam Gravels on the upper River Severn, Wales, river archive data were applied to establish the role of inter-annual flow variation on community composition. Generalised Linear Models were created for cursorial and fossorial specialists associated with the habitat and revealed differing effects of high and low flow events. Fossorial rove beetles (Staphylinidae) were shown to benefit most strongly from prolonged, low flows during the summer months and weakly from increased raised flows in the previous year, and that of sampling. Cursorial ground beetles (Carabidae) showed positive responses to high flow events occurring in the previous year and the year of sampling. It is suggested that different adaptations are responsible for the response variations, ground beetles utilise strong survival mechanisms and high dispersal abilities to colonise new habitat created in winter and move to optimum sites when threatened by local inundation. Rove beetles benefit in the short-term from local stability, but also require a level of habitat disturbance and movement cues. These results further demonstrate the importance of irregular flows within rivers to maintain complex arthropod communities. Long-term regional changes in weather patterns or anthropogenic alterations to river hydrology may change population levels and structure.

4.1 Introduction

Exposed riverine sediments are a highly disturbed habitat intrinsically reliant on variable flow regimes for their maintenance. They are characteristic of rivers that exhibit natural flow regimes where ERS habitat is created by repeated inputs of eroded sediments that are subjected to frequent reworking by high flow events (Plachter and Reich, 1998). As such they are devoid of established vegetation and autochthonous nutrients (Bates et al., 2009). Although highly disturbed, the habitat possesses a community of associated specialist invertebrates adapted to the pressures it imposes (Fowles, 1989, Sadler et al., 2004, Van Looy et al., 2005). Repeated disturbance resulting from high flow variability is the key pressure subjecting riparian biodiversity to repeated inundations (Plachter and Reich, 1998, Ward and Tockner, 2001). Whilst these are essential for long-term maintenance of the habitat, the potential for increased mortality in populations utilising the resource may rise with the severity of the flows. Anthropogenic alteration of rivers via channel modification, impoundment and abstraction lead to variations in the timing, frequency and magnitude of high and low flows, causing changes to the physical and vegetative structure of downstream riparian areas (Toner and Keddy, 1997). There is a growing body of evidence demonstrating that modification of natural flows also has a detrimental impact on ERS macroinvertebrate communities, via the removal of high-flow, habitat-creating events which promote dispersal (Hering et al., 2004), low-flow events that allow between patch movement by poor dispersers (Lambeets et al., 2010, Stelter et al., 1997), and overall reduction in diversity under regulated flows, which are typically moderated, causing channel and ERS stabilisation (Bonn et al., 2002, Lambeets et al., 2008, Paetzold et al., 2008, van Looy et al., 2007). With an increasing implementation of river restoration projects (Gunther and Assmann, 2005, Jahnig et al., 2009, Tockner et al., 1998), the long-term impact of naturally changing flow regimes is less well understood. This is an important omission as current global scenarios predict possible long-term changes to future river regimes, emphasising more frequent and aseasonal high magnitude events. This study aims to examine how specialist invertebrates react to natural or semi-natural variations in flow over several years, as an indication of how communities may be altered by long-term changes in flow regimes resulting from climate change.

4.1.1 Flooding responses of specialist invertebrates

Mechanistic and morphological adaptations to mitigate inundation pressures have been well documented in specialist species. These incorporate both avoidance and survival strategies, including submersion tolerance (Andersen, 1968), flight (Desender, 2000) and life-cycle plasticity (Plachter and Reich, 1998). Whilst these adaptive strategies provide advantages for specialists, they can be expected to be most efficient under an optimum, intermediate level of inundation frequency and magnitude (Ward and Tockner, 2001). A degree of mortality within populations subjected to disturbance is the norm; where the population possesses adaptive advantages, these losses are minimised and a viable population maintained (Petraitis et al., 1989). Where flow regimes are modified by regulation, populations of specialist species are impacted (Bonn et al., 2002, Lambeets et al., 2008, Paetzold et al., 2008) most likely due to a long-term reduction in the quality and quantity of available habitat as a result of flow stabilisation (Naiman et al., 2008). This may occur even with an increase in prey availability (Greenwood and McIntosh, 2008). Repeated extreme events have however potentially catastrophic consequences for patchily distributed populations with limited dispersal abilities, as shown by populations of the specialised ERS grasshopper *Bryoderna tuberculata* (Stelter et al., 1997) and spider *Pardosa agricola* (Lambeets et al., 2010). Both species exhibit vulnerability to repeated high flow events, which serve to cause local extinctions, their limited dispersal abilities preventing subsequent recolonisation of habitat from isolated populations. Extreme or prolonged changes in the flow regime of a river may also alter community structure (Gunther and Assmann, 2005), as species respond differently to events of changing duration and magnitude. ERS ground beetle populations exhibited a temporary collapse following a major flood event before rebounding to very high levels. Hering et al. (2004) suggested that this is indicative of the group's colonisation abilities.

ERS invertebrate studies have often focused on ground beetle assemblages and responses, due to their larger size, ease of identification and cursorial behaviour (Anderson and Hanssen, 2005, Desender, 1989). They do, however, represent only one component of the associated community, with often smaller and fossorial rove beetles providing a major contribution to the assemblage diversity (Eyre et al., 2001, Sadler and Bell, 2002). The adaptations of these two groups differ both morphologically and behaviourally (Chapter 3) allowing simultaneous use of the resource whilst minimising competitive interactions. As such, it is likely that their responses to different flow regimes will also vary.

4.2 Aim, objectives and hypotheses

This chapter uses a unique long-term dataset of ERS species abundance and river flow data to assess how inter-annual variations in the flow regime alter community structure. It has three linked objectives.

- Collate and categorise existing data sets from 2002 – present of specialist Coleoptera abundance from Llandinam Gravels, mid-Wales.
- Collate historic flow data from upstream river gauge station (Dolwen) to delineate variations in annual flow regimes, defining the duration, occurrence and magnitude of low, median and high flow events.
- Use statistical modelling to define models that best predicted the components of flow regime that exerted strongest influence on specialist fauna abundance.

The hypotheses of the study is that local populations of specialist Coleoptera associated with ERS will demonstrate long-term variations in abundance that can be explained by inter-annual changes in flow regime, with the magnitude, timing and duration of high and low flow events particularly important. It is also expected that the population responses will vary between taxonomic families.

4.3 Methodology

Samples of Coleoptera fauna were collected annually from Llandinam Gravels on the upper River Severn using a standardised hand searching and excavation method. The sample sites are within an extensive stretch of ERS found along the Upper Severn between Llandinam (SO025885) and Caersws (SO035925). Situated downstream of the confluence of the Severn and the impounded Clywedog, the river has a maintained minimum flow (Higgs, 1987), but retains enough features to be classed as a ‘wandering gravel’ river (Church et al., 1987). Samples from each of six adjacent habitat patches (Figure 4.1) were undertaken three times a year (between May-August) from 2002 – 2010 (excluding 2005 and 2007). Standard hand-searching protocol was followed, with two samples taken per bar (one upstream, one downstream) from a quadrat of 1.5m x 1.5m. The removal of surface armour and repeated wetting with water reveals all Coleoptera present, which are collected with an aspirator (Andersen, 1995, Bates et al., 2007a). All specimens were identified to species and classified by the level of fidelity to the ERS habitat (Sadler and Bell, 2002). Data used in this study was a combination pre-existing data, and new data collected in 2009-2010 to supplement the existing data set.

Flow data were obtained from the Centre for Ecology and Hydrology’s National River Flow Archive for the Dolwen gauging station (SN996851). From these data, exceedence levels of 10% (16.521 m^3/s^{-1}), 50% (3.862 m^3/s^{-1}), and 70% (2.569 m^3/s^{-1}) were used to derive high, median and low flow thresholds, and the number, duration and magnitude of events in each year calculated. These flow metrics were chosen as they define the extent and rate of habitat turnover, and dictate the level of abiotic inundation pressure imposed on ERS specialists (sensu Olden and Poff, 2003, Richter and Richter, 2000). The inundation parameters used in model creation encompass the mechanisms which both maintain and rework the habitat (which may be a beneficial process) and those which are potential threats to ERS invertebrates. The role of previous years' events is included as inundation or ERS restructuring may reduce reproductive success and suppress subsequent adult generations.

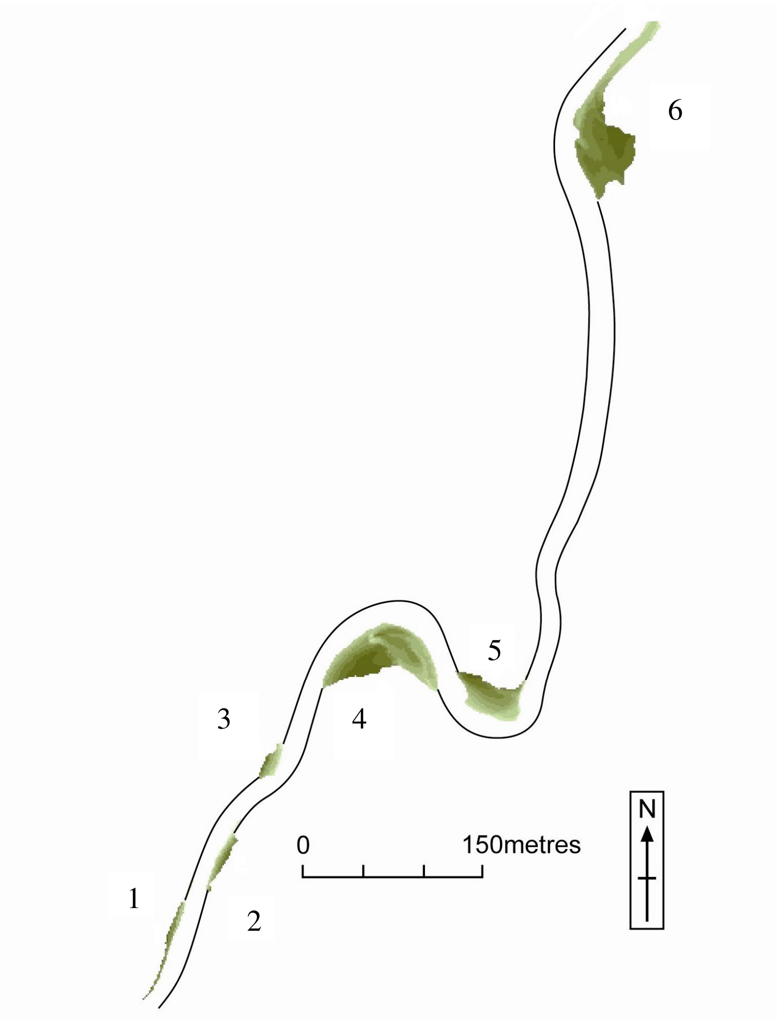

Figure 4.1: Relative positions of habitat patches 1-6 (based on DGPS survey taken in 2009) sampled from 2001-2010 at Llandinam Gravels, SO023873. Patch 1 is upstream, with the river flowing northwards.

Prior to the analysis the data were carefully explored to identify outliers in the explanatory variables, collinearity between the explanatory variables, and variables requiring transformation (Zuur et al., 2010).

The pool of hydrological variables that captured the key components of the flow regime (i.e. magnitude, frequency, duration and timing of high (Q_{10}), median (Q_{50}) and low flow (Q_{70}) events) were initially analysed using Spearman's correlation to identify those with strong relationships to species abundance metrics. Correlation was also used to seek explanatory variables that were strongly correlated ($Rs>0.4$). These were removed from the analyses.

Generalised Additive Models (GAM) were used to establish trends in abundances of Coleopteran families over time, allowing for non-linear changes. Generalised Linear Models (GLM) with a Poisson distribution were run for three response taxa: (i) ground beetle abundance, (ii) rove beetle abundance, and (iii) the most abundant ground beetle, *Bembidion atrocaeruleum*, and a range of explanatory (hydrological) variables. The most important explanatory variables were selected using a drop 1 selection process to select the most probable, significant combination of variables (Zuur et al., 2007). Model validation was performed visually using plots of standardised residuals against fitted values to assess homogeneity, histograms of the residuals to verify normality, plots of residuals against each explanatory variable to establish independence (after Zuur et al., 2010). No patterns were visible in any of the plots.

Optimum model selection from the range of possible models was undertaken using Akaike's Information Criterion (AIC) (Burnham and Anderson, 2002), with weighting also providing all models lying within a 95% confidence interval (see Chapter 2 for detail).

4.4 Results

The species data comprised 1604 rove beetles, 8547 specialist ground beetles (of these 6090 were single species, *Bembidion atrocaeruleum)*.

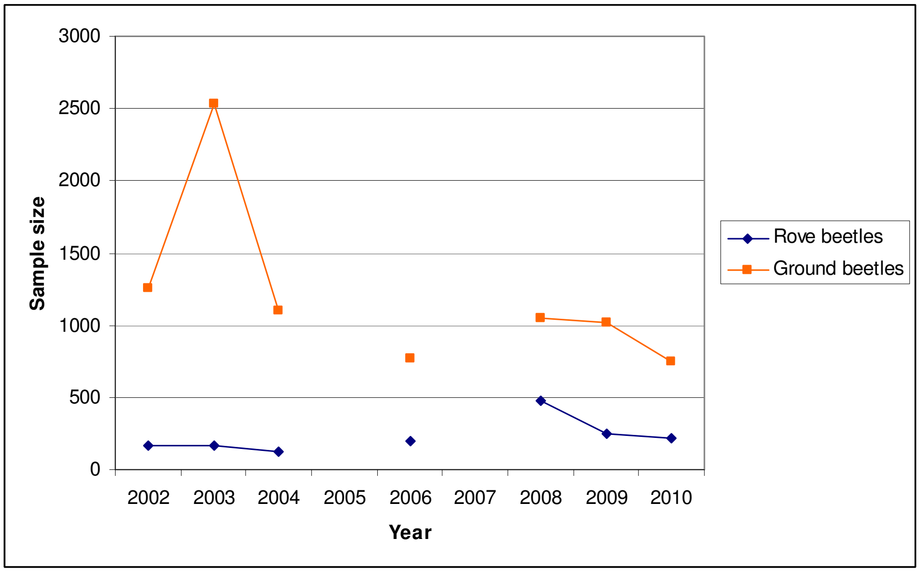

Figure 4.2: Abundance data of Coleoptera sampled from Llandinam Gravels 2002-2010 (data missing from 2005 and 2007), with ground beetle populations peaking in 2003 and rove beetles in 2008.

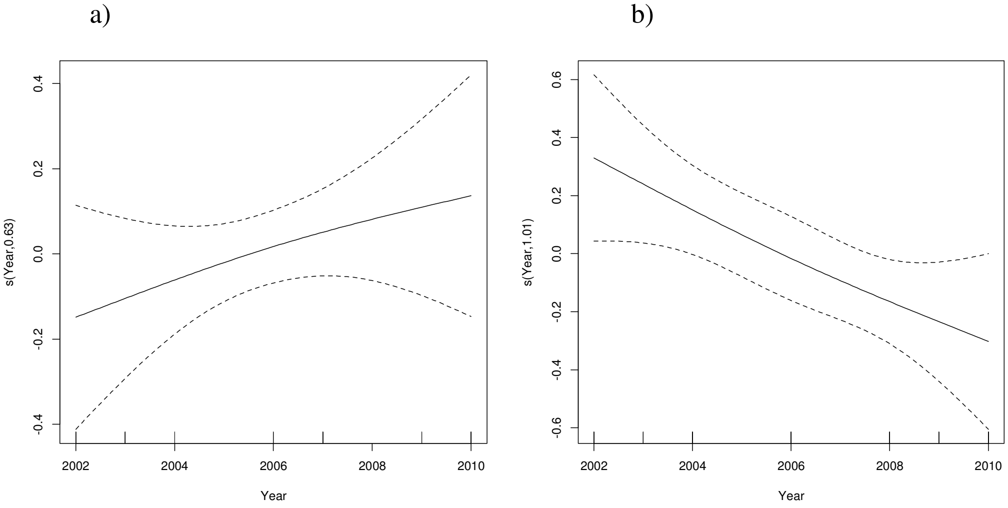

Figure 4.3: Abundance trends over time for rove beetles (a) and ground beetles (b). Rove beetles show a non-significant (F: 1.183; df 0.63; p: 0.25,) increase over time, and ground beetles exhibit a significant decrease (F: 5.222: df: 1.009; p <0.05,).

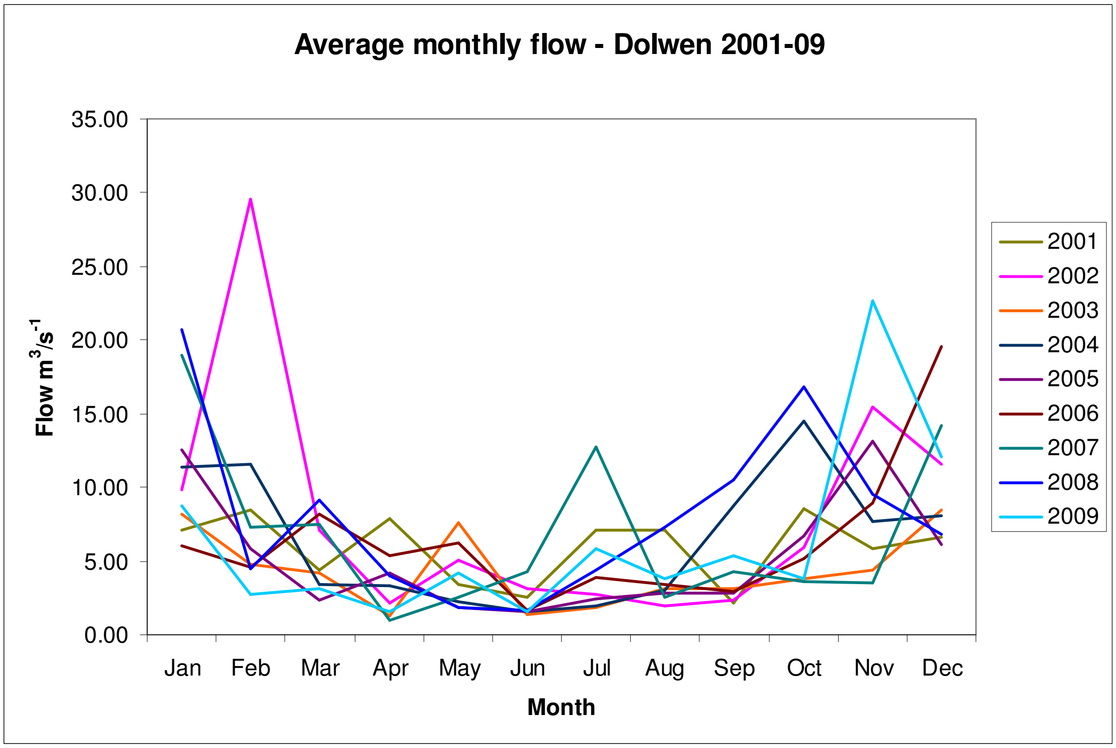

Figure 4.4: Average monthly flows recorded from Dolwen gauging station (2001-2009), showing heightened average winter flows, with raised individual events. The reduced summer flows are consistent, excepting extreme years such as 2007 and 2008.

Model validations were conducted using Akaike weights to produce a list of ranked models lying within the 95% confidence intervals (Appendix 3), with models of best fit (Table 4.1) selected by AIC weighting and significance. Rove beetle validations give the optimum model as the duration of the lowest flow in the year of sampling. Ground beetle validations produce a best-fitting model that is a combination of the number of high flow events in the previous year, the magnitude of the highest flow event in the previous summer and the duration of the maximum flow in the year of sample. *B. atrocaeruleum* validations produce a best-fitting model that is a combination of the number of high flow events in the previous year, the magnitude of the highest flow event in the previous year and the duration of the maximum flow in the year of sample. Rove beetles demonstrate the largest number (7) of possible models (within 95% confidence interval), half of which feature duration of lowest flow; ground beetles have five possible models within the 95% confidence interval, all of which contain the number of Q_{10} events and maximum magnitude of flow in the previous summer. *B. atrocaeruleum* has three possible models within the 95% confidence interval, all of which contain duration of maximum flow in the year of sampling

Table 4.1: GLM models for rove beetles, specialist ground beetles and *B. atrocaeruleum* using Poisson distribution (dLF = duration of lowest flow in sample season; p10% = no of 10% exceedence events in year before sampling; dMF = duration of maximum flow in sample season; MpSum = Magnitude of highest flow in summer before sampling; MpM = magnitude of highest flow in year before sampling).

	Model	Std E	Z	Pr	Dev	Dev/ df	AIC
Rove beetle	dLF	0.0047	2.893	**<0.005**	19.19	0.56	151.66
Ground beetle	P10% + dMF + MpSum	0.197	13.996	**<0.001**	33.6	1.05	201.06
B. atrocaeruleum	P10% + dMF + MpM	0.218	11.658	**<0.001**	46.27	1.45	204.67

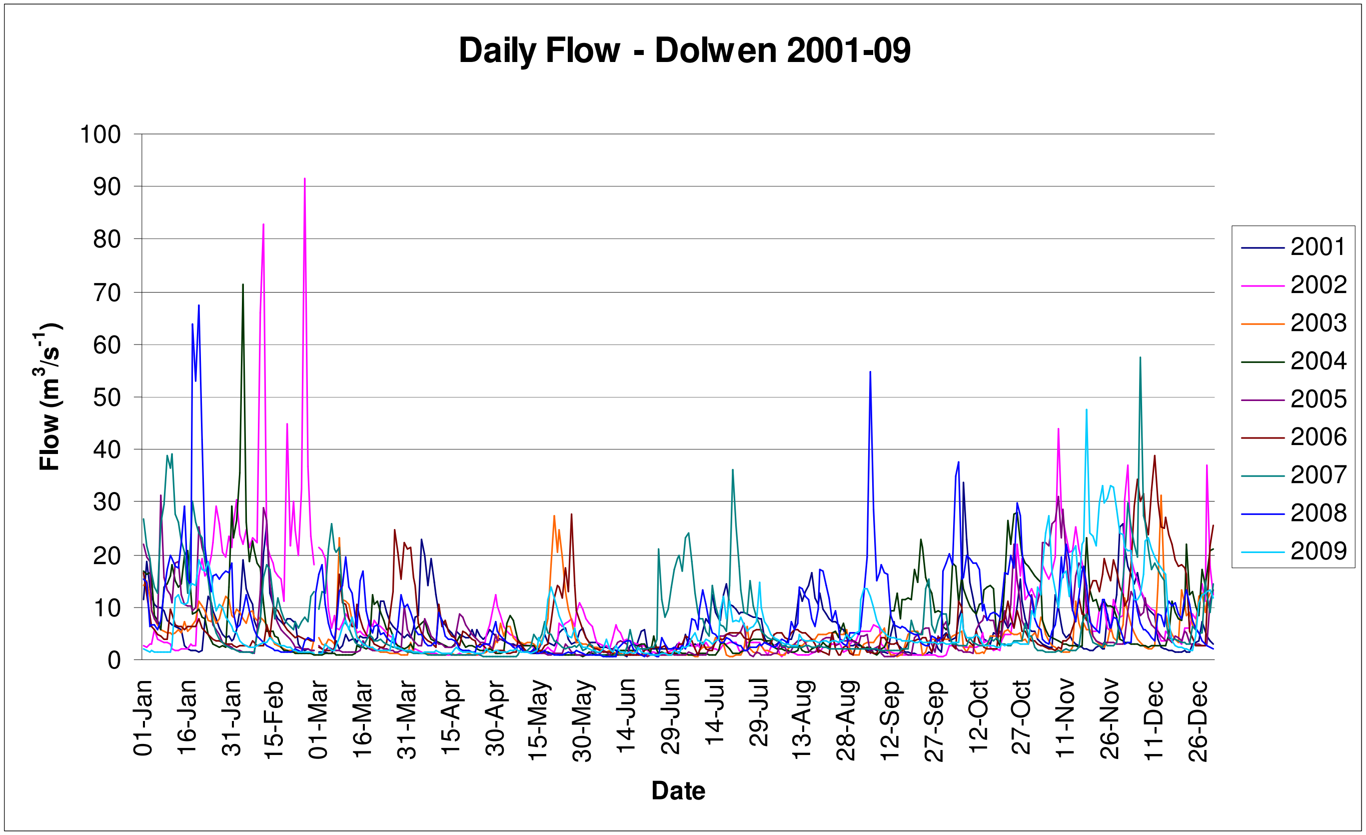

Figure 4.5: Daily flows recorded from Dolwen gauging station (2001-09) showing individual flood pulses: summer high flow events have varying characteristics each year, with 2007 having prolonged high flows in June and July whereas 2008's flow is larger, but of short duration and at the end of the active season in September. Other years lack these summer high flows all together.

4.5 Discussion

Flow variability is vital in sustaining riverine ecosystem complexity (spatial and temporal) (Arthington et al., 2006), although long-term, anthropogenic-induced change has the potential to alter community structure (Greenwood et al., 1999, Poff and Zimmerman, 2010). Both aquatic and riparian assemblages are altered by high and low flow events, with high flows in particular resetting successional processes (Harris et al., 2000), reducing local densities in the short-term (Suren and Jowett, 2006) and potentially benefitting individual species in the medium-term (Hering et al., 2004). The flow data for the Severn exhibits patterns characteristic of a surface, rain water fed river system, with maximum flows consistently observed in autumn and winter (Figure 4.4) but with inter-annual variations varying the maximum and minimum monthly flows within this pattern. These high flows normally coincide with the overwintering strategy of many specialist invertebrates, which seek sites away from the riparian edge to hibernate, ensuring that during an essential period of quiescence, they are removed from the inundation pressures of high flow events (Andersen, 1968, Andersen, 2006). Daily data (Figure 4.5) highlights the role of individual events, which vary both in magnitude and duration. Very high magnitude events are typically of short duration (hours), whilst moderately raised flows can be comparatively stable and persist for several weeks. Within the annual pattern, there remain wide variations. The magnitude of winter flows in 2002, 2004 and 2008 is much greater that in other years (and therefore habitat restructuring will have been more pronounced). Similarly, some summers are characterised by unusually high flow events (2007 and 2008), where others show prolonged low summer flows (2004 and 2005), altering the potential environmental stress during the active period from year to year. The timing, magnitude and duration of these variations can be expected to differently impact ERS communities. High flow winter events rework and restructure the habitat. Whilst summer events of a lower magnitude have been suggested as important in spatially varying resource availability (Paetzold et al., 2005, Paetzold and Tockner, 2005). Any high flow event in the active period potentially reduces habitat, raises mortality and increases patch emigration, both passively by downstream transportation (Andersen, 1968), and actively via dispersal (Desender, 2000). Whether these mechanisms enhance or reduce the integrity of local communities will be dictated by the extent of the inundation pressure imposed (frequency and magnitude) and the ability of species to evade or survive.

In Chapter 3 it is demonstrated that a variety of morphological forms are possessed by ERS specialist Coleoptera these dictate their responses to the various pressures of the environment particularly inundation. These results presented in this chapter indicate how these morphological forms, can be used to predict community responses to inter-annual changes in flow regimes, indicating likely long-term changes in population structure under different hydrological scenarios.

Initial model selection grouped the two most abundant families sampled, allowing the responses of cursorial ground beetles and fossorial rove beetles to be examined separately. Generalised Addditive Models (Figure 4.3) indicate differing long-term population trends between rove beetles and ground beetles, the former increasing and the latter declining. ERS ground beetles are almost universally macropterous (Plachter, 1986) and are capable dispersers within the habitat. The life cycle of rove beetles is less well understood, but connectivity modelling (Chapter 3) indicates that they have reduced dispersal capabilities and are reliant on a complex habitat mosaic. Inundation responses model differently between ground beetles and rove beetles. Abundance data (Figure 4.2) shows the former fluctuating between 700-1000 each year, with a single year (2003) when abundance peaks around 2500. Rove beetles are consistently less abundant (150-250), but exhibit a peak of nearly 500 in 2008. The best-fitting model (Table 4.4) indicates that rove beetle abundance is most positively associated with the duration of the lowest flow during the season of sampling (i.e. a period of prolonged stability free from inundation pressures, (a variable that occurs in half of the models falling within the 95% confidence interval)). Other (less significant) models falling within this confidence interval (Table 4.1) include the role of the number of Q_{10} events in both the season of sampling and the previous year, both having a weak positive influence on abundance. This grouping contains mostly small (less than 5mm) cryptic species, found via excavation of the substrate. The best-fitting model therefore indicates that stability favours adult generations (but not subsequent generations), whilst disturbance has a less important, but at least partially beneficial influence on long-term rove beetle abundance. Ground beetles respond positively to a combination of high flow parameters, the number of Q_{10} events in the previous year, the duration of the highest flow in the season of sampling and the magnitude of the highest flow in the previous summer (parameters consistent within all of the models lying within the 95% confidence intervals, Table 4.2). These parameters include both habitat reworking events (magnitude) and potential inundation pressures (summer events). The strength of adaptations possessed by ERS ground beetles throughout their lifecycle appears to maximise their fitness to a very high level of disturbance. The optimum model includes extensive habitat provision via high flow events, even when occurring during the active period of their lifecycle. Several summers within the data record contain short duration/high magnitude summer events which would cause local inundation. The ability of eggs, larvae and adults to survive immersion (Andersen, 1968), coupled with flight responses and recolonisation abilities (Bonn, 2000, Hering et al., 2004) maintain the integrity of individual generations at all stages of their lifecycle and maximise their potential to utilise newly available habitat resources.

There is some evidence that even within the tribe Bembidinii, there are subtle adaptive and behavioural differences that allow species to partition resources (Andersen, 1988), one of which involves spatial positioning within the ERS habitat (Bates et al., 2007b), that alters resource utilisation and may be responsible for longitudinal variations in community structure (Chapters 5 and 6). *B. atrocaeruleum* (the most abundant ground beetle sampled) exhibits a mobile behaviour within the habitat, which optimises utilisation of headwater ERS. Due to this dominance (and specialised behaviour) the species was modelled individually, providing the smallest range of models (3) within the 95% confidence interval (Table 4.3). The optimum model was (unsurprisingly) similar to that derived for all specialist ground beetles, except magnitude of previous summer's highest event was replaced was by the magnitude of the previous year's highest event. Magnitude represents the ability of the river to rework the ERS habitat, higher magnitudes exposing larger areas of new habitat. The inclusion of this parameter within the model reinforces the suggestion made in Chapter 4 that *B. atrocaeruleum* possesses optimum adaptations for the headwater ERS habitat, reflecting its ability to colonise newly available resource, a trait which is present, but less pronounced when all specialist ground beetles (with varying levels of adaptation) are modelled.

4.5.1 Conclusion

The models demonstrate the importance of fluctuating flow regimes in structuring ERS assemblages. Both families studied are more or less beneficiaries of disturbance (as both a force for habitat creation and dispersal promotion). The stronger the dispersal potential, the better able a group is to take advantage of these habitat characteristics. Temporal changes in local abundances are (at least in part) a result of differing responses to variations in flow regime. Ground beetles are highly adapted, strong dispersers and rapidly take advantage of the resources made available by major restructuring events, with evidence that the most strongly adapted are best positioned to make this rapid response. The causes of the positive response of rove beetles to seasonal stability are uncertain, but are likely to be due to reduced local mortality and emigration, coupled with strong toleration of the thermal and humidity gradients present within the habitat (sensu Andersen, 2006), which would be exaggerated during such stability. There is however no indication that this translates into increased fecundity via raised abundance in subsequent generations. Whether this is a trend that would emerge over a succession of stable, low summer flows could only be tested with a longer dataset.

The loss of stochasticity in flow regimes has repeatedly been demonstrated to have a detrimental impact on stream and riparian diversity, with loss of peak flows in particular leading to an increasing ‘terrestrialisation’ of the riparian zone (Poff and Zimmerman, 2010). Where species are functionally dependent on ERS, the stochastic nature of unregulated flows is essential for maintaining the riparian disturbance regime characterised by frequently arrested succession. These results demonstrate the positive influence of high flow events on ERS specialists, and indicate the mechanism by which observed population losses have occurred on regulated rivers. The predicted rise in intense rainfall events over coming decades will however potentially benefit communities in less regulated rivers, with increasing habitat reworking a likely outcome. Highly adapted species are dependent on the environmental pressures that exclude non-specialists from the ERS habitat, an increase in these pressures will further benefit specialists that are best positioned to utilise the resource.

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5

The impact of inundation on aquatic nutrient utilisation by riparian beetles

Stable Isotope Analysis (SIA) was used to investigate the role of inundation pressures on the dietary composition of an assemblage of predatory riparian beetles inhabiting exposed riverine sediments (ERS) on the Upper Severn, mid Wales. With potential prey originating from both aquatic and terrestrial sources, inundation stresses were shown to cause differing variations in dietary composition according to behavioural and morphological adaptations to the habitat. Stream edge species showed a consistent aquatic dominated diet regardless of inundation pressures. Mobile species increased the level of aquatic subsidy with increased inundation pressures. In-land species either exhibited a consistent terrestrial diet under all inundation levels or switched to a strong terrestrial based diet with the onset of moderate pressures. Seasonal changes in dietary composition are also evident, reflecting overwintering strategies. Resource uptake is controlled by morphology and behaviour which reflect species' toleration of inundation pressures. These adaptations enforce a complex, overlapping partitioning of resources and habitat, creating micro-niches which enhance the diversity and abundance of specialist ERS beetle fauna.

5.1 Introduction

The aquatic-riparian interface is an important transfer zone, characterised by reciprocal, varying flows in nutrients and food resources (Bastow et al., 2002, Briers et al., 2005, Burdon and Harding, 2008, Collier et al., 2002). Terrestrial inputs are a major nutrient resource (Richardson et al., 2009), both as a primary carbon source in headwater streams (Vannote et al., 1980) and as a subsidy for macroinvertebrates (Jardine et al., 2008). Higher trophic levels also benefit; fish consume terrestrial invertebrates, and fruit and seeds that fall into the stream (Correa et al., 2007), and this can account for up to 50% of the annual energy budget for juvenile salmonids (Baxter et al., 2005). The reciprocal aquatic subsidy (Figure 5.1) is as important for terrestrial mammals (Ben-David et al., 1998), reptiles (Sabo and Power, 2002), birds (Iwata et al., 2003) and arthropods (Kato et al., 2004). In some systems this process can facilitate extreme but temporally constrained inputs, such as the Pacific coast salmon returns of North America (Wipfli et al., 1998). Of chief concern to this study is the role of emergent or stranded aquatic insects which are actively predated or scavenged by specialist arthropods of ERS (Hering and Plachter, 1997).

Much of the resource utilisation at this ecotone is passive or reactive (i.e. increased predator density is a reaction to prey abundance rather than obligative habitat and resource use), as such the habitat supports regular influxes of locally itinerant species (Baxter et al., 2005). This results in temporary spatial shifts in predation and foraging with a concurrent switch in diet (from terrestrial to aquatic prey). The Coleoptera fauna associated with British ERS have been extensively documented in recent years with an increasing knowledge of species' behaviour and lifecycles (Eyre et al., 2001, Sadler and Bell, 2002, Sadler et al., 2005). That the habitat hosts an associated fauna indicates that this fauna will possess a suite of characteristics optimising their utilisation of the environment and the resources it provides. These 'specialist' Coleoptera are known to be at least partially dependent on aquatic prey, with some evidence that their abundance is linked to emergence levels (Paetzold et al., 2006). Whether the subsidy causes the fluctuations in Coleoptera abundance or is an example of synchronous lifecycles is unclear, particularly as there is evidence that the proportion of aquatic subsidy is proportionate to stream productivity, suggesting an obligative plasticity in prey selection (Hering and Plachter, 1997, Paetzold and Tockner, 2005).

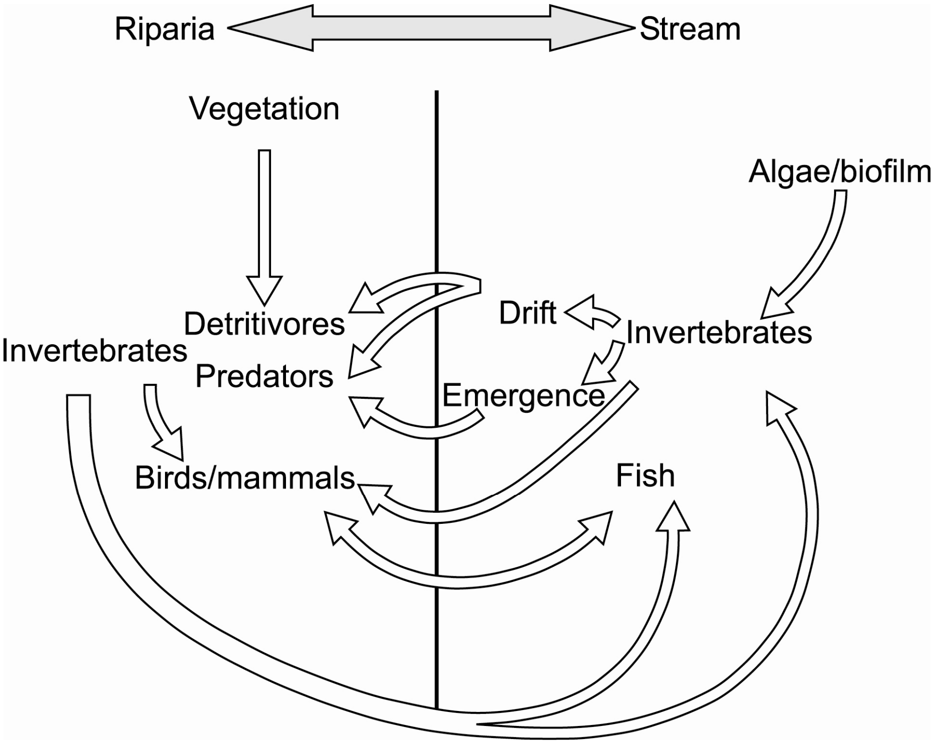


Figure 5.1: Simplified representation of nutrient exchanges and sources across the aquatic-riparian ecotone.

A common understanding of specialisation is that morphological adaptations serve to position species into functional groups, allowing them to co-exist within a habitat due to differing resource utilisation (Ribera et al., 2001). This positioning may be evinced spatially, as with fossorial and cursorial Coleoptera (Andersen, 1988), or temporally, where species exhibit the same limiting resource but with diel separation (Kocarek, 2001, Lundgren et al., 2009). The more 'adverse' the environment, the stronger the adaptive measures that are required (Lytle et al., 2008, Parmesan et al., 2000). This exclusion process is known as 'habitat filtering' (Cornwell et al., 2006) and it effectively reduces the pool of potential species that can occupy a habitat and utilise its resources.

The filters imposed by ERS have been much studied and the adaptations Coleoptera utilised (especially ground beetles) to overcome them have largely been identified. Physical disturbance and inundation (Plachter and Reich, 1998), reworking of habitat patches, low nutrient availability, extremes of temperature and humidity all play a part in suppressing long-term colonisation by non-adapted species (Sadler and Bates, 2008). The suite of characteristics exhibited include high reflectivity (Desender, 1989), flattened bodies (Andersen, 1985), avoidance behaviour, spatial positioning (Andersen, 1983) and seasonal alterations of habitat (Andersen, 2006). Many of these adaptations enable species to tolerate the high levels of disturbance caused by repeated inundations. Whilst there is a strong seasonally predictive element to these (during autumn-winter high rainfall periods in the UK), high flow events are possible year round. Most specialists possess a lifecycle that ensures avoidance of seasonal inundation by movement to higher sites to overwinter (Andersen, 1968). The spring-summer active period will however occasionally be subjected to extreme flow events that inundate all or part of the habitat.

Morphological adaptations can give some indication of the strategies employed by different groups to ensure survival of these extreme events, for instance specialist ground beetles have increased wing and leg length (relative to body length) than rove and click beetles associated with the habitat, enabling greater and more rapid dispersal. This allows the ground beetles to utilise active movement (either flight or running) away from rising waters more effectively than other families (Desender, 1989). The shorter legs and wings of rove and click beetles indicate other avoidance strategies may be preferentially employed (Chapter 3). An obvious strategy is to avoid the habitat that is most frequently inundated, as with *Fleutiauxellus maritimus*, which utilises elevated areas of habitat away from the stream edge (Bates et al., 2005) and therefore the need to employ costly avoidance mechanisms. Other adaptations reduce the danger of immersion, delaying the need for escape in the event of rapid inundation. Rove beetle species (particularly *Stenus sp.*) produce hydrophobic discharges promoting movement across the water surface, couple with enlarged and flattened tarsal segments, increasing contact area with the water (Betz, 1998, Betz, 2002). These adaptations also appear to influence the dietary selection of different species, a consequence of variations in the likelihood of encountering prey types and increased/decreased efficacy of foraging in different microhabitats (Andersen, 1988, Bates et al., 2007b, Bauer and Pfeiffer, 1991).

Inundation avoidance or survival adaptations are specific to the ERS environment but, concurrently, inundation temporarily deprives the specialist species of their optimum habitat. Under these conditions the refugia utilised may provide suboptimum conditions which alter resource acquisition. The complex morphology of the habitat means that individual patches will exhibit marked variations in inundation susceptibility, which in turn drives variations in sediment deposition and vegetative colonisation, all characteristics of the dynamic 'riverine landscape' (Ward et al., 2002). Whilst organisms make individual responses to flood pressures, the morphology of individual patches will produce 'response trends' that are idiosyncratic to the structure of each patch.

Previous invertebrate studies have examined the strength of the aquatic subsidy to Aranea (Briers et al., 2005, Burdon and Harding, 2008, Collier et al., 2002), Orthoptera (Bastow et al., 2002), Formicidae and Coleoptera (Paetzold et al., 2005), most of these studies, however, have not distinguished between specialists and transitory species present in the study area (although see Paetzold et al., 2005). The apparent similarities of the species typically found in riparian Coleopteran communities have been suggested as a rare example of a lack of 'intrageneric isolation' (Thiele, 1977) with multiple species occurring in the same niche. Work on micro-habitats has demonstrated how apparently similar species are able to operate in close proximity (Desender, 1989). Differences in the way species utilise the aquatic subsidy when subjected to varying levels of environmental pressure may further demonstrate the existence of these micro-habitats and delineate their boundaries.

Partitioning of resources, particularly food resources, allows species co-existence with minimal competition (Andersen, 1988, Bell, 1971). Data on Coleoptera diet have been derived using gut content analysis (Davies, 1953, Hering and Plachter, 1997) and provided useful *a priori* information on potential food sources (from an otherwise large pool). A pre-requisite of consumption is availability, a factor not just of presence but also size and emergence pathway, which are specific for both consumer and prey (Hering and Plachter, 1997). Prey preferences can either be morphologically driven or opportunistic. *Stenus* species possess an additional extendable and adhesive set of mandibles, well adapted to catching Collembola (Bauer and Pfeiffer, 1991). The presumed aphid-based diet of Coccinellidae is also known to incorporate opportunistically the larval stages of both Coleoptera and Lepidoptera (Evans, 2009). Ground beetles largely appear to be opportunistic feeders, if they encounter prey, the main selection criteria is size. This may explain observed variations in dietary content between differently-sized species; where smaller species fed on chironomids and larger species predating emerging stoneflies (Paetzold et al., 2005).

What is known about the adaptive strategies, prey selection by riparian Coleoptera and inundation pressures allow hypotheses to be developed that resource acquisition will vary between adaptive groups and according to inundation pressures, which can be tested by observing variations in dietary composition.

SIA has been suggested as a means to unravel the complexities of multi-source food webs, allowing investigation of trophic positioning (Anderson and Cabana, 2007) and identifying contributions of multiple sources (Inger et al., 2006). These techniques are especially applicable to the ERS habitat which demands high levels of specialism from its permanent inhabitants yet simultaneously recruits large numbers of itinerant visitors from neighbouring terrestrial habitats. The suggestion that riparian gravel bars form a disproportionately subsidised habitat due to their low productivity relative to adjoining systems (Marczak et al., 2007) may aid investigation of trophic positioning, resource utilisation and functional groupings be amplifying variations between differently subsidised groups.

5.2 Study aim, research questions and hypotheses

The aim of this study is to examine how inundation alters nutrient uptake pathways by specialist riparian Coleoptera. The strength of specialism varies between species, as such pressures imposed by the system may induce differing responses that can be detected via changes in resource acquisition. Observed variations may illuminate the extent of resource partitioning within the ERS ecotone and the presence of multiple niches.

1. ERS is a complex boundary between the aquatic and the terrestrial. How efficient is this boundary at absorbing aquatic subsidies, and does this change under differing conditions or over time? Particularly, how do pressures of inundation and spatial positioning create local and temporal variations in aquatic subsidies?
2. Specialisation is an important element of the Coleoptera fauna associated with ERS and many of the adaptations are associated with inundation survival or avoidance. To what extent do these adaptations drive prey selection by controlling interaction with the productive stream edge?
3. Can the use of trophic enrichment be used to establish the presence of resource partitioning within Coleoptera assemblages, and explain high levels of diversity and abundance?

The study hypothesises that it is possible to detect variation in prey selection (via SIA) between different functional groups of Coleoptera, and that the level of aquatic prey will be predicted by the strategies utilised to overcome inundation pressures imposed by local hydrology.

5.3 Methodology

5.3.1 Assessing dietary proportions through SIA

SIA is a widely used mechanism for assessing variation in dietary composition both spatially and within assemblages. ^{13}C and ^{15}N are naturally occurring isotopic forms of Carbon and Nitrogen 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). 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 however a standard trophic enrichment rate has been accepted at 2.3‰ ± 0.16‰ for $\delta^{15}N$, and 0.5‰ ± 0.13‰ for $\delta^{13}C$ (McCutchan et al., 2003). Isotopic date are initially plotted to give a visual estimation of trophic positioning, via isotopic positioning. The extent of the spread of isotopic values is seen to indicate the distribution of the population sampled, and the variation within food sources, known as the 'total area' (Layman et al., 2007). As an indicator of the most prevalent values this process is heavily influenced by outlying data points. A refinement which removes this influence test the data within a Bayesian framework, thereby incorporating a level of probability into the distribution and providing the most probable values of the majority of the population (Jackson et al., 2011). Mixing models are also applied to the data to estimate probable contributions after ecologically informed *a priori* selection of potential prey items (Phillips et al., 2005).

5.3.2 Data collection

An extensive run of ERS occur along a 7km stretch of the upper River Severn between the villages of Llandinam and Caersws, mid Wales (Figure 5.2). Twenty individual gravel bars were selected along this gradient for terrestrial sampling, representing a diverse range of sizes and profiles. Care was taken to avoid bars where livestock had access due to potential for nutrient enrichment and community alteration, as observed on the River Tywi (Bates et al., 2007a).

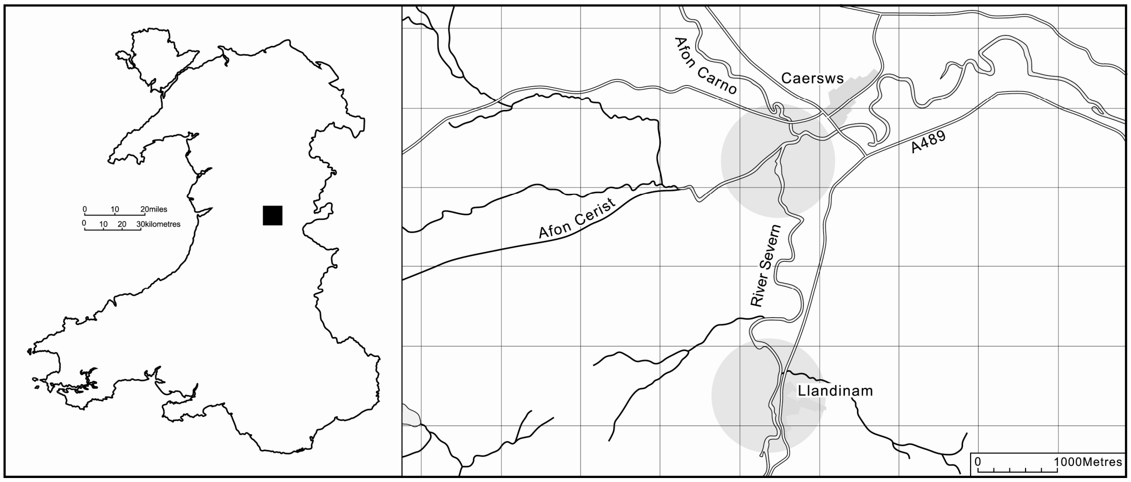


Figure 5.2: Study area of the River Severn, mid-Wales, with sampling areas shaded.

Each site was mapped using a Leica Geosystems 1200 DGPS during a period of low flow in April 2009. These data were used to produce contour maps of each habitat patch in ArcGIS (Figure 5.3 and 5.4). Contour levels were set at 20cm and compared with data from a permanently installed pressure transducer recording river depth every 15 minutes throughout the study period (April 2009-April 2010). For each 20cm increase in river depth extent of habitat submerged was calculated, up to 1m, representing the greatest depth recorded the study species' active period). Bankfull (> 1.5m) occurred only during winter when invertebrates are absent from the habitat. Habitat patches were classified by inundation susceptibility (1: low; 2: moderate; 3: high) based on the percentage of habitat inundated at (or before) a 1m increase in river depth (<50%: low; 51-90%: moderate; > 90%: high).

Samples of terrestrial Coleoptera (consumers) and potential prey (aquatic and terrestrial) were collected three times during the period (June 2009, September 2009 and April 2010). Consumer samples were collected at the stream edge and at the point where perennial vegetation established. Potential terrestrial prey (Collembola and Aphids) were collected by hand from the substrate and host plants. Aquatic prey were collected using a standard 3 minute kick sample with a 500 μm net. Three samples were taken from each of four points in the reach. All samples were kept alive until they were returned to the laboratory at the University of Birmingham, where they were frozen. Samples were then identified to species (Coleoptera) or family (sources) prior to removal of gut contents and drying of organisms (> 48 hours at 65°C).

5.3.3 SIA sample preparation

Each sample was divided, with one half undergoing lipid extraction. Doing this avoids difficulties arising due to lipid depletion in $\delta^{13}C$ values; extraction provides greater accuracy and therefore reliability than post-analysis mathematical correction (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 ± 0.05mg; Nitrogen: 0.6mg ± 0.05mg) into tin cups prior to combustion.

Samples were combusted at 920°C before being passed through a reduction column in an Elementar Pyrocube, the isotopic composition of sample gases was then determined on an Isoprime continuous flow mass-spectrometer. Within-run reproducibility was better than 0.07 per mil for both $\delta^{13}C$ and $\delta^{15}N$. The two techniques were analysed on separate sub-samples rather than by ‘peak-jumping’ (i.e. measuring $\delta^{13}C$ and $\delta^{15}N$ in the same combustion), avoiding observed influences of the lipid extraction process on $\delta^{15}N$ values (Logan et al., 2008).

5.3.4 Trophic and nutrient proportion analysis

Species data were analysed separately and by functional group, as defined by morphological similarity (Chapter 3). Analyses were conducted to determine how dietary composition was influenced by season, inundation and sampling position (stream edge or inland), following testing for significant differences by multivariate analysis of variance. Inundation analysis excluded specialist rove and click beetles, and in-land ground beetles (with no known affinity to the ERS habitat) due to a lack of individual organisms retrieved from high inundation sites. Sample sizes were large enough to allow species-specific analysis of specialist ground beetles with an affinity to the habitat: *Bembidion atrocaeruleum*, *B. decorum*, *B. punctulatum*, *B. tetracolum* and *Paranchus albipes*.

Data were entered into a Bayesian mixing model available as an open source R package, SIAR v4 (Parnell et al., 2008). The SIAR model is fitted via a Markov Chain Monte Carlo (MCMC) method, producing simulations of plausible values of dietary proportions of sources. The SIAR MCMC was run with 500,000 iterations, the first 50,000 being discarded before thinning by 15 to reduce autocorrelation. The resulting probability density function distributions of feasible consumption solutions allow identification of the most probable (median) solutions, with feasible solutions captured by the total range of credibility intervals. Trophic positioning was visualised using a Bayesian probability framework to evaluate most likely distributions of isotopic values by functional group (Jackson et al., in press).

5.4 Results

Samples were derived from 1368 terrestrial Coleoptera, 786 potential aquatic prey and 195 potential terrestrial prey. Some samples comprised multiple organisms (3-5) due to small size of individuals. Isotopic values were obtained for 50 terrestrial prey samples, 262 aquatic prey (which following exploration were reduced to 130) and 366 predatory terrestrial Coleoptera. Once isotopic analysis was complete, samples were grouped by species and functional group (Table 5.1) before statistical analysis.

Table 5.1: Members of Coleoptera functional groups, assigned according to morphological indications of mobility potential and affinity to habitat.

	Summary	Member Species
Group 1	Specialist ground beetles: Headwaters	*B. atrocaeruleum* *B. decorum*
Group 2	Specialist ground beetles: Lower reaches	*B. punctulatum*
Group 3	Ground beetles: Low affinity	*B. tetracolum* *P. albipes*
Group 4 species	Ground beetles: No affinity	All other ground beetle
Group 5	Other specialists Headwaters	*Stenus* species *C. 5-punctata*

5.4.1 Habitat morphology and inundation susceptibility

The contour maps (derived from digital elevation models (DEM)) of both Llandinam (Figure 5.3) and Caersws (Figure 5.4) coupled with stage data provide indicators of inundation susceptibility at each site for any given rise in river depth. Peak river depth was consistently higher during the autumn and winter periods; maximum winter flows (2.2m) submerged all sites, maximum summer flows (1.4m above base levels) left some ten sites with available habitat. Six sites experienced total inundation during April – October 2009 (Figure 5.6), whilst the five least affected lost less than 50% of available area under the highest flows. Concurrently, the duration of inundation events varies between bars; those with shallow profiles experience prolonged inundation of several weeks during the raised levels in July, whilst the short-lived peaks created more extensive flooding, but typically for a duration of a few hours, rather than days or weeks. Inundation susceptibility was obtained by transforming the DGPS data of each habitat patch into DEM with 20cm contour maps defined. Sequential 20cm rises on habitat area are illustrated (Figure 5.5) for a highly susceptible patch (Site 1), indicative of the between patch variability in inundation susceptibility (Table 5.2)

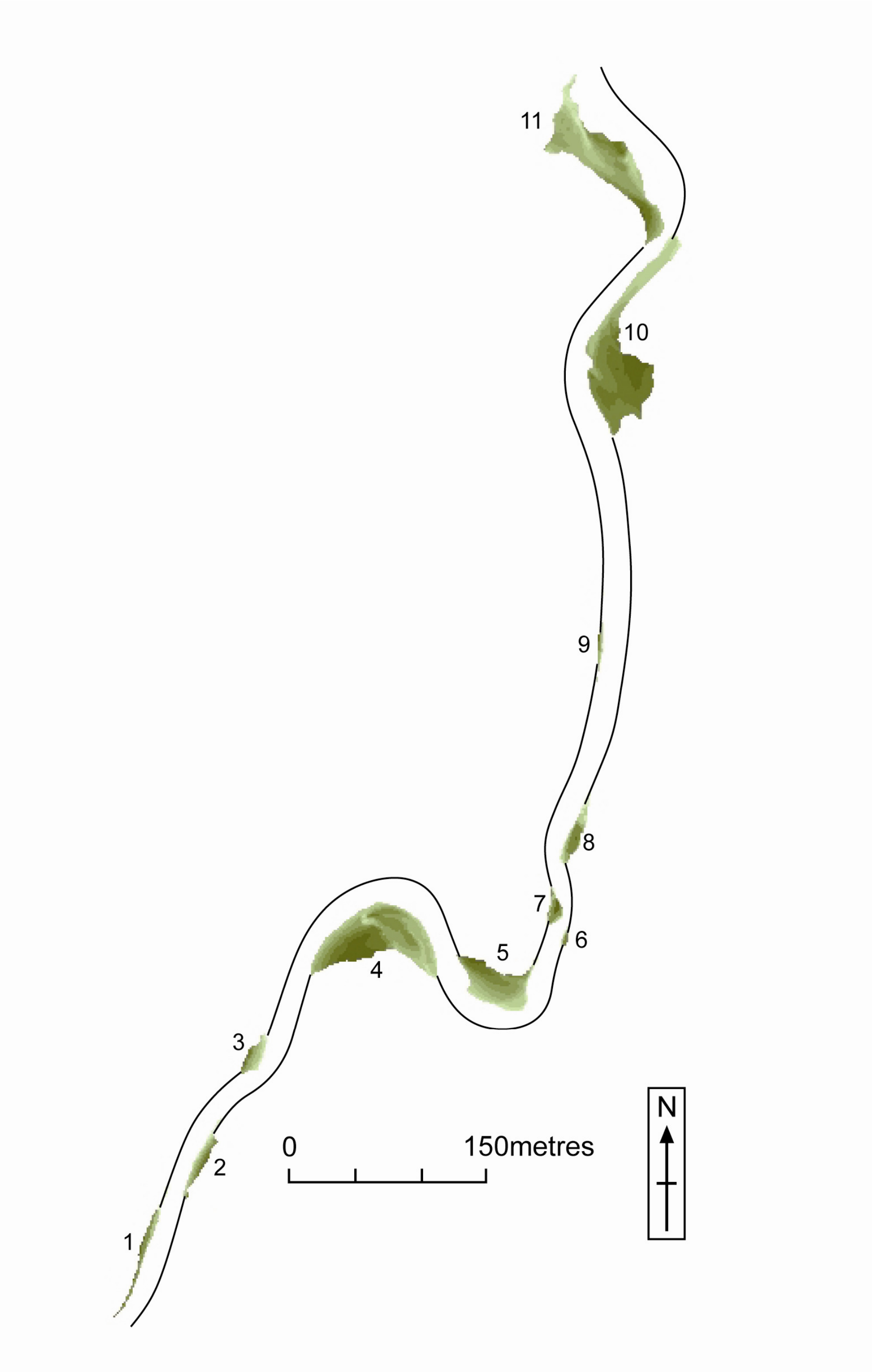


Figure 5.3: DEM of Llandinam reach of the River Severn, showing patches 1-11, incorporating a range of low, moderate and high inundation risks. River flows from south to north. Lowest elevations are coloured light green, highest, dark green, with each contour representing a 20cm increase.

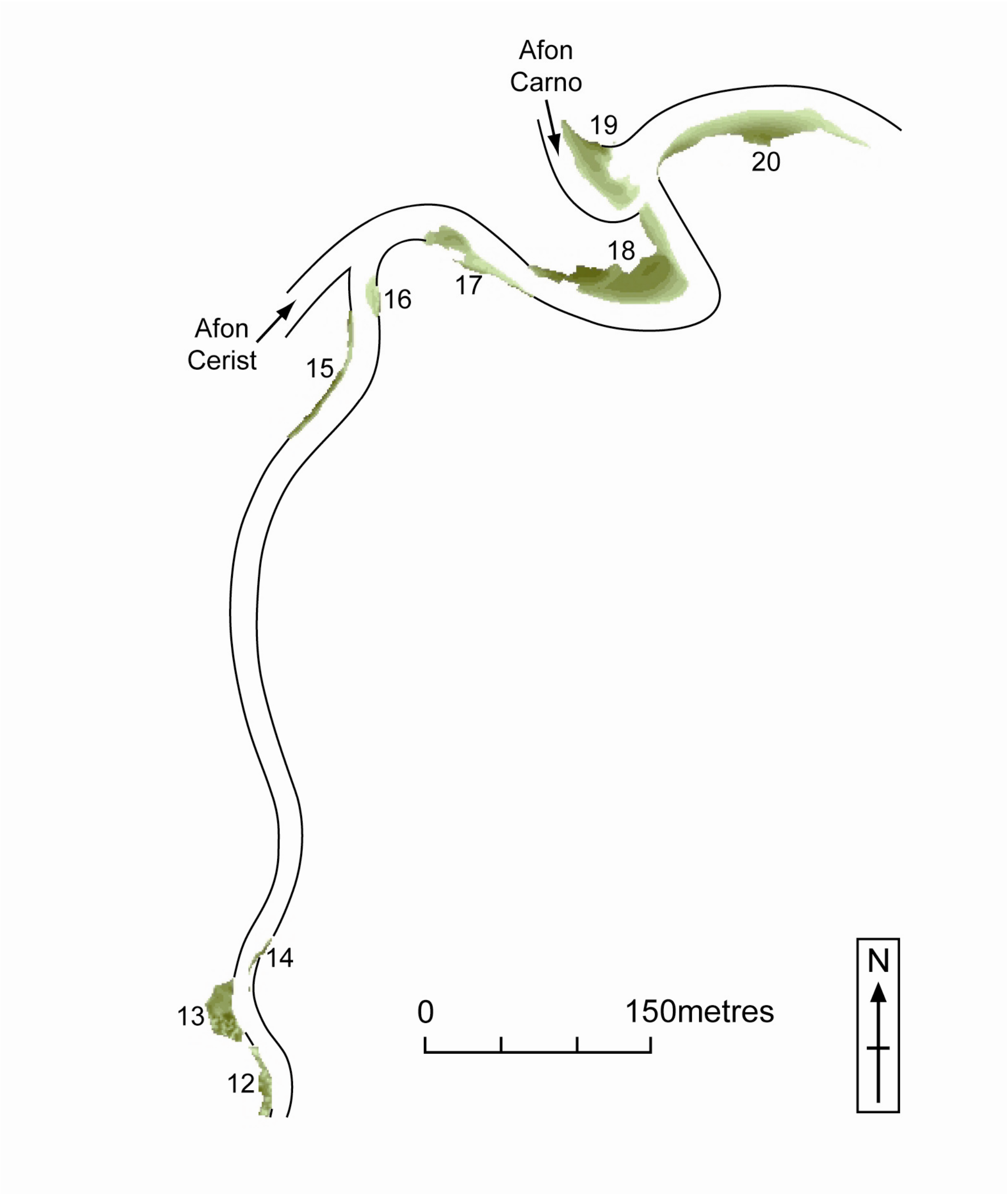


Figure 5.4: DEM of Caersws reach of the River Severn, incorporating each of the three inundation risk levels, and showing confluences of the Afon Cerist and Afon Carno. River flows from south to north. Lowest elevations are coloured light green, highest, dark green, with each contour representing a 20cm increase.

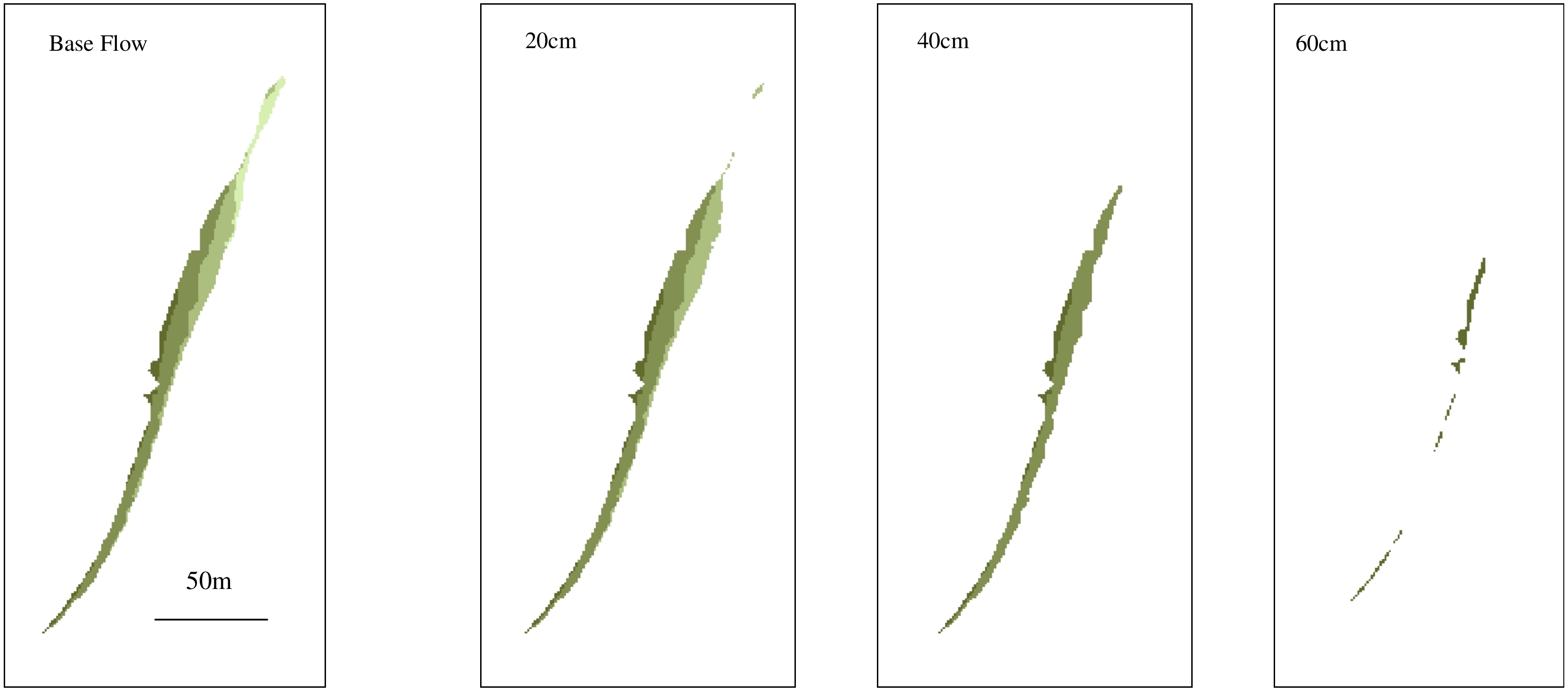
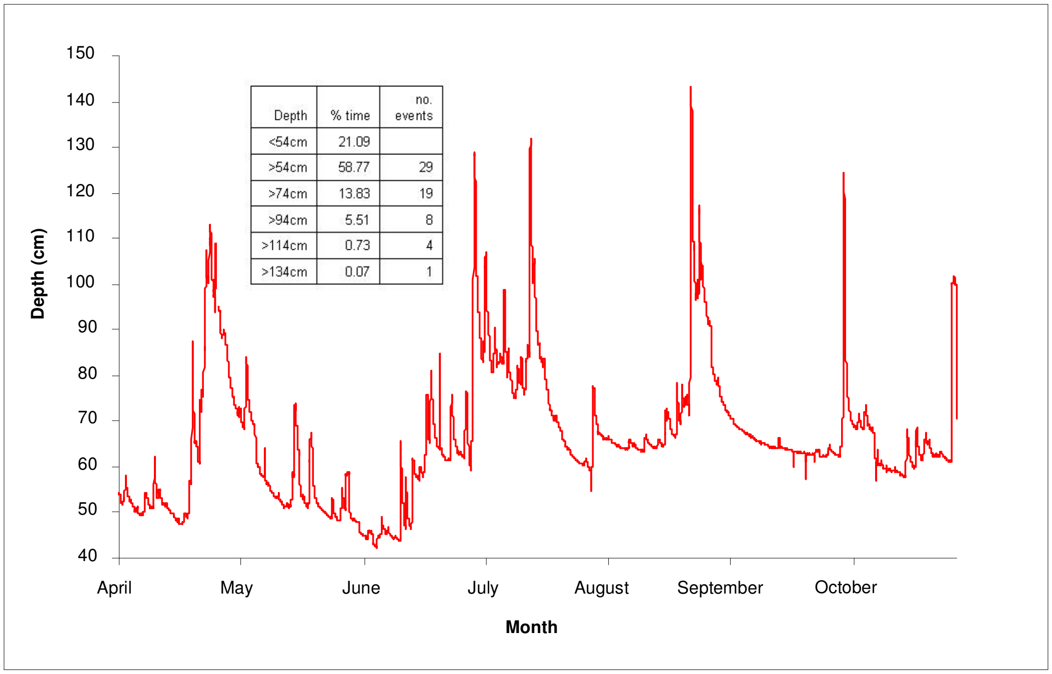


Figure 5.5: Sequential loss of habitat from base flow with each incremental 20cm rise on a habitat patch (no. 1) with a high inundation susceptibility. River flows upwards, to the right of the habitat patch depicted. Area to the left is grazed pasture.

Table 5.2: Percentage of habitat submerged with each 20cm rise in stream depth for each habitat patch. Data given up to 1m (maximum summer depth) or until all habitat patch is submerged if this is less. Inundation classes are coloured mild (blue), moderate (green) and high (red)

Patch	<20cm	<40cm	<60cm	<80cm	<1m	%
1	11	27	53	9	-	**100**
2	13	14	17	22	20	**86**
3	12	21	23	21	12	**89**
4	0	5	16	18	19	**58**
5	3	8	14	12	16	**53**
6	13	22	27	34	4	**100**
7	10	30	45	15	-	**100**
8	19	25	20	36	-	**100**
9	19	25	20	34	1	**100**
10	1	2	13	6	6	**28**
11	2	5	6	13	25	**51**
12	2	4	9	11	13	**39**
13	0	1	2	4	6	**13**
14	2	4	9	11	13	**39**
15	47	53	-	-	-	**100**
16	17	50	22	4	3	**96**
17	6	19	23	21	25	**93**
18	1	5	11	11	12	**40**
19	8	14	25	27	18	**92**
20	4	15	16	15	12	**62**

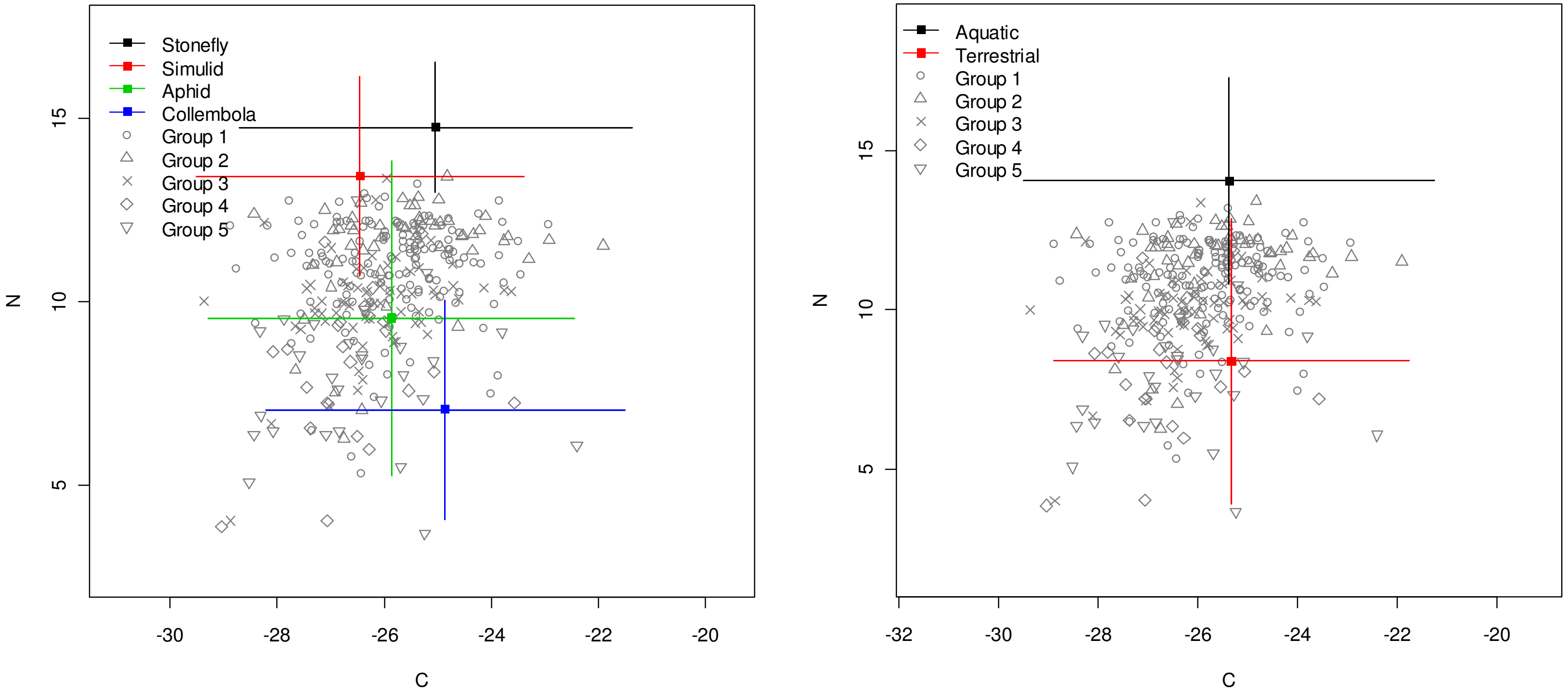


Depth	% time	no. events
<54cm	21.09	
>54cm	58.77	29
>74cm	13.83	19
>94cm	5.51	8
>114cm	0.73	4
>134cm	0.07	1

Figure 5.6: Daily variations in river depth (using calibrated pressure transducer data), showing high flow peaks, frequencies and durations.

5.4.2 Isotope data

Isotopic data for Coleoptera consumers showed a range of -29.9 to -21.9 δ^{13}C and 3.67-13.76 δ^{15}N, with potential sources showing ranges of -26.72 to -21.63 δ^{13}C and 4.07 to 12.63 δ^{15}N (aquatic), and -29.03 to -22.34 δ^{13}C and 1.44 – 8.26 δ^{15}N (terrestrial) using pooled data from the three sampling periods. Seasonal variation in source data were significant for δ^{13}C (F: 10.871; df: 2; p <0.001) and δ^{15}N (F: 3.331; df 3; p 0.038); with Autumn 2009 less enriched than Summer 2009 (δ^{13}C: p <0.001; δ^{15}N: p 0.03) and Spring 2010 (δ^{13}C only, p <0.001). The Coleoptera δ^{15}N signature was significantly different between samples from the stream edge and inland, with stream edge samples more enriched (F:11.955; df: 2; p 0.001).



5.7a) 5.7b)

Figure 5.7: Biplots of δ^{13}C and δ^{15}N values derived for potential source prey; Springtails and Aphids (terrestrial), and Blackflies and Stoneflies (aquatic), with individual consumer values by morphological group. 5.7a shows prey values according to family, whilst 5.7b shows combined values for terrestrial and aquatic groups; the majority of all consumer values lie within those indicated by potential prey, suggesting multiple sources are being utilised.

Both the 4- and 2-source biplots (Figures 5.7a and 5.7b) show the positioning of the terrestrial consumers between the $\delta^{15}N$ enriched aquatic sources and the relatively depleted terrestrial sources, providing the first indication that populations are consuming prey from both systems. Mean $\delta^{13}C$ values for aquatic and terrestrial sources are identical, suggesting that the two systems still possess an archetypal headwater signal, where aquatic consumers are largely reliant on allocthonous carbon in the absence of sufficient in-stream primary production. Stoneflies show greater $\delta^{13}C$ and $\delta^{15}N$ enrichment than simulids, reflective of the multiple feeding strategies in the family, in comparison to reliance on fine particulate matter. Aphids demonstrate relative depletion of $\delta^{13}C$ and enrichment of $\delta^{15}N$ when compared with Collembola, which in turn reflects their reliance on nitrogen rich sap and Collembola utilisation of carbon rich detritus.

There are also indications that the terrestrial subsidy may have a stronger influence than has been recorded in the potential sources with several consumers lying outside the range of source data (Figure 5.7a and 5.7b). Although these data points may be an indication that sampling of sources was incomplete (Layman et al., 2007), the data points represent groups 3, (n=1), 4 (n=2) and 5 (n=5), and also show a strong terrestrially skewed signal. Variation in Collembola signals is know to be wide (especially between taxa) and there are data to suggest they often exhibit very low $\delta^{15}N$ (Chahartaghi et al., 2005). The lowest $\delta^{15}N$ value for the Collembola sampled here is 1.44 ‰, which lies outside the standard errors depicted within the biplots, but does incorporate the lowest Coleoptera value.

Isotopic position was visualised for morphological groups (Figure 5.8). Morphological groups show the strongest δ^{15}N enrichment (indicative of increased aquatic subsidy) in specialist ground beetles, with the stream-edge dwelling, floodplain ground beetles (Group 2) having the highest level, followed by mobile, headwater ground beetles (Group 1). Medium enrichment is exhibited by ground beetles with a weak affinity to the ERS resource (Group 3), whilst the lowest levels (reflecting greater uptake of terrestrial sources) are exhibited by non-affiliated ground beetles (Group 4) and *Stenus sp.* and *C. 5 punctata* (Group 5). Although group ellipses exhibit overlap (reflecting variation in population prey selection) the trends show increasing utilisation of aquatic resources with stronger inundation resilience adaptations.

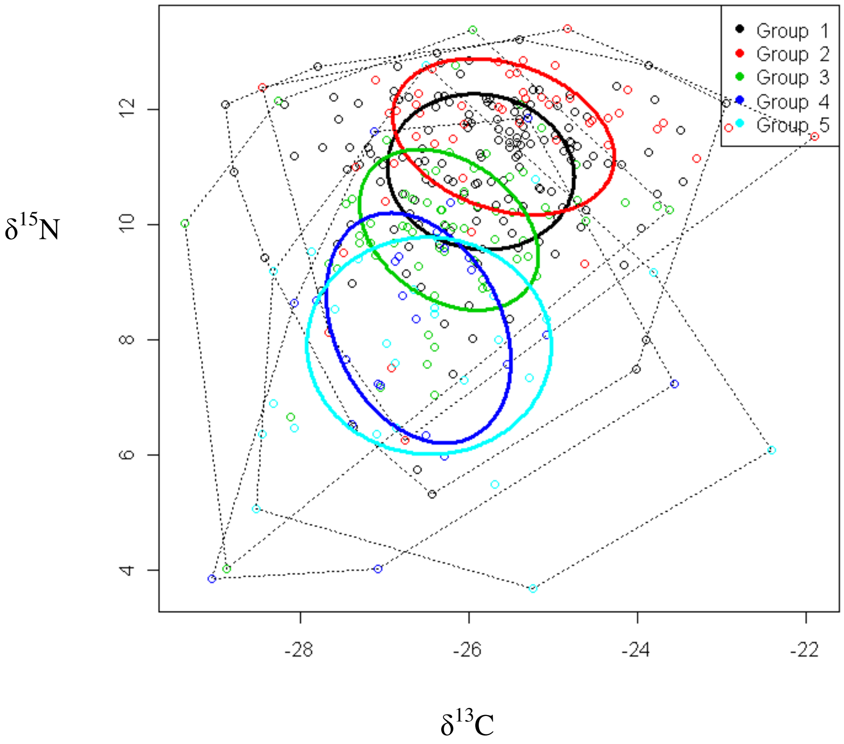
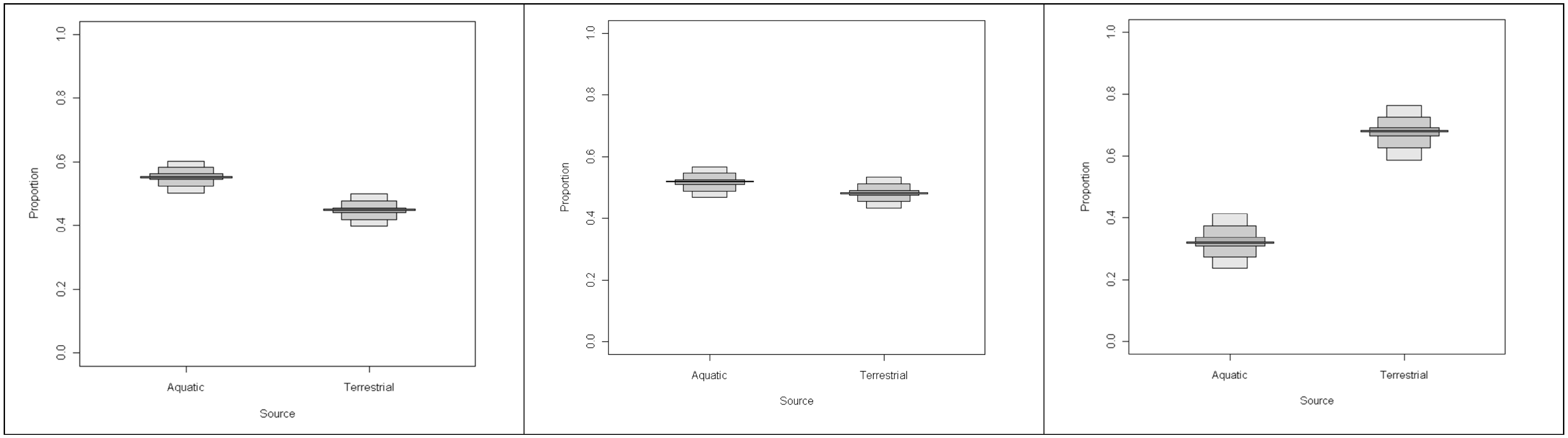


Figure 5.8: Isotopic positions of morphological groups visualised using convex hulls (dotted lines showing extent of whole population) and standard ellipses (solid lines) showing range of most probable population values.

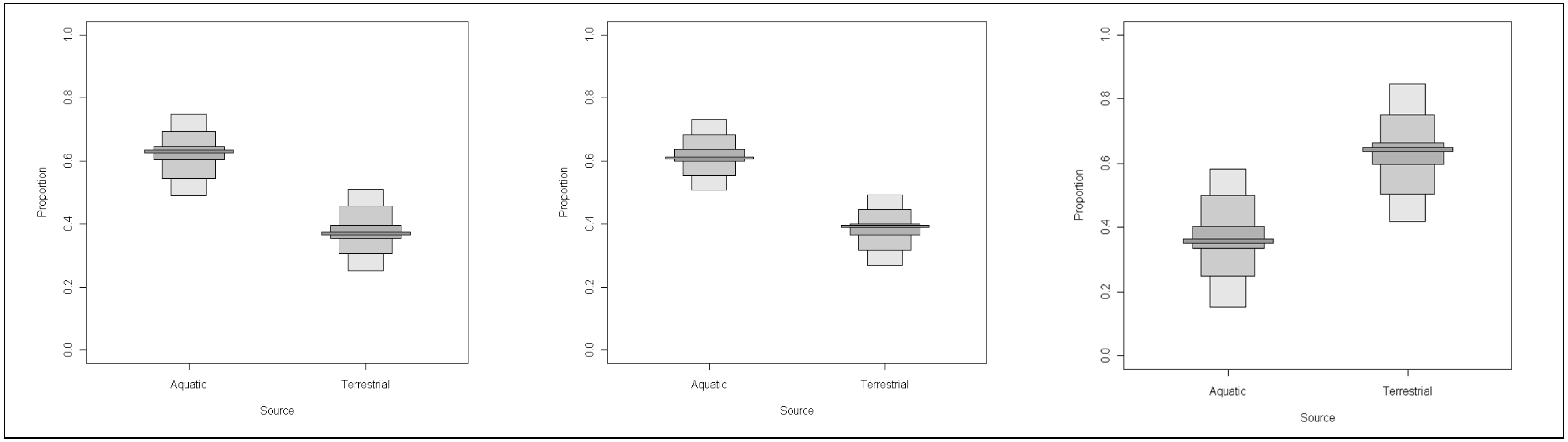
5.4.3 Variations in dietary composition.

Probability density functions provide the most likely contribution levels to each group under differing regimes, with surrounding extent of plausible values. Representative visualisations are shown in Figures 5.9-5.11, with summaries of median values of nutrient proportions in Tables 5.3-5.5.

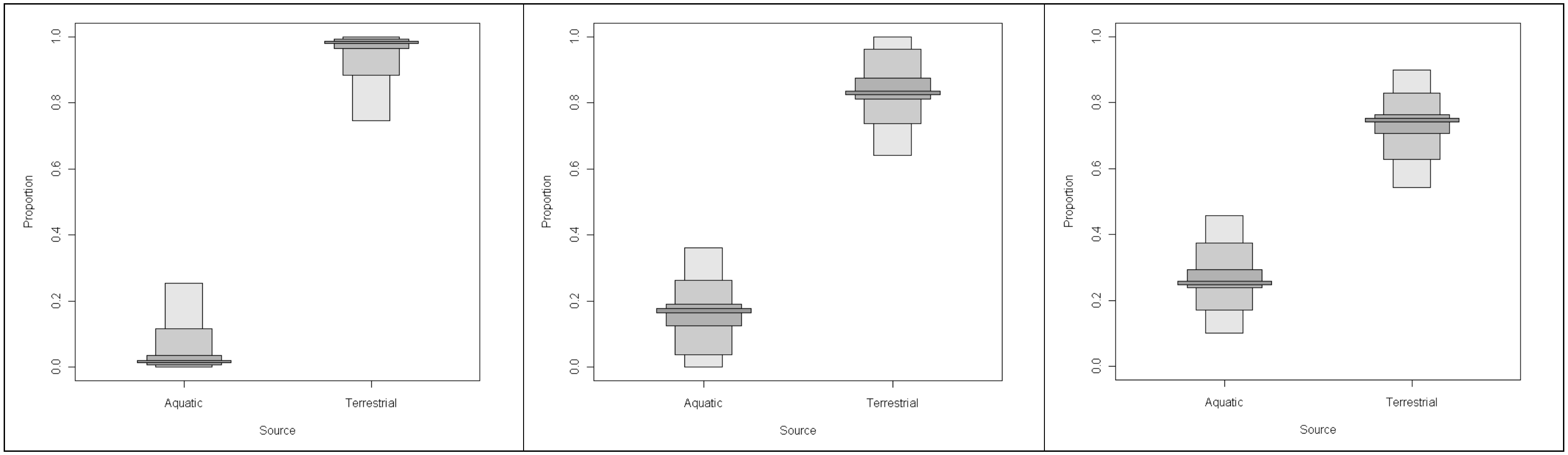
The headwater specialist ground beetles (Group 1, Figure 5.9a) have a consistent ~50:50 split in aquatic and terrestrial subsidies in both summer and autumn. In spring, the mean proportions change to 32:68 split. The specialist ground beetles associated with floodplains (Group 2, Figure 5.9b, Table 5.3) exhibited a mean aquatic subsidy higher than Group 1 in summer and autumn but also exhibited a seasonal shift toward terrestrial subsidies in the spring (~60:40 in summer and autumn, 35:65 in spring). Group 3, low affinity ground beetle species show a lower uptake of aquatic prey compared with Groups 1 and 2. The summer and autumn proportions are again steady between 32-36:64-68, and also show a spring reduction in aquatic prey (to 25%). The final two groups, in-land ground beetles (Group 4, Figure 5.9c) and *Stenus* sp. and *C. 5-punctata* (Group 5) show similar patterns; in the summer terrestrial prey accounts for almost 100% of dietary contributions, with the spring diet incorporating 20-25% aquatic prey. Ground beetles show a small increase in aquatic prey in the autumn (to 15%) but *Stenus* sp. and *C. 5-punctata* show no uptake. Both groups do increase their aquatic prey use in the spring to 24% for ground beetles and 20% for *Stenus* sp. and *C. 5-punctata*.



a) Specialist headwater ground beetles



b) Specialist floodplain ground beetles



c) In-land ground beetles with no ERS affinity

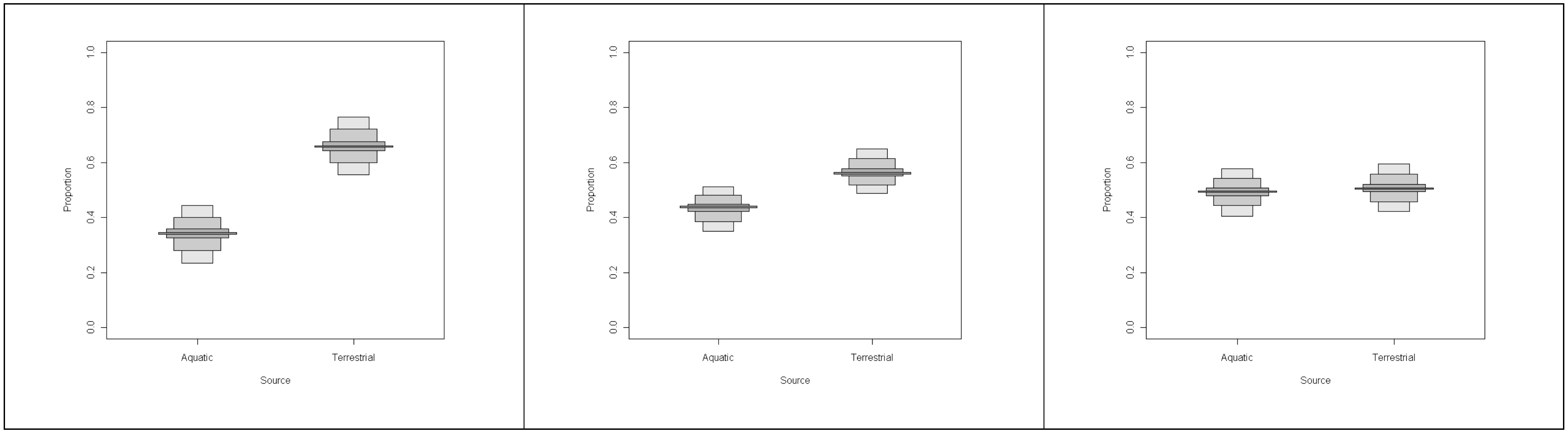
Figure 5.9: Seasonal variations (summer, autumn and spring) in dietary proportions of specialist headwater (a) and floodplain (b) ground beetles (Groups 1 and 2), and ground beetles with no habitat affinity (c) (Group 4).

5.4.4 Impact of inundation

Species from Groups 1-3 were analysed for changes in nutrient sources according to the three inundation risk levels. Individual species were analysed to establish any species-specific responses, as well as functional group responses (Figure 5.10). *B. atrocaeruleum* (Group 1, Figure 5.10a) showed a 35:65 ratio of aquatic: terrestrial sources under low inundation risk, changing under high risk to 55:45. *B. decorum* (Group 1) showed a 60:40 split under low risk, switching to a 45:55 ratio under high risk. *B. punctulatum* (Group 2, Figure 5.10b) exhibited a shift from 60:40 to 35:65. *B. tetracolum* (Group 3, Figure 5.10c) had a 50:50 ratio in low risk patches switching to a 15:85 ratio in high risk sites. Finally *P. albipes* exhibited a small change from 45:55 to 35:65.

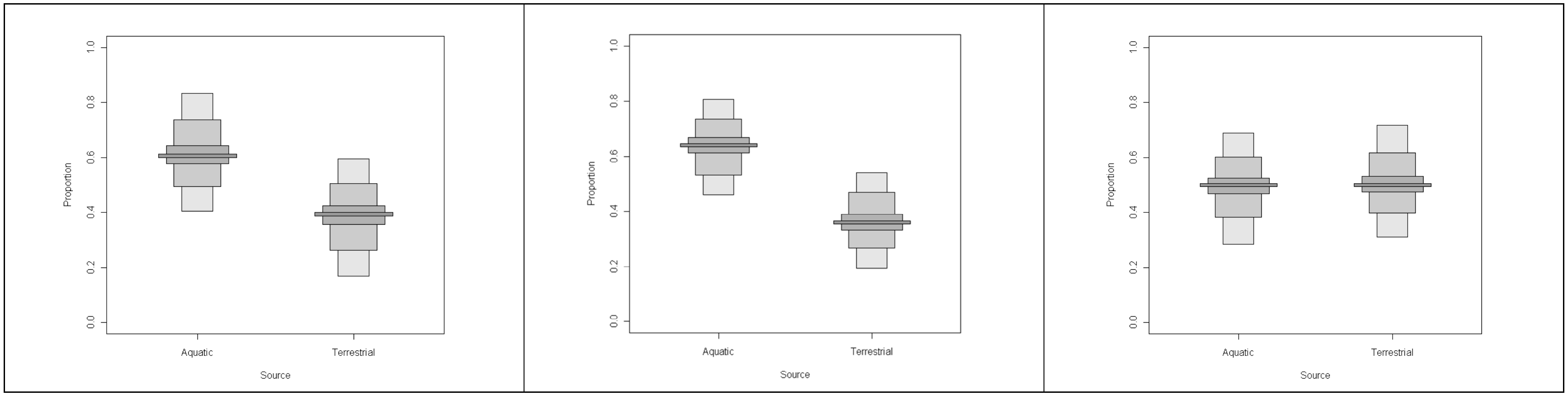
5.4.5 Effect of lateral positioning

Comparison of dietary composition according to proximity to the stream edge produces varying data between groups. Group 1, headwater specialist ground beetles, exhibited strongest variation, with samples taken at the stream edge having a 50:50 aquatic:terrestrial composition, whilst samples from the vegetated areas in land switching to 30:70 proportions (Figure 5.11). This was the only group that exhibited a large switch in dietary proportions according to position. Group 2 (floodplain specialist ground beetles) dropped its aquatic proportions from 60% to 52% inland, Group 3 (low-affinity ground beetles) showed no change between sample positions (~30% aquatic prey), whilst Groups 4 and 5 showed a stable uptake of predominantly terrestrial sources (70% for ground beetles with no affinity to the habitat and >95% for *Stenus sp*. and *C. 5-punctata* beetles).



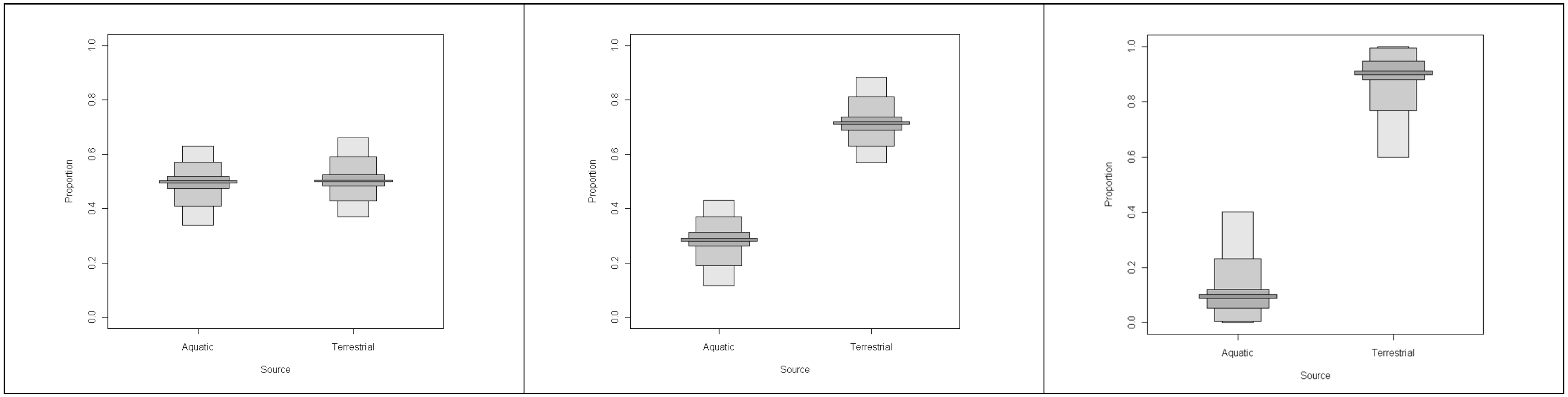
Low Medium High

a) *B. atrocaeruleum*



Low Medium High

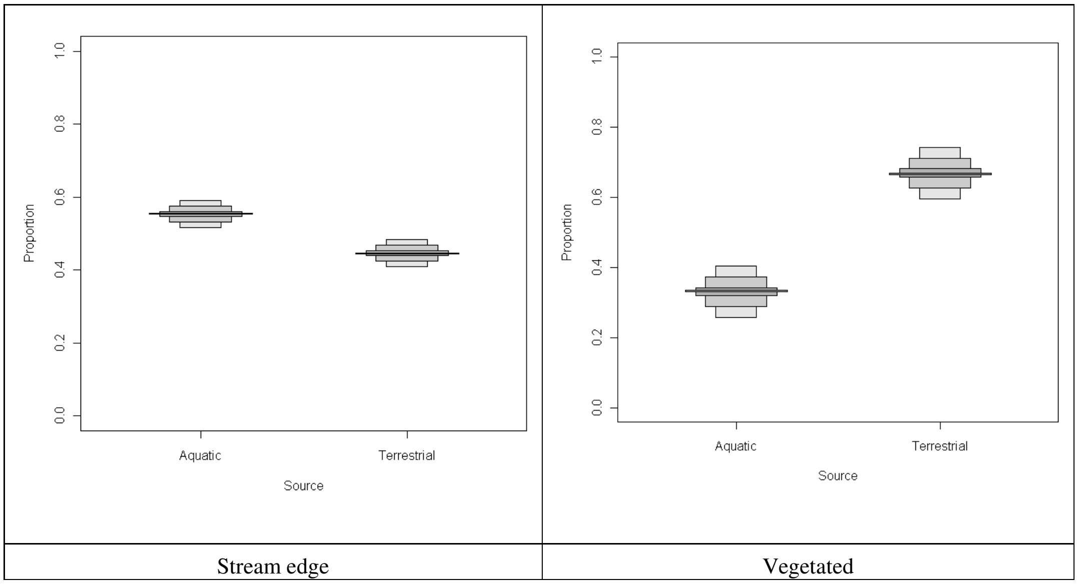
b) *B. punctulatum*



Low Medium High

c*) B. tetracolum*

Figure 5.10: Probability density functions of ground beetle species from each of the groups with a level of affinity to the ERS habitat, *B. atrocaeruleum (a)*, *B. punctulatum* (b) and *B. tetracolum (c)*, showing variation in dietary composition according to inundation pressures.



Stream edge

Vegetated

Figure 5.11: Probability density function of dietary proportions of headwater specialist ground beetles (Group 1) exhibiting switch in dietary contributions with change in sampling position.

Table 5.3: Median values of seasonal aquatic and terrestrial prey contributions according to Coleoptera functional group

Group	Season	Aquatic %	Terrestrial %
Headwater ground beetles	Spring	32	68
	Summer	58	42
	Autumn	55	45
Floodplain ground beetles	Spring	35	65
	Summer	60	40
	Autumn	60	40
Low-affinity ground beetles	Spring	25	75
	Summer	32	68
	Autumn	32	68
Stenus sp. & C. 5-punctata	Spring	20	80
	Summer	5	95
	Autumn	5	95
In-land ground beetles	Spring	75	75
	Summer	0	100
	Autumn	20	80

Table 5.4: Median values of aquatic and terrestrial prey contributions according to inundation pressures on three representative species

Species	Inundation pressure	Aquatic %	Terrestrial %
B. atrocaeruleum	Low	35	65
	Medium	42	58
	High	55	45
B. punctulatum	Low	60	40
	Medium	62	38
	High	45	55
B. tetracolum	Low	50	50
	Medium	30	70
	High	15	85

Table 5.5: Median values of aquatic and terrestrial prey contributions to functional groups according to lateral positioning.

Group	Position	Aquatic %	Terrestrial %
Headwater ground beetles	Stream edge	50	50
	In-land	70	30
Floodplain ground beetles	Stream edge	60	40
	In-land	52	48
Low-affinity ground beetles	Stream edge	30	70
	In-land	30	70
Stenus sp. & C. 5-punctata	Stream edge	5	95
	In-land	5	95
In-land ground beetles	Stream edge	30	70
	In-land	30	70

5.5 Discussion

This study demonstrates that resource acquisition within the ERS habitat has spatial and seasonal variations that are specific to functional groups. The ‘adverse’ (Lytle et al., 2008) conditions of the habitat demand high levels of adaptation from its permanent residents, whilst limited primary production has created resource partitioning and dietary plasticity allowing highly adapted species to utilise the resource in spite of its environmental pressures. Conversely, species with weaker or lacking adaptations show less resource flexibility and find themselves excluded from the habitat under high environmental stress. Even between specialised groups, behavioural responses vary, in turn altering resource acquisition under different regimes and suggesting resource partitioning at very fine scales, which creates highly defined functional groups adapted to varying environmental pressures.

Morphological characteristics have been successfully used to delineate functional groups in Coleoptera (Chapter 3 and Ribera et al., 2001). SIA analysis tests the validity of these morphological groupings by establishing differences in resource acquisition and stress responses. Behavioural variations in ERS specialists have been observed, with species demonstrating microspatial positioning (Bates et al., 2007b), habitat resource partitioning (Andersen, 1988) and microclimate preferences (Henshall et al., 2011). Until now there has been little understanding of how these ‘choices’ guide resource acquisition. The importance of the aquatic subsidy to riparian arthropod communities has been well demonstrated. Paetzold (2006) showed between taxa variations in and dependence upon the aquatic subsidy amongst ground dwelling arthropods (ants, beetles and spiders), although further classification within taxa was not conducted. Within that study beetles were shown to utilise the aquatic subsidy, although it was not a limiting factor – a trait which is repeated in this study where both headwater and floodplain specialist ground beetles exhibit dietary plasticity. Where family groups have been examined, variations in dietary composition have been observed according to size and family (Hering and Plachter, 1997, Paetzold et al., 2005). In the community studied here, there is very little variation in size (the larger *P. albipes* being the exception), so variations in dietary composition are being influenced by other factors, the suggestion being that morphologically driven resource partitioning is a reflection of the strength of adaptations to the habitat.

Initial exploration of the likely sources was conducted using *a priori* knowledge of coleopteran dietary preferences; emergent aquatic insects especially Plecoptera and Diptera (Hering and Plachter, 1997, Paetzold et al., 2005); Collembola (Bauer and Pfeiffer, 1991, Betz, 1998); aphids and Coleoptera larva (Evans, 2009). This allowed the elimination of non-contributing sources (Ephemeroptera, Trichoptera and the abundant *G. viridula* larvae from the terrestrial zone), their absence from the diet is likely to be a result of emergence pathways and feeding strategies, which reduce the likelihood of consumers encountering them). Dominant sources were consistently simulids, Plecoptera, Collembola and aphids with proportions varying between groups. Chironomids were never indicated as an important prey source in this system (compare Hering and Plachter, 1997) but similarly sized simulids were. This is likely to be a function of prey availability, chironomid abundance being much lower than simulids in all the kick samples (typically < 5 compared to several hundred).

The community splits initially into species deriving a greater proportion of their diet from aquatic resources or terrestrial resources, with further seasonal and inundation responses. The need for inundation tolerance within the habitat has been well described (Sadler and Bates, 2008), these data demonstrate that the strength of adaptive mechanisms also provide advantages in sourcing nutrients. Stream edge (floodplain) species and mobile (headwater) species utilise the aquatic resource under all levels of inundation pressure, with mobile species increasing their utilisation with increased inundation (a reflection of reduced ERS area and increased interaction with the stream edge). Modelling of species' positioning within the larger river corridor (Chapter 3) suggests the mobile species have a stronger affinity with headwater habitat than stream edge species. Mobility within the habitat protects a proportion of the population from rapid inundations, associated with flashy headwater systems. Stream edge species trade off the increased resources derived from aquatic sources with increased likelihood of inundation. Although well adapted to survive these pressures, distribution models for these species show a preference for downstream habitat where flows show less rapid fluctuations. *Stenus sp.* and *C. 5-punctata* utilise the inundation avoidance strategy by positioning themselves above all but the highest events. Under these conditions they are excluded from the habitat. This positioning is also shown to remove their access to an aquatic subsidy, as they exhibit a stable dietary composition regardless of position or season (the small input of aquatic nutrients is likely to be an opportunistic response to very high local emergence levels (Hynes, 1961)). Where adaptations are weak or missing, species that opportunistically utilise the aquatic resource exhibit a rapid switch to a terrestrially dominated diet under high stress, or show negligible utilisation of the resource at all (demonstrating their vagrant status within the habitat).

There is strong evidence that nutrient acquisition is a key element in the structuring of ERS Coleoptera communities, and that inundation pressures have different implications according to the strength of adaptations for the environment. Inundation frequency structures riparian arthropod assemblages, with intermediate levels demonstrably enhancing species richness. Unusually or artificially raised and lowered levels of inundation degrade habitat and associated communities in both the short- and long-term (Greenwood and McIntosh, 2008, Hering et al., 2004, Lambeets et al., 2010). Much of the research into inundation responses has been on lowland, modified European rivers (e.g Lambeets et al., 2008, Paetzold et al., 2008) In contrast, the system in this study is a headwater, semi-natural river, with maintenance of minimum flows but retention of natural, surface-water fed flashiness. It and many similar systems within the UK are characterised by high species diversity (Sadler and Bates, 2008) along with high levels of rarity (Luff, 1998, Sadler and Bell, 2002). Rarity is likely to be (partly) due to a heightened reliance on habitat connectivity (Chapter 3), which in turn is a reflection of levels of inundation tolerance. This study demonstrates that reduced inundation tolerance in the species studied also controls dietary choice. Lambeets et al (2009) argued for the need to understand and include the functional responses of specialist invertebrates in management and conservation practice. Understanding how near-pristine communities are structured by natural, intermediate inundation pressures adds to our stock of knowledge for inclusion in the restoration and protection of our rivers.

Within the species study, dietary plasticity is also evident in highly specialised groups, occurring spatially and seasonally. The disturbed nature of the habitat favours species which are able to exploit resources opportunistically when their preferred sources are unavailable. The cumulative advantages of ERS adaptations can be visualised to explain success and abundance of Coleoptera functional groups in the study's headwater habitat (Figure 5.12). Species which have a strong affinity with the habitat possess different adaptations, some of which provide multiple advantages. The most abundant group (Headwater specialist ground beetles) utilises within habitat mobility, high inundation tolerance and dietary plasticity, whilst the least abundant has fixed microspatial positioning, fixed nutrient sources and reduced inundation tolerance.

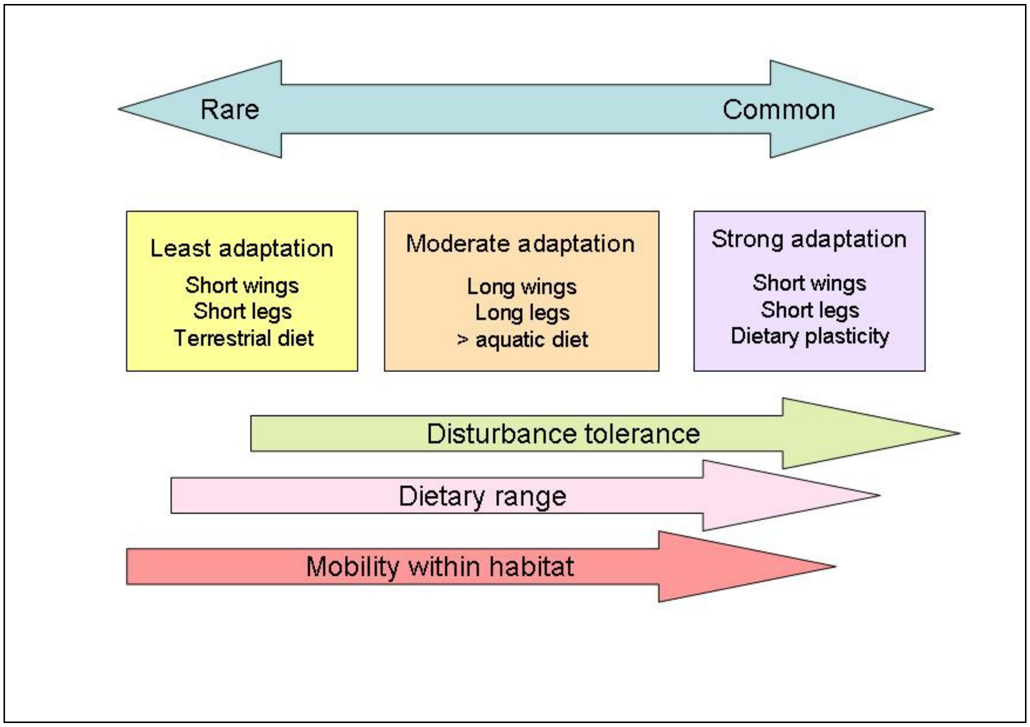


Figure 5.12: Functional adaptations as drivers of distribution and abundance of specialist Coleoptera within a head water ERS network.

5.5.1 Conclusions

The variation in nutrient sourcing between functional groups refutes Thiele's (1977) 'lack of intrageneric isolation'. The ERS habitat supports a complex Coleoptera assemblage with multiple species, often derived from within the same genus. Notwithstanding, this study, in combination with morphological observations, demonstrates the presence of overlapping functional groupings within these assemblages, where highly similar species utilise subtle adaptive variations to partition the spatial and nutrient resources. There are indications that although these variations permit overlapping populations, they favour some species in the studied environment. If this is evidence of geographical positioning through adaptation, then it can be demonstrated by further research into the less abundant groups for which headwater habitat is predicted to be optimal. The presence of low levels of adaptation within specialist species is counterintuitive to the demands of the habitat. In natural river systems however, the required complex network of habitat will be maintained, reducing pressures on metapopulations and allowing species to occupy a specific ERS niche. SIA has provided a valuable insight into community dynamics of ERS Coleoptera which have previously been viewed in terms of how they 'cope' with the demands of their environment. This study demonstrates that these demands benefit the most highly adapted species and force multiple microhabitat and resource selection decisions which enhance the complexity and richness of the Coleoptera assemblages of ERS.

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6

Longitudinal variations in the utilisation of aquatic resources by ground beetles along a 150km length of the River Severn

Longitudinal variations in assemblage structure have been observed in Coleoptera fauna inhabiting exposed riverine sediments on Welsh rivers. Stable Isotopes Analyses of $\delta^{13}C$ *and* $\delta^{15}N$ *were used to identify changes in dietary composition of different functional groups of specialist ground beetles (Carabidae) according to sampling position. The three defined groups exhibited an increasing utilisation of aquatic subsidies in downstream samples, but species associated with headwater habitat switched to a terrestrially dominated diet in the lowest sample sites. Floodplain associated species demonstrated the greatest increase in uptake of aquatic prey downstream, followed by inundation-averse weakly associated species. Behavioural and morphological adaptations specific to functional groups establish differing optimum disturbance regimes and change the efficiency of resource acquisition on a longitudinal gradient.*

6.1 Introduction

At the interface of river and riparia a reciprocal exchange of nutrients maintains a complex and diverse ecotone exhibiting marked spatial and temporal variation (Baxter et al., 2005, Burdon and Harding, 2008, Gray, 1993). One factor driving the complexity of this exchange is the morphological variation in habitats associated with riparian areas which instigate specific ecological responses. The level of structural complexity enhances the interchange, with wooded riparia supporting elevated populations of web-building spiders (relative to wooded areas away from the river) (Nakano and Murakami, 2001) and simultaneously supplying riverine consumers with a supply of terrestrial food (Correa et al., 2007, Richardson et al., 2009). Increased spatial complexity in meandering streams locally increases the surface area and subsequent densities of emerging aquatic prey, promoting a aggregative response in insectivorous birds (Iwata et al., 2003). Exposed riverine sediments offer a superficially less complex environment, but have also been shown to facilitate extensive two way subsidies, with terrestrial consumers extensively utilising aquatic emerging or stranded insects. This uptake can be an opportunistic, temporary response to increased emergence, a common strategy in non-specialised ants (Paetzold et al., 2006) or preferential, and ensuring a dominant contribution of aquatic nutrients, a strategy employed by specialised spiders and beetles (Greenwood and McIntosh, 2008, Hering, 1995). In Chapter 5 it is demonstrated that Coleoptera preferentially utilising the resource also possess strong morphological and behavioural adaptations that facilitate this uptake. These adaptations concurrently enable these specialist species to overcome the environmental pressures imposed within the disturbed ERS habitat (Andersen, 1988, Desender, 1989).

In England and Wales, the ERS resource is predominantly confined to rivers with high stream power and flashy surface fed flow regimes, which leads to a geographical concentration in north and south west England and Wales (Chapter 2). The resource persists in these rivers into low altitude flood plains where anthropogenic modifications have not broken lateral and longitudinal connectivity of river and floodplains, as has been observed in some European systems (Bonn et al., 2002, Van Looy et al., 2006). Where this longitudinal continuity persists, the characteristics of the habitat change downstream, as loss of stream power, flashiness and sediment sorting and fining reducing the frequency and complexity of ERS, typically confining the habitat to meanders, with grain size much reduced in comparison to headwater patches (Church, 1992, Gurnell et al., 2009, Petts et al., 2000). The exceptions to this exponential reduction come when fresh sediment inputs are received from tributary supplies (Benda et al., 2005, Knighton, 1980) or the river channel flows through geological forms which increase the local sediment load (e.g. Rice, 1957)

Much of the research on English and Welsh ERS invertebrate fauna has utilised the abundant and complex northern and western habitat (e.g. Bates et al., 2005, Henshall et al., 2011, Sadler et al., 2005), with the collected data demonstrating existence of diverse, complex and vulnerable assemblages of ERS dependent species. (Bates et al., 2009, Sadler and Bell, 2002). Chapter 3 showed that downstream restructuring of Coleopteran assemblages occurs, especially within ground beetle populations, whilst Chapter 5 suggests that this longitudinal positioning may be a function of strategies for nutrient acquisition traded against inundation risk. Flashy, headwater areas of the

ERS provide a complex and well connected habitat mosaic, where individual patches are susceptible to stochastic high flow events. If the observed differences in longitudinal communities do reflect strategies that are responses to inundation threats, then the lower altitude habitat (which stream edge species show a preference for) should exhibit a less stochastic flow regime which reduces the threat of inundation and increases potential for the uptake of aquatic resources. This is (generally) what is expected with downstream progression. Headwater systems typically possess high and erratic rainfall, draining rapidly over steep catchments. When they descend to lower altitudes, raised ground water inputs and increased timings of surface runoff buffer the rate of discharge change (Bridge, 2003).

Alongside hydrological changes downstream, changes occur in nutrient availability and productivity (Junk et al., 1989, Vannote et al., 1980, Ward and Stanford, 1983). Headwater streams support an abundance of organisms in defiance of their reduced primary productivity; terrestrial carbon has been suggested as the subsidy which enables this biomass, entering as vegetative matter which is processed by guilds of shredders and gatherers. Downstream, primary productivity rises and the reliance on terrestrial carbon declines (Vannote et al., 1980, Wallace et al., 1997, Wallace and Webster, 1996). With increasing distances from headwaters, nutrient supplies within the river channel become a complex synthesis of upstream 'leakage', flood-pulse contributions from the floodplain, and in-stream productivity (Thorp and Delong, 1994). The sequestration and movement of nutrients along this gradient is further complicated by spatial variations in nutrient spiralling (Newbold et al., 1982), and groundwater and hyperheic interactions (Boulton et al., 1998, Dahm et al., 1998, Tockner and Stanford, 2002). These processes can cause highly localised changes in nutrient availability; increased velocity or dilution (via groundwater inputs) can increase biotic retention of nutrients and compress spiralling (Mulholland et al., 1995), which in turn reduces primary production (Trudeau and Rasmussen, 2003). Substrate variations can change basal algal communities, altering the relative contributions of aquatically and terrestrially derived carbon (Cabana and Rasmussen, 1996, England and Rosemond, 2004).

6.1.1 Stable isotopes, nutrient sources and dietary composition

Stable isotope analysis (SIA) utilising carbon and nitrogen provides a mechanism for identifying the relative contribution of possible nutritional sources, with naturally occurring lighter, abundant forms (^{12}C and ^{14}N) of both elements being preferentially metabolised and excreted by consumers. This process causes a predictable increase in isotopic concentrations in consumers, which can be used to assign trophic positions (Hood-Nowotny and Knols, 2007). Whilst the precise values of enrichment vary between species, individuals and tissues (Post, 2002, Vander Zanden and Rasmussen, 2001), a standardised enrichment rate has been established for whole invertebrates; at 2.3 ± 0.16 ‰ $\delta^{15}N$ and 0.4 ± 0.13 ‰ $\delta^{13}C$ (McCutchan et al., 2003).

The importance of the reciprocal exchange across the aquatic:terrestrial interface is well established, and has been shown to influence the structure of both communities (Correa et al., 2007, Jardine et al., 2008, Kato et al., 2004, Nakano and Murakami, 2001). Terrestrial consumers utilise the subsidy at all trophic levels, as herbivores and predators or scavengers (Burdon and Harding, 2008, Greenwood and McIntosh, 2010). The subsidy is spatially (Hering and Plachter, 1997) and seasonally (Paetzold and Tockner, 2005) variable and can be altered by changes in the flow regime (Greenwood and McIntosh, 2010). SIA has been shown to be a valuable tool in identifying dietary composition from multiple potential souces (Hood-Nowotny and Knols, 2007, Inger et al., 2006, Peterson and Fry, 1987) and spatial variation in diet within populations (Ainley et al., 2003, Sierszen et al., 2006). Chapter 5 demonstrated that the technique can be applied to examine local variations in dietary composition and elucidate differences in functional responses to environmental stresses. This study hypothesises that functional responses are consistent within species across a longitudinal gradient, representing permanent nutrient acquisition strategies which are best adapted to specific levels of inundation stress. These functional responses combine with behavioural adaptations to dictate the positioning of functionally specific optimum habitat along the gradient.

6.2 Aims, objectives and hypothesis

The ERS habitat persists along the River Severn from its headwaters on Plynlimon in the Cambrian Mountains to lowland patches in Shropshire (approximately 150km). The resource changes from a complex and abundance mosaic in the headwater reaches, to isolated, single patches in the Shropshire floodplain. Longitudinal changes in the ground beetle fauna of ERS are also exhibited. Using SIA (δ^{13}C and δ^{15}N) the study aims to investigate whether changes occur in the dietary composition of riparian beetles inhabiting the ERS along a longitudinal gradient and how these changes (if they occur) are related to functional group. The hypothesis, based on data from preceeding chapters, is that floodplain specialist ground beetles will show an increased uptake of aquatic prey with downstream position, as their behavioural adaptations coincide with optimum conditions; mobile, headwater specialists may be disadvantaged under these conditions.

Objectives

- Analyse samples of riparian predatory Coleoptera and their potential prey (both aquatic and terrestrial) from ERS habitat occurring along the 150km distribution on the River Severn.

- Establish whether changes occur in prey sources along the longitudinal gradient and whether changes vary between functional groups observed in headwater studies.

- Assign the relative importance of environmental pressures versus species' traits in determining prey selection via dietary plasticity.

6.3 Methodology

6.3.1 Study sites and sample collection

Fifteen ERS habitat patches were sample from five positions along the 150km continuum of ERS on the River Severn from its headwaters above Llanidloes in mid-Wales to Shropshire (Figure 6.1). Samples of dominant ground beetle beetles and potential terrestrial prey (collembola and aphids) were collected by hand from each sample site in June 2009, August 2009 and April 2010. Samples of potential aquatic prey were also collected at the same time, using a standardised three minute kick sample using a 500µm net. This sampling method ensured consumers, and potential terrestrial and aquatic prey were obtained simultaneously at each site in summer, autumn and spring.

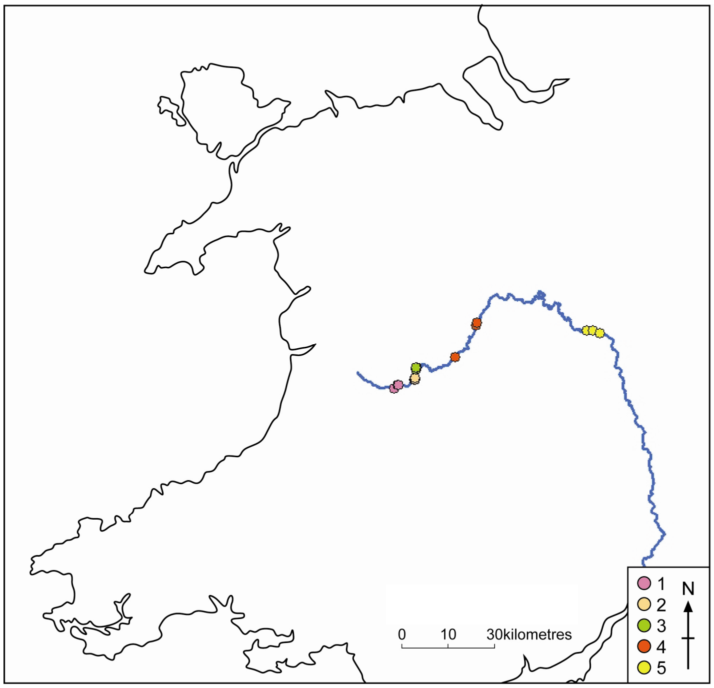


Figure 6.1: Relative positions of 15 sampling points along the River Severn, grouped in threes according to longitudinal position (1-5), moving from beneath Llyn Clwyedog, downstream to Llandinam, Caersws, Abermule and Welshpool, and Ironbridge (Sampling points with close proximity overlap on the map).

6.3.2 Sample processing

All invertebrates were kept alive until they were returned to the laboratory where they were frozen prior to identification (to species for Coleoptera and to family for potential prey). Gut contents were removed and samples were then dried for 24 hours at 60°C before being ground and split into two sub-samples, with one half undergoing lipid extraction. A 2:1 mix of ethanol:methanol was added to ground samples for a minimum of 30 minutes before centrifuging and removal of the solvent and dissolved lipids. This process was repeated three times and the remaining samples then dried at 60°C for > 24 hours (Folch et al., 1957). Individual samples were weighed (carbon 0.2mg ± 0.05mg; nitrogen 0.6mg ± 0.05mg) into tin cups prior to combustion.

Samples were combusted at 920°C before being passed through a reduction column in an Elementar Pyrocube, the isotopic composition of sample gases was then determined on an Isoprime continuous flow mass-spectrometer. Within-run reproducibility was better than 0.07 per mil for both $\delta^{13}C$ and $\delta^{15}N$. The two techniques were analysed on separate sub-samples rather than 'peak-jumping'.

6.3.3 Data Analysis

Consumer samples were assigned to one of five functional groups (headwater specialist ground beetles, floodplain specialist ground beetles, weak affinity ground beetles, non-specialist ground beetles and specialist non-ground beetles), defined using morphological measurements and distribution models (Chapter 3). Variance in stable isotope signatures was initially tested using Multivariate Analysis of Variance (with a post-hoc Tukey test), to explore variations between spatially distinct populations of consumers and potential sources

Data were then entered into a Bayesian isotope mixing model available as an open source R package, SIAR v4 (Parnell et al., 2010a). SIAR models were fitted using a Markov Chain Monte Carlo method (MCMC) to produce plausible values of dietary proportions of sources consistent with the data using a Dirichlet prior distribution. The SIAR MCMC was run with 500,000 iterations, the first 50,000 being discarded before thinning to reduce autocorrelation. The resulting probability density functions of the feasible dietary proportions allow identification of the most probable solutions based on median values, the total range of credibility intervals describing possible proportions of potential sources (Parnell et al., 2010b). Trophic positioning was visualised using a Bayesian probability framework to evaluate most likely distributions of isotopic values by functional group (Jackson et al., 2011).

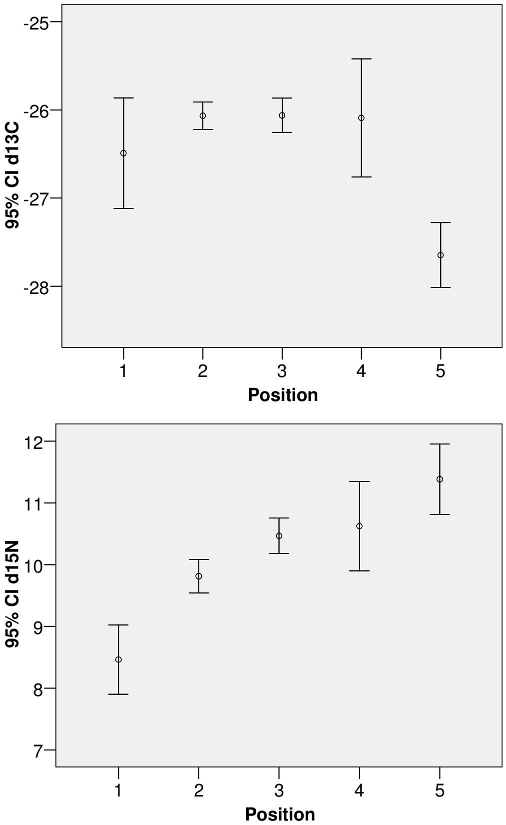
6.4 Results

A total of 719 analyses were undertaken on 572 Coleoptera, 182 potential aquatic prey and 65 potential terrestrial prey. Coleoptera comprised 327 ground beetles with known affinity to the habitat, and 145 other predatory beetles (phytophagous click beetles were not included in the analyses). Source samples were derived from between 3-5 amalgamated individuals. All samples were classified according to the longitudinal position at which they were collected and the date.

Prior to functional group analysis, changes in community isotopic signal were explored. Downstream changes were observed in Coleoptera and aquatic source isotopic signals; with $\delta^{13}C$ (Figure 6.2a) showing consistent values until Position 5 (Sheinton, Buildwas and Ironbridge) when they were lower (F: 9.16; df 4; $p < 0.001$). Post hoc testing showed the difference between Position 5 and all others to be significant (1: p 0.006; 2: $p < 0.001$; 3: $p <0.001$; 4: $p <0.001$). $\delta^{15}N$ (Figure 6.2b) showed consistent variation between sampling positions (F: 13.025; df 4; $p < 0.001$) which represented progressive enrichment downstream. Position 1 was significantly lower than all other sampling positions, Position 2 was significantly different from 3 (significance values from post hoc testing shown in Table 6.1).

Table 6.1: Post-hoc Tukey test results of between sampling position variation in Coleoptera $\delta^{15}N$.

Position	1	2	3	4	5
1	-	**0.004**	**< 0.001**	**0.002**	**< 0.001**
2	**0.004**	-	**0.011**	0.423	0.379
3	**< 0.001**	**0.011**	-	0.998	0.082
4	**0.002**	0.423	0.998	-	0.653
5	**< 0.001**	0.379	0.082	0.653	-

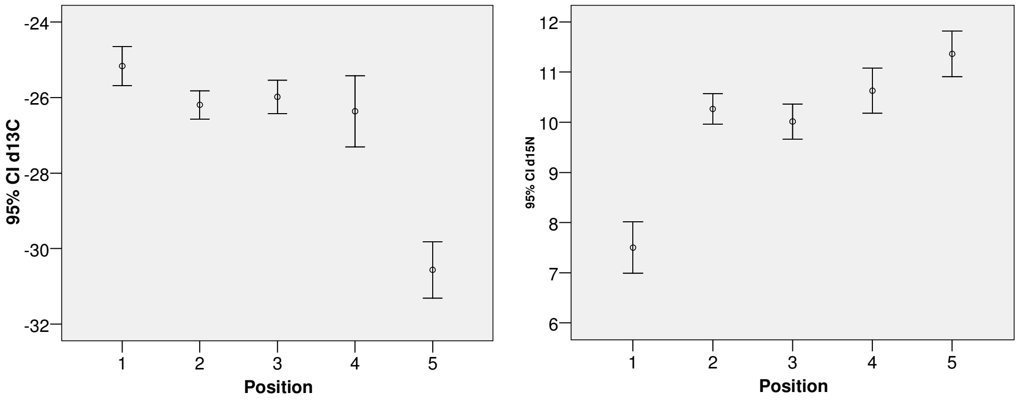


6.2a: $\delta^{13}C$ by sampling position

6.2b: $\delta^{15}N$ by sampling position

Figure 6.2: Coleopteran isotopic variation (2 SE) between sampling position, showing position 5's relative $\delta^{13}C$ depletion in comparison to other sampling position (6.2a) and the downstream enrichment of $\delta^{15}N$ (6.2b).

Similar isotopic patterns were observed in community changes in potential aquatic prey. Samples from Position 5 also showed a significant depletion in δ^{13}C (F: 37.058; df: 4; $p < 0.001$), with variation from all positions significant at < 0.001 in post-hoc testing (Figure 6.3a). Downstream enrichment of δ^{15}N (Figure 6.3b) was also evident, ($p < 0.001$) with variation significant between Positions 1 and 2 (p 0.001), 4 (p 0.001) and 5 ($p < 0.001$); Positions 2 and 5 (p 0.018) and 3 and 5 (p 0.01).

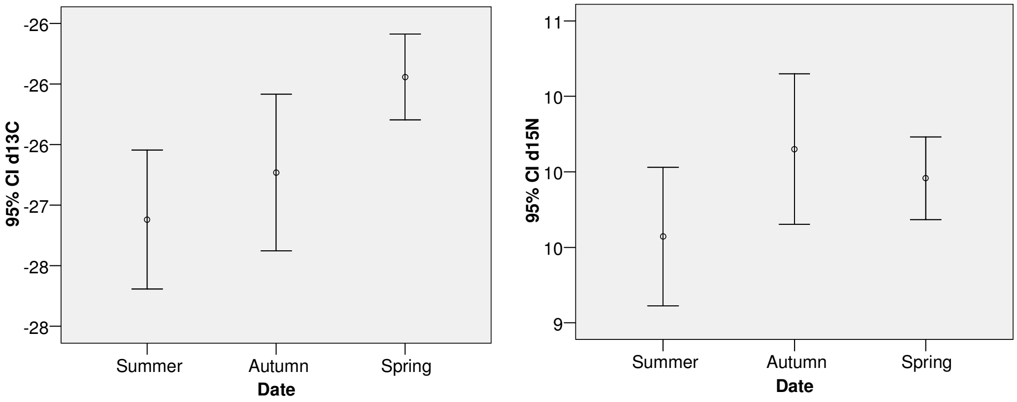


6.3a: δ^{13}C by sampling position

6.3b: δ^{15}N by sampling position

Figure 6.3: Changes in isotopic values (2 SE) of potential aquatic prey, showing Position 5's relative δ^{13}C (6.3a) and downstream enrichment trend of δ^{15}N (6.3b)

Interseasonal variation in isotopic values of potential prey was significant (F: 5.571; df 4; $p < 0.001$) with post-hoc testing showing significant difference ($p < 0.001$) between summer and spring δ^{13}C values (Figure 6.4a), and between summer and autumn δ^{15}N values (p 0.018) (Figure 6.4b).



6.4a: $\delta^{13}C$ by sampling position 6.4b: $\delta^{15}N$ by sampling position

Figure 6.4: Seasonal changes in isotopic values of potential prey (2 SE). Spring shows relative enrichment of $\delta^{13}C$ (6.4a), autumn shows relative enrichment of $\delta^{15}N$ (6.4b).

Ellipses of probable isotopic values were consistent with the data presented in Chapter 5, with the same vertical positioning of functional groups (Figure 6.5). Specialist ground beetles, (defined in Chapters 4 and 5), show greatest $\delta^{15}N$ enrichment (an indication of the relative contribution of aquatic prey to the diet) with Group 2 (floodplain specialist ground beetles) more enriched than Group 1 (headwater specialist ground beetles). Group 3 (ground beetles with a weak affinity to the habitat) occupy a median level of enrichment, Groups 4 (in-land ground beetles) and 5 (specialist rove beetles) showing least enrichment and therefore greater utilisation of terrestrial prey.

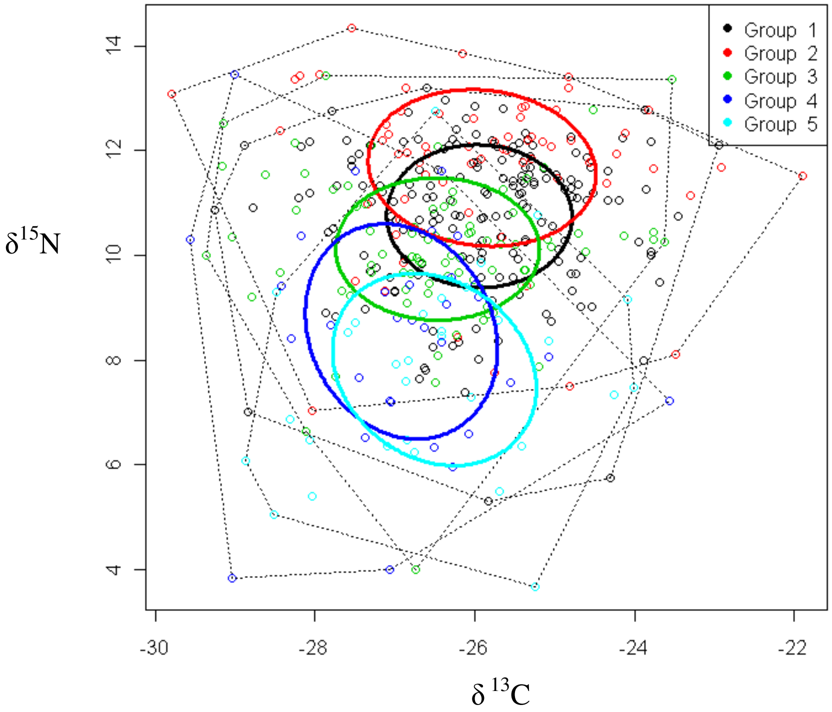
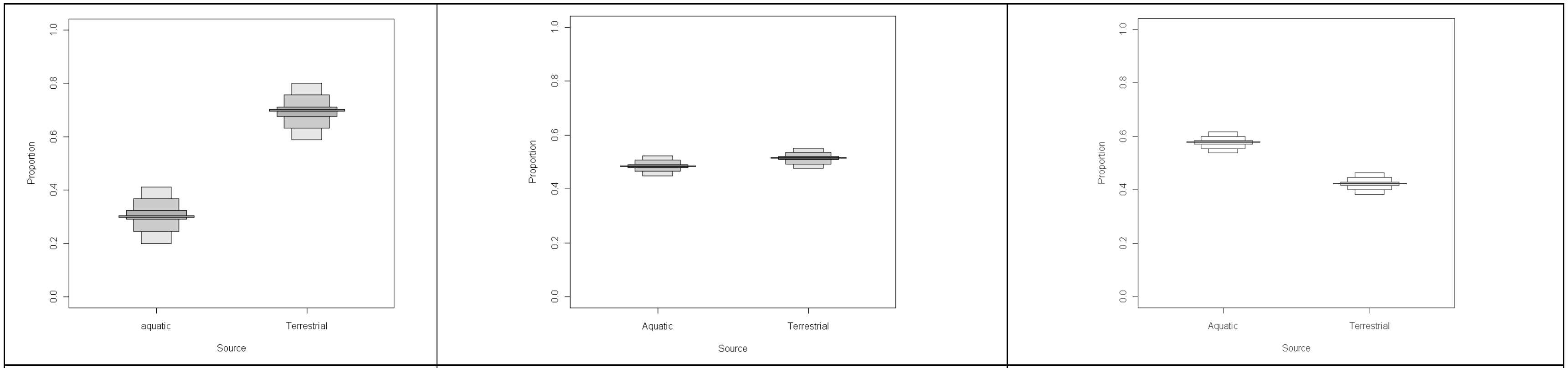


Figure 6.5: Variations in trophic positioning according to functional group (1: Headwater specialist ground beetles; 2: floodplain specialist ground beetles; 3: low-affinity ground beetles; 4: inland ground beetles; 5: specialist rove beetles. Dotted lines represent total distribution of data values, ellipses represent probable distributions.

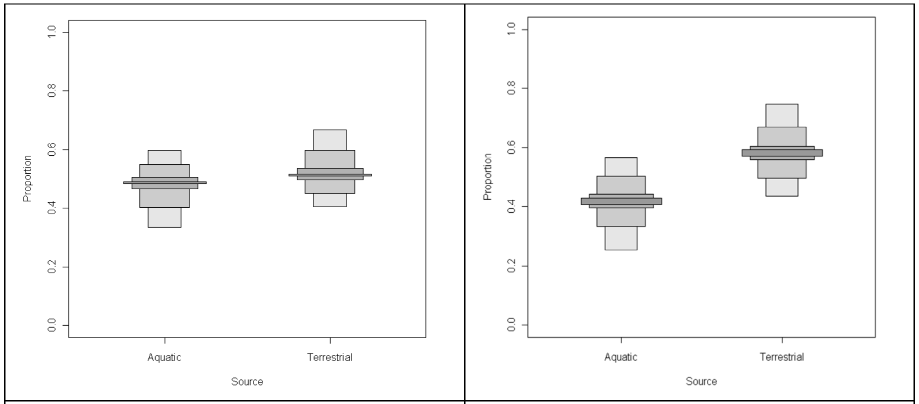
There are slight indications of carbon enrichment in the diet, although the range of possible values does not suggest a strong variation between functional groups. The three dominant ground beetle groups (1-3) were analysed to establish how functionality affected their resource acquisition spatially, with the data being visualised via a Bayesian probability density functions. Group 1, headwater ground beetles showed a gradual increase in use of aquatic prey downstream (Figure 6.6), until the final sampling position, where terrestrial prey dominates the diet. In headwater sites, the proportions are around 30:70 aquatic:terrestrial, this rises to a maximum of 65% aquatic in Position 4 (Abermule and Welshpool). In Position 5, the terrestrial component rises to 60%.

Floodplain specialist ground beetles (Group 2) were absent from the first headwater sampling position. At their first sampling point, aquatic sources show a small dominance (52%) but this changes to 75% aquatic composition of diet in all other sampling positions (Figure 6.7). Group 3 (low affinity ground beetles) were also missing from the headwater sample sites. They exhibited a switch from a terrestrial prey dominated diet in position 2 (65%) to an aquatic prey dominated diet in the lowest sites (around 60%) (Figure 6.8).

Group 3 (low affinity ground beetles) were also missing from the headwater sample sites. They exhibited a switch from a terrestrial prey dominated diet in position 2 (65%) to an aquatic prey dominated diet in the lowest sites (around 60%) (Figure 6.8).

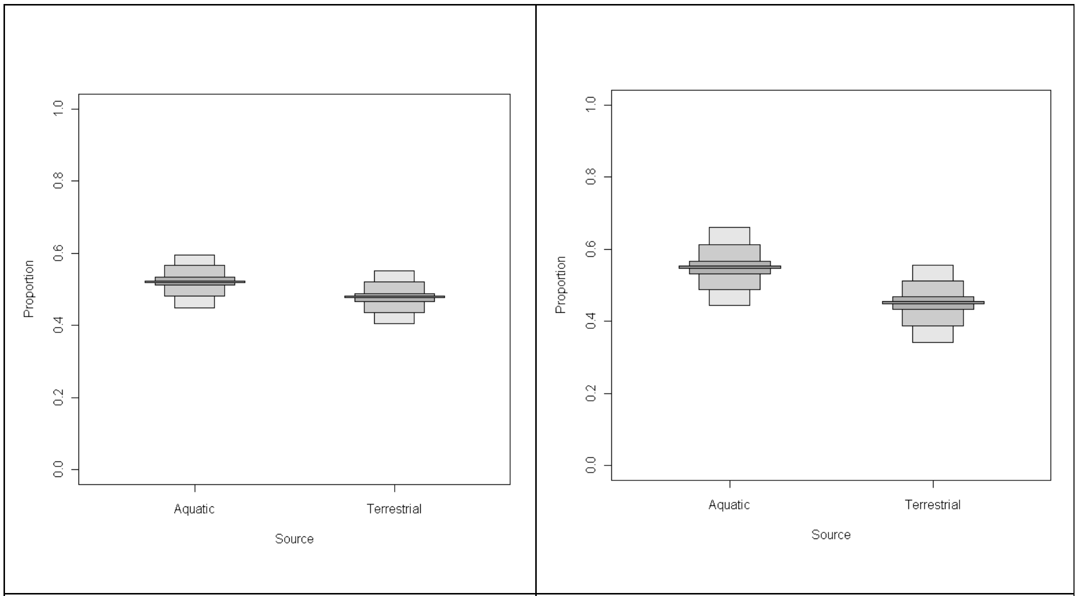


Position 1 | Position 2 | Position 3

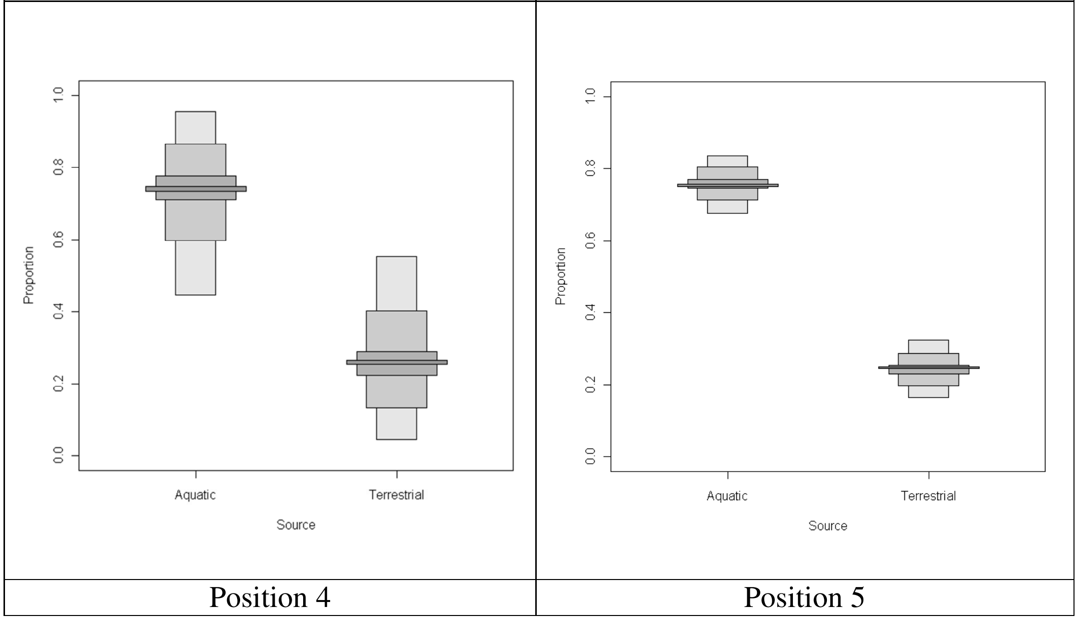


Position 4 | Position 5

Figure 6.6: Headwater specialist ground beetle dietary composition according to sampling position (1-5) showing switch from aquatic dominated prey in headwaters (Position 1), to a balanced aquatic:terrestrially sourced diet (Positions 2-4) before a final switch back to an aquatically dominated in the furthest downstream sampling points (Position 5)

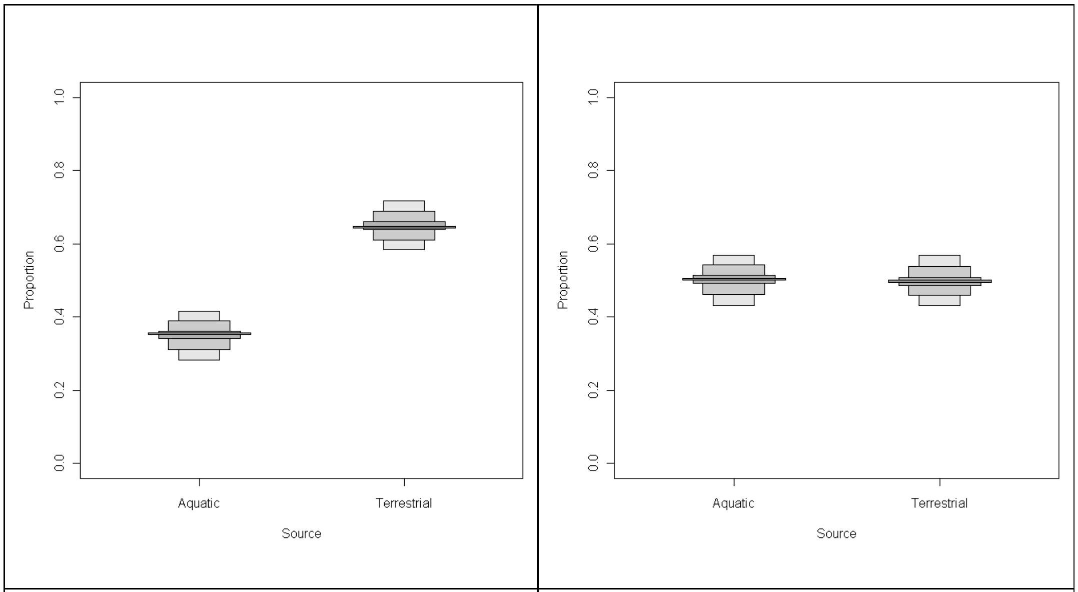


Position 2 Position 3

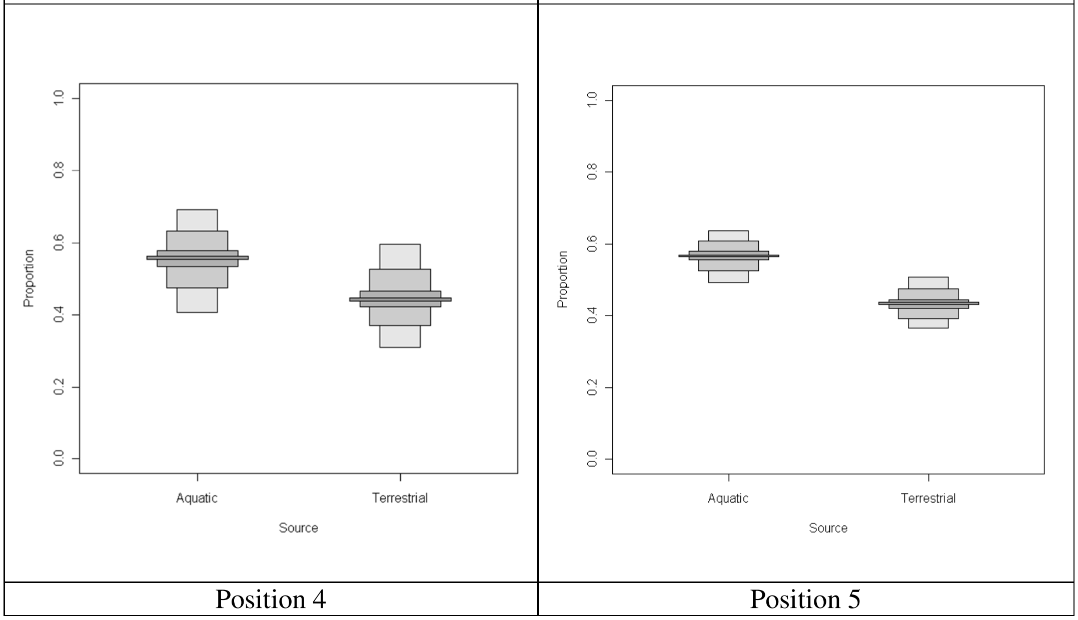


Position 4 Position 5

Figure 6.7: Floodplain ground beetle dietary composition according to sampling point, showing increasing aquatic contributions with downstream progression (2-5). No individuals were sampled at Position 1.



Position 2 Position 3



Position 4 Position 5

Figure 6.8: Dietary composition of low affinity ground beetles according to sampling position, shifting from aquatic dominated diet in sampling positions nearest to headwaters before stabilising with a small dominance of aquatic prey downstream.

6.5 Discussion

The spatial variations in the isotopic signatures of sources and consumers indicate the complexity of the river's nutrient supply along a longitudinal gradient. The downstream $\delta^{15}N$ enrichment is indicative of both natural and anthropogenic processes, with retention of naturally-derived nitrogen supplemented by additions from urban and agricultural sources (Carpenter et al., 1998). Even headwater signatures which possess raised $\delta^{15}N$ in comparison to pristine site studies (Milner et al., 2000) indicate the influx of anthropogenic nitrogen at an early stage (with water treatment, agricultural and landfill inputs entering the river at or downstream of Llanidloes). The depleted $\delta^{13}C$ values in the lowest sample points provide the strongest evidence of floodplain complexity over-riding simplistic models of nutrient transfer longitudinally, with possible causes including groundwater influx (Tockner and Stanford, 2002) and substrate changes altering algal production (England and Rosemond, 2004). These spatially distinct isotopic signatures preclude homogenisation of the data set.

Seasonal variations occur only within aquatic samples, demonstrating the presence within the riverine system of enrichment processes reflecting annual cycles of productivity (sensu Yoshioka et al., 1994). This variation is not however significantly reflected in consumer signals – which may be a reflection of lifecycles, as adults function in autumn and spring with an intervening period of diapause (Andersen, 2006).

Variations in the response of functional groups complement observations of a headwater community (Chapter 5), and provides data that matches subsidy levels seen on European rivers (Hering and Plachter, 1997, Paetzold et al., 2005). Trophic positioning initially confirms the stability of prey selection within the different functional groups within the entire dataset. The generic terms assigned to the three ground beetle groups with a level of affinity to the habitat are indicative of their distributions based on morphological and abundance data (Chapter 3). This study tests the validity of these terms by examining changes in resource acquisition under changing circumstances. All three groups exhibit an increase in the proportions of aquatic prey in their diets as they are sampled downstream. The level of this increase varies between groups, and in the headwater specialists switches to a terrestrial dominance in the sites sampled furthest downstream. The downstream ERS resource is poorly connected and less complex, relative to the headwater resource (Chapter 2) and inundation pressures are likely to occur over more defined seasonal scales (Bridge, 2003). The composition and quantity of the aquatic subsidy will also be different, with increased (Grubaugh et al., 1997) productivity increasing the potential subsidy. The observed uptake in all three functional groups will be (at least partly) explained by raised local productivity. The observed switch to terrestrial prey in headwater specialists argues however that the level of subsidy is not the only factor selecting prey selection.

Behavioural differences in the species are known, with *B. punctulatum* from the floodplain grouping exhibiting stable positioning at the stream edge, in comparison to *B. atrocaeruleum* (grouped in the headwater species) which is mobile in ERS habitat).

In Chapter 5 it is argued that this elasticity of positioning benefits *B. atrocaeruleum* in habitat which has very high levels of disturbance. Preferential spatial positioning comes with trade-offs; increased access to the aquatic subsidy or decreased risk of disturbance exposure and the relative costs of this risk change with longitudinal position. Floodplain specialists are positioned at the stream edge, constantly available to intercept the subsidy, whereas only a proportion of local populations of headwater species will be in that position at any given point. As the numbers of emerging insects rapidly decline away from the stream edge (Briers et al., 2005, Petersen et al., 1999) access to the subsidy is curtailed in mobile species; as floodplain species benefit from their optimum habitat and potentially significantly reduce prey numbers (Paetzold and Tockner, 2005), headwater species are excluded from resource utilisation and turn to terrestrial prey. Under less flashy flow regimes, the benefits of raised aquatic subsidies outweigh inundation risks for those species spatially positioned to take advantage of them. The reduced flashiness of floodplain rivers may also explain the longitudinally raised aquatic subsidy in low-affinity species. Data in Chapter 5 indicated that these species have high aversion to inundation risk, but are opportunistic consumers of aquatic prey where that risk is reduced. The relative stability of floodplain flows therefore allows them to utilise the raised subsidy, and, given their larger size, they can consume larger prey, thereby avoiding direct competition with specialist species.

Several studies on ERS specialists have stressed the importance of intermediate levels of disturbance in maintaining stable and diverse assemblages (Greenwood and McIntosh, 2008, Lambeets et al., 2008). The dietary shifts observed in this study indicate that what can be classed as ‘intermediate’ is directly related to the adaptations that are possessed to ameliorate the impacts of that disturbance. Headwater specialists have greater tolerance of inundation pressures which benefit local populations under disturbance levels that are too high for floodplain specialists and low-affinity species. But under differing conditions, the same adaptations disadvantage previously highly adapted species.

6.5.1 Conclusions

This study has demonstrated the presence of longitudinal structuring processes in specialist Coleopteran assemblages along the River Severn that have been suggested by abundance data (Chapter 3) and isotopic data from a headwater dataset (Chapter 5). The data show that the strength of the aquatic subsidy has spatial and functional group variations that are driven by behavioural adaptations that delineate the conditions of optimum habitat. The adaptations serve to reduce competition and allow species to coexist within individual habitat patches, although differently benefitting individual species according to local pressures. The results show a longitudinal complexity within ERS specialist Coleoptera that has not previously been demonstrated and emphasis the need to maintain the longitudinal cohesion of the ERS resource.

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7

Conclusion

The combined conclusions of the different elements of the research are presented: ERS invertebrates form complex multi-dimensional assemblages with reliance on an equally complex habitat resource. Further research areas are proposed, along with potential limitations.

7.1 Exposed riverine sediments and their associated invertebrates: landscape integrity and community cohesion.

This research project has enabled a landscape-scale approach into the controls of ERS Coleopteran assemblages, looking beyond the autecology of individual species to explain the diversity of the communities associated with the habitat. Understanding how the resource is occupied and utilised across gradients of longitude, connectivity and increasing terrestrial stability provides insights into the consequences of habitat degradation on resident assemblages at a riverine scale and as such can inform future conservation and resource management strategies.

The reliance of associated species on the habitat constrains possible distributions because of the characteristics of rivers with which the resource is associated. Whilst current ERS distributions are in part a function of historical degradation, they are also strongly dictated by hydrogeomorphological forces and underlying geology. The regional distribution of habitat initially predicts the occurrence of complex formations of ERS, and the likelihood (in the absence of downstream channel modifications) of sediment transport to provide floodplain habitat within rivers. Knowledge of the location of a river's headwaters provides at least enough information to establish its potential to contain ERS i.e. does it exhibit a steep incline? Is it predominantly rainfall/surface water fed? What is the sediment store within the catchment? The long term impacts of impoundment, abstractions of sediments and water, and engineering works on within-channel sediment movements are well understood, and therefore the potential for degradation and loss of ERS habitat where new schemes are implemented can be viewed within the context of the catchment in which they are taking place. A database now exists which covers all major distributions of ERS in England and Wales, by river. Although positions are liable to change with natural habitat turnover, in the absence of changes to the channel or flow regimes, overall amounts are likely to remain constant over time. Similarly, in rivers where it is absent, restoration procedures can only be expected to reintroduce the ERS habitat where the characteristics of the river support its presence.

When species' distributions are modelled, lateral and longitudinal complexity emerges at local and regional scales, with data indicating the presence of multiple levels of specialisation that fit species into functional groups and these groups to specific environmental regimes. Consequentially assemblage structure can be predicted spatially, and the factors producing rarity (chiefly dependence on habitat complexity and connectivity) understood. However, they also enable us to understand why morphologically similar species achieve peak abundances under differing environmental scenarios.

The intrinsic role of flooding is much discussed in relation to the formation and maintenance of ERS, and the pressures it places upon associated species. The long-term impacts of differing regimes reveal the variation in adaptations and inundation resilience between families, and further explain levels of rarity, local spatial positioning and resource utilisation. Dichotomous responses to inundation frequency between rove beetles and ground beetles within the same habitat patches demonstrate how a variable flow regime can temporarily benefit one family. Under natural conditions, interannual fluctuations in rainfall are reflected in the responses of Coleoptera, low flows benefitting rove beetles, high flows benefitting ground beetles. Prolonged stabilisation of the regime, in either direction, therefore has the potential to reduce the habitat suitability for different elements of the ERS community; it is the inherent, exaggerated stochasticity of the environment that enforces long-term assemblage diversity.

Inundation is also shown to be a driver in directing prey selection amongst ERS specialists, or rather, the adaptations employed to avoid inundation stresses. Inundation has a role in altering temporal structure of associated assemblages, but also spatial structure. The occurrences of morphological and behavioural adaptations that favour survival or avoidance dictate the efficiency of aquatic prey utilisation. Weaker adaptations and stronger inundation aversion position species away from high risk areas (such as the stream edge), reducing aquatic prey availability and enforcing a reliance on terrestrial prey. Highly adapted species demonstrate greater uptake of aquatic prey, as their survival mechanisms and avoidance strategies enable a successful trade off between the risks of inundation and the benefits of resource acquisition. The impact of minor changes in behaviour becomes evident when resource acquisition is studied at a larger scale; longitudinal variations in assemblages are a reflection of subtly different responses to inundation threat. In flashy, headwater systems, a slight increase in risk aversion (shown by increased within-habitat mobility) reduces aquatic prey uptake, but enhances local abundance. The risks of the trade off are not high enough to favour permanent stream edge positioning under this regime. In the floodplains, where the demands of the regime alter, the risks of stream edge positioning are reduced, and these species are favoured.

By combining the factors controlling ERS distribution and influencing local and regional assemblages, it is possible to conceptualise (Figure 7.1) the longitudinal structuring of the ERS community as a consequence of the combined processes of hydrology, resource availability and adaptive strategies. This mechanism reinforces the need to view specialist invertebrates of ERS at a regional and catchment scale, with the whole diversity of the system intrinsically reliant on the sustained connectivity of habitat and populations along the headwater:floodplain gradient.

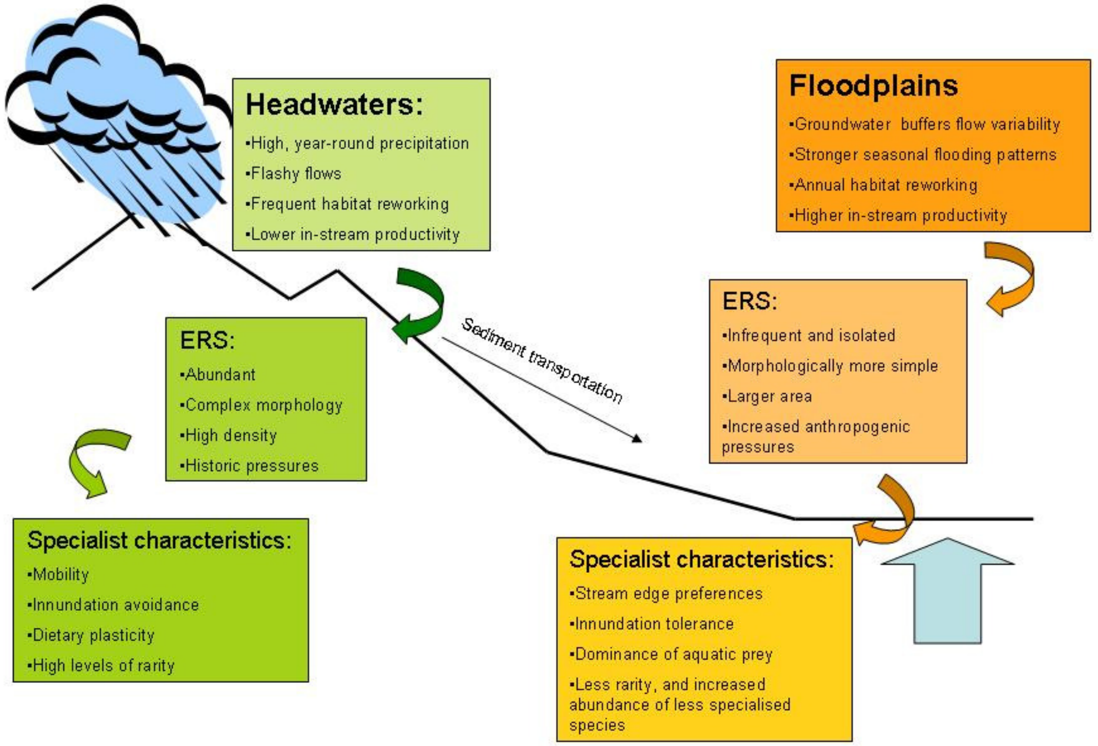

Figure 7.1: Conceptual model of processes structuring specialist invertebrate communities on English and Welsh ERS; demonstrating the complexity of biotic and abiotic factors enforcing local population controls defining longitudinal variations in habitat and associated specialist.

7.2 Limitations observed within the research

This research project has established the extent of the ERS resource within England and Wales and goes some way to explaining the complexities of associated Coleopteran assemblages. It establishes the importance of habitat complexity at both local and regional scales and emphasises that ERS communities are spatially structured according to highly refined levels of specialisation, creating multiple overlapping niches and maximising assemblage diversity.

However, several limitations were observed within the research that should be taken in to consideration in future research planning, and in applying outcomes of the project:

- Assessment of the ERS resource was undertaken using aerial photography, which included differing seasons and flow levels. As such the database is likely to be an underestimation of the total extent of the resource, with habitat patches either submerged or obscured by tree canopies. The database provides information on relative variations in ERS resources between rivers, but accurate assessments can only be obtained by groundtruthing.

- The accepted sampling method of ERS invertebrates uses pitfall traps to collect data on abundance and diversity but is vulnerable to data loss via inundation and anthropogenic or animal disturbance (Andersen, 1995). 2008 included two months of high river levels with subsequent interruptions of data collection, notwithstanding the inherent sampling weaknesses. The quality of the dataset would have been improved by including sampling through hand searching to complement the passive trapping method.

- SIA analysis remains a developing area of ecological study, both in its techniques and statistical analysis. Whilst the consensus is for tissue specific analysis (e.g.Wehi and Hicks, 2010), the small size of the invertebrates in this study precluded such detailed work, which will have reduced the accuracy of the data. Similarly, debate is still occurring on the most valid analytical approach to derive mixing models (Jackson et al., 2011, Jackson et al., 2009, Semmens et al., 2009, Parnell et al., 2010). Bayesian techniques have been shown to provide truthful representations of ecological processes, but it is likely that this is an area which will be subject to ongoing development.

- One absence in the SIA dataset comes from a lack of information on the small, fossorial Staphylinid species associated with the habitat. As one of the principle morphological forms associated with the habitat (and containing many of the rarer species), understanding their resource utilisation would have completed the picture of resource partitioning within the habitat. Size, habitat choice and relatively lower abundance did not supply enough specimens for valid analysis, and as such a knowledge gap remains in this area.

7.3 Suggestions for areas of future research

The roles that habitat complexity and continuity have in structuring ERS assemblages provide suggestions for the development of future research themes.

- Modelling of species distributions and habitat selection, although borne out by SIA data, can be further tested by incorporating larger datasets from disparate sites. Anthropogenic influences within the catchments study appear to have a largely indirect impact on assemblages via historic reductions in habitat. The inclusion of more replicate river systems is needed to test this observation, and would indicate whether regionally isolated communities show similar responses to natural and anthropogenic pressures. The presence of differing flow regime shapes and magnitudes observed within the ERS river subset also offers the opportunity to assess the role of these factors in predicting assemblage structure within rivers where data are available.

- Much interpatch movement is assumed to be linear, with individuals moving within their river corridor. If this is the case, then individual rivers' communities are vulnerable in the event of reach scale disturbances. Whilst different species are known to have differing levels of dispersal ability, the extent to which between river exchanges of individuals occur is unknown. If these are rare events, then reach scale extinction events will be long term. Genetic tools provide methods to assess the relatedness of separate populations (Lagisz et al., 2010). Microsatellites for the abundant species *B. atrocaeruleum* have been identified and are currently being tested for reproducibility. Once testing is complete, these will enable within and between river genetic changes to be studied, providing information on short-term, inundation driven movements within local populations, and the longer-term rate of exchange between populations.

- River restoration projects offer the potential to reintroduce ERS habitat to degraded systems (Gunther and Assmann, 2005). The ability of species to recolonise new habitat is poorly understood – and will be related to their interpatch movement potential and the relative isolation of new habitat from source populations. Understanding the rates of movement for an abundant species will provide an indication on the re-establishment timescales of a basic assemblage structure.

- Ever-developing techniques in SIA will enable more sophisticated research in prey acquisition by specialists. The whole body technique used in this study should be improved by tissue specific studies which would enable analysis of responses to emergence patterns, and can potentially demonstrate any variations between adult and larval dietary composition (Tallamy and Pesek, 1996). As many of the requirements of larval specialist Coleoptera are unclear, any increase in knowledge of this stage of the lifecycle would provide an invaluable aid in their conservation.

- The SIA data shown here indicate variations in behaviour and nutrient acquisition according to longitudinal positioning within the river, which in turn reflect differing strategies in inundation avoidance and survival. ERS specialist distributions are a reflection of early Holocene colonisations (Thiele, 1977), with populations following retreating glaciers and utilising newly disturbed landscapes. Current distributions reflect species' tolerance of disturbance levels and may provide a chronosequence of colonisation. This could be tested by examining ERS assemblages within contemporary disturbed environments, where stream (and habitat) age is known. The presence of temporal changes in populations (along with any variation in prey selection) would provide information on fine-scale successional processes.

7.3 References

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8

Appendices

Appendix A

Chapter 2 multiple linear regression model validations of for ERS area and density, giving models of best fit, and all models lying within 95% confidence interval following weighting and ranking.

Definition of variable terms:

Shape: Annual shape of discharge (as defined in Chapter 2)

Magnitude: Magnitude classification (as defined in Chapter 2)

Q_{10}: Average number of Q_{10} events annually

Slope: Descent of river, m/km^{-1}

Abstraction: Anthropogenic abstraction for drinking/agriculture

Dam: Upstream impoundment

Natural: No know anthopogenic influences on river

Table 1: Ranked models of explanatory variables within 95 confidence interval following validation and derivation of Akaike weights: Area of ERS/km^{-1} of river

Rank	Shape	Magnitude	Q_{10}	Slope	Abstraction	Dam	Natural	AIC	Weight
1			✓		✓			-7.19	0.38
2		✓		✓	✓			-5.94	0.2
3			✓					-5.47	0.16
4			✓	✓				-3.71	0.07
5				✓	✓			-2.9	0.04
6			✓	✓	✓			-2.26	0.03
7		✓						-1.8	0.02

Table 2: Ranked models of explanatory variables within 95 confidence interval following validation and derivation of Akaike weights: Number of bars/km^{-1} of river.

Rank	Shape	Magnitude	Q_{10}	Slope	Abstraction	Dam	Natural	AIC	Weight
1				✓		✓		-23.46	0.412
2				✓	✓	✓		-5.47	0.165
3			✓	✓				-5.28	0.161
4				✓			✓	-4.11	0.161

Appendix B

Chapter 3 GLM model validations of morphological groups' responses to connectivity variables, giving model of best fit, and all models lying within 95% confidence interval following weighting and ranking.

Definition of variables

Upstream	Distance from nearest upstream habitat patch.
Downstream	Distance from nearest downstream habitat patch.
1km area	Total area of ERS within 0.5km of habitat patch up and downstream.
No. bars	No of habitat patches 0.5km of habitat patch up and downstream.
Dist. Down	Distance of sample site from headwaters.

Table 1: Ranked models with AIC scores and Akaike weights for headwater ground beetles, showing all combinations of explanatory variables lying within the 95% confidence interval.

Rank	Upstream	Downstream	1km Area	No. bars	Dist. Down	AIC	Weight
1					✓	82.91	.226
2				✓		82.96	.22
3			✓			83.15	.201
4			✓		✓	84.73	.091
5			✓	✓		84.9	.084
6				✓	✓	84.92	.083

Table 2: Ranked models with AIC scores and Akaike weights for floodplain ground beetles, showing all combinations of explanatory variables lying within the 95% confidence interval.

Rank	Upstream	Downstream	1km Area	No. bars	Dist. Down	AIC	Weight
1					✓	77.77	.446*
2			✓		✓	79.73	.167*
3	✓		✓	✓	✓	80.04	.143*
4			✓	✓	✓	81.03	.087*
5	✓		✓		✓	81.37	.074*

Table 3: Ranked models with AIC scores and Akaike weights for specialist click and rove beetles, showing all combinations of explanatory variables lying within the 95% confidence interval.

Rank	Upstream	Downstream	1km Area	No. bars	Dist. Down	AIC	Weight
1				✓	✓	93.49	.383*
2				✓		94.82	.197*
3					✓	96.2	.099*
4			✓		✓	96.34	.092*
5			✓	✓	✓	96.71	.077*
6		✓	✓	✓	✓	97.51	.051*

Table 4: : Ranked models with AIC scores and Akaike weights for low-affinity ground beetles, showing all combinations of explanatory variables lying within the 95% confidence interval.

Rank	Upstream	Downstream	1km Area	No. bars	Dist. Down	AIC	Weight
1		✓				73.72	.383*
2		✓	✓			74.79	.173*
3		✓			✓	75.54	.119*
4		✓	✓		✓	76.31	.081*
5	✓		✓	✓	✓	76.5	.073*
6			✓	✓	✓	77.19	.052*
7	✓			✓	✓	77.54	.044*

Appendix C

Chapter 4 GLM model validations of responses to flow variations, giving model of best fit, and all models lying within 95% confidence interval following weighting and ranking.

Definition of variables:

PQ_{10}: Number of Q_{10} events occurring in the year before sampling.

$PSQ_{10:}$ Number of Q_{10} events occurring in the previous summer.

$PSQ_{50:}$ Number of Q_{50} events occurring in the previous summer.

$CQ_{10:}$ Number of Q_{10} events occurring in the year of sampling.

$CQ_{50:}$ Number of Q_{50} events occurring in the year of sampling.

$CSQ_{10:}$ Number of Q_{10} events occurring in the season of sampling.

$CSQ_{50:}$ Number of Q_{50} events occurring in the season of sampling.

$CSQ_{70:}$ Number of Q_{70} events occurring in the season of sampling.

dMF: Duration of maximum flow in the year of sampling.

dLF: Duration of lowest flow in the year of sampling.

mpsum: Duration of maximum flow in the summer before sampling.

mpm: Duration of maximum flow in the year before sampling.

Table 1: Potential models of rove beetle response to hydrological metrics validated, weighted and ranked.

Rank	PQ_{10}	CSQ_{10}	CSQ_{50}	CSQ_{70}	dLF	AIC	Weight
1					✓	151.66	.247
2		✓		✓		152.57	.157
3	✓				✓	153.35	.106
4		✓			✓	153.65	.091
5			✓			153.66	.091
6	✓		✓			153.67	.09
7	✓	✓				153.79	.085
8	✓			✓	✓	155.34	.039

Table 2: Potential models of specialist ground beetle response to hydrological metrics, validated, weighted and ranked.

Rank	PQ_{10}	CQ_{10}	PSQ_{50}	dMF	mpsum	AIC	Weight
1	✓			✓	✓	201.06	.374
2	✓		✓	✓	✓	203.04	.139
3	✓	✓	✓		✓	203.08	.136
4	✓	✓		✓	✓	203.24	.126
5	✓	✓	✓	✓	✓	205.01	.052

Table 3: Potential models of *B. atrocaeruleum* response to hydrological metrics validated, weighted and ranked.

Rank	PQ_{10}	psQ_{50}	CQ_{10}	CQ_{50}	Mpm	dmf	AIC	Weight
1	✓				✓	✓	204.67	.64
2				✓		✓	206.88	.212
3				✓	✓	✓	208.87	.078

Appendix D