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Squeezed out: the consequences of riparian zone modification for specialist invertebrates

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Abstract

While anthropogenic biodiversity loss in fresh waters is among the most rapid of all ecosystems, impacts on the conservation of associated riparian zones are less well documented. Riverine ecotones are particularly vulnerable to the combined 'squeeze' between land-use encroachment, discharge regulation and climate change. Over a three-year period of persistent low discharge in a regulated, temperate river system (River Usk, Wales, UK; 2009-11), specialist carabid beetles on exposed riverine sediments (ERS) were used as model organisms to test the hypotheses that catchment-scale flow modification affects riparian zone invertebrates more than local habitat character, and that this modification is accompanied by associated succession among the Carabidae.

Annual summer discharge during the study period was among the lowest of the preceding 12 years, affecting carabid assemblages. The richness of specialist ERS carabids declined, while generalist carabid species' populations either increased in abundance or remained stable. Community composition also changed, as three (*Bembidion prasinum*, *B. decorum* and *B. punctulatum*) of the four dominant carabids typical of ERS increased in abundance while *B. atrocaeruleum* decreased.

Despite significant inter-annual variation in habitat quality and the encroachment of ground vegetation, beetle assemblages more closely tracked reach-scale variations between sites or catchment-scale variations through time.

These data from multiple sites and years illustrate how ERS Carabidae respond to broad-scale discharge variations more than local habitat character. This implies that the maintenance of naturally variable flow regimes is at least as important to the conservation of ERS and their dependent assemblages as are site-scale measures.

Key words: Beetles, Climate change, *Bembidion*, Discharge, Exposed Riverine Sediments, Regulation.

Introduction

Much conservation emphasis in river systems has focussed on the wetted channel, where global rates of anthropogenic extinction and impairment are faster than in nearly any other ecosystem (Paetzold *et al.* 2008; Tockner *et al.* 2010). Species and habitats in the riparian zone are, however, also at risk from impairment through processes ranging in scale from local to regional (Ballinger & Lake 2006; Jonsson *et al.* 2013; Capon *et al.* 2013; Mantyka-Pringle *et al.* 2014). As with river channels, riparian zones are hotspots for human activity (Strayer & Dudgeon 2010) that cause 'squeeze' from several directions. For example, terrestrial land-use change alters habitat extent from the landwards direction at local to catchment scales (Strayer & Findlay 2010); flow modification, impaired water quality and flood-risk management, on the other hand, alter habitat quality at the water-body to catchment scale (e.g., Bates *et al.* 2006; Paetzold *et al*. 2008; Larsen *et al.* 2009). Climate change alters thermal regimes and flow patterns over whole regions (Capon *et al*. 2013; Mantyka-Pringle *et al*. 2014). Although the ecological importance of riparian zones is recognised (Strayer and Findlay 2010), the consequences of 'riparian squeeze' and flow stabilisation for specialist riparian organisms are poorly understood.

Exposed riverine sediments (ERS; i.e., sand and shingle bars exposed above a river's typical base flow) and their specialist Carabidae have been the focus of recent efforts to understand the importance of the conservation of riparian habitats and their vulnerability to change (e.g., Eyre & Luff 2002; Sadler *et al.* 2004; Bates *et al.* 2009; O'Callaghan *et al.* 2013). Formed from fluvial sediment transfer, and river bed movements during regular flood events and high discharge (Bates & Sadler 2005; Bates *et al.* 2005; Bates *et al.* 2006; O'Callaghan *et al*. 2013), the distribution and extent of these habitats has declined in temperate regions (e.g., Baiocchi *et al.* 2012; O'Callaghan *et al*. 2013) with consequences for their specialist arthropods (Greenwood & McIntosh 2010; McCluney & Sabo 2012). Specifically, areas of ERS epitomise habitats at risk from riparian squeeze, where changing flood frequency affects their stability and dynamics (e.g., Amoros & Bornette 2002; Van Looy *et al.* 2005; Bates *et al*. 2006; Rolls *et al.* 2012). Whilst there have been studies of succession within ERS carabid assemblages along environmental gradients (Gray 1989; Braun *et al*. 2004; Ulrich *et al*. 2008), few studies have considered assemblage character and dynamics over several years, particularly with the aim of appraising the relative 'squeeze' effects of flow stabilisation and habitat encroachment on ERS carabid dynamics. Persistent low river flows are expected to i) expose new areas of riverine sediment and inhibit dynamics, while ii) allowing the development of terrestrial vegetation growth (Gergely *et al*. 2001; Bates *et al*. 2006), with consequences for the extent and condition (e.g., wetness) of available habitat for arthropod functional ecology (Fowles 2004).

Ideally, assessing ecological succession among ERS Carabidae demands an in-depth understanding of individual species's ecology and life history traits. Whilst limited literature does exist on single species or narrow groups of carabids (e.g., Andersen 1968, 1989; Manderbach & Hering 2001; Bates & Sadler 2005; Gerisch 2011; Fowles 2004), this is not comprehensive. Carabid life histories remain generally poorly understood (Luff 2005, 2007). Consequently, species succession within assemblages in response to habitat change cannot be supported with evidence of functional succession, though aspects such as body size offer some clues. Studies have shown that mean individual body size of carabids decreases along gradients of increasing environmental disturbance (Gray 1989; Braun *et al.* 2004; Ulrich *et al.* 2008), and might therefore be inferred to increase with increasing environmental homogeneity. Mean Individual Biomass (MIB; Schwerk *et al.* 2006), defined as the average of total biomass from the total number of individuals in the sample (Schwerk & Szyszko 2007), can reveal differences among assemblages in habitats of different successional age, quality or natural state (Cardenas & Hidalgo 2007; Schwerk & Szyszko 2007; Jelaska *et al.* 2011; Kwiatkowski 2011). In previous studies (Cardenas & Hidalgo 2007; Jelaska *et al*. 2011), significant temporal changes in MIB values have been used to indicate faunal ecological succession, with higher MIB indicating more mature habitats or later succession stage. On ERS, similar patterns are anticipated where, over time, smaller, specialist Carabidae are replaced by larger, generalist species.

Here, we report a study investigating changes in the distribution and abundance of carabid beetles on ERS in the catchment of the River Usk, Wales (UK), over a three-year period during which annual river discharge declined year-on-year and no inundation events occurred. We tested the hypotheses that i) catchment scale changes in flow affect carabid assemblages more than local habitat character, and ii) that successive periods of low river discharge are accompanied by ecological succession within ERS carabid assemblages.

Study Area and Methods

Rising on the Black Mountain in the Great Forest European Geopark (51.90 N, 3.72 W; 500m above ordnance datum), the River Usk flows through the temperate and relatively maritime Brecon Beacons National Park in Wales, UK (*Figure 1*). It forms an important near-natural feature often lined with ash (*Fraxinus excelsior*), alder (*Alnus glutinosa*), oak (*Quercus petraea*) and willow (*Salix* species) trees, within a pastoral and afforested landscape. The River Usk is classified as over-licensed for water abstraction, meaning that if all abstraction licences issued were used to their full allocation, unacceptable environmental damage would occur in the river at low flows (EAW 2007). The river's morphology has been modified by dredging and river bank alterations (EAW 2009). At the time of study, river water quality was classified as 'very good' with respect to its chemistry, biology and pollutants (EAW 2008). With its steep upper catchments, discharge in the Usk closely tracks rainfall patterns (*Supplementary Material A*) but flows are also regulated by impoundment and abstraction (DCWW 2014). Large sections of the river are designated as a Special Area of Conservation (SAC, EC 1992) and a Site of Special Scientific Interest (SSSI, for a range of conservation features, including rare invertebrates.

By inspection, six sites were selected for detailed study (51.9N, 3.00W, *Figures 1, 2*) within the middle reaches of the River Usk. They ranged in area from *circa* 600 m^2 to 14,500 m^2. Each area of ERS, formed of point or side bars of exposed, deposited bed material, was selected for study based on likely extent of exposure, inundation following rainfall, accessibility and close proximity to other sites. Each site was formed by areas of shingle isolated by flowing water and hence could be considered to be distinct.

Beetle Sampling and Collection

During the summers of 2009, 2010 and 2011, searches for Carabidae were made among ERS sediments at 50 m intervals along each shoreline using a hand rake, collecting all beetles found using an aspirator (Sinnadurai 2014). The zone within a few metres of a river's wetted perimeter provides an "activity zone" where ERS specialists are present in higher densities (Bates & Sadler 2005; Bates *et al.* 2005; Sadler *et al.* 2006; Bates *et al.* 2007b; Paetzold *et al.* 2008). Samples were taken from locations positioned perpendicularly and adjacent to the water's edge, extending 2 to 3 m up-shore during a 10-minute search period at each sample location. The 50 m intervals and 10-minute searches achieved a standardised sampling intensity irrespective of patch size (Sinnadurai 2014). Sample visits to the same locations were repeated on three occasions each year during early, mid- and late summer (April/May, June/July and August/September, respectively). Beetles were preserved on site in labelled glass vials, and subsequently identified to species wherever possible (Luff 2007). All individuals were counted to determine assemblage composition.

Determining Ecological Succession: Composition and Mean Individual Biomass

A species' Mean Individual Biomass (MIB) was examined using the equation:

$$\ln y = -8.92804283 + 2.55549621 \times \ln x$$

where y is an individual beetle's live estimated body weight (mg) and x the body length of that individual (Schwerk & Szysko 2007). Species' Mean Individual Biomass (MIB) were determined by incorporating Luff (2007)'s average body lengths into this formula. Mean Individual Biomass was determined for: species abundance from each site each year; all ERS' specialists sampled each year; generalist species sampled each year; all species present in > 5% of sample locations each year; ERS specialists present in > 5% of sample locations each year; and generalist species present in > 5% of sample locations each year. Specialist Carabidae of ERS were identified after Fowles (2004) on the basis of both stenotypic species as well as other species for which bare sediment is fundamental to some stage of their life cycle. All other Carabidae were treated as generalists. All larvae found were from the wetted activity zone, within 2 m from the water's edge. Given that larval distribution is dependent upon female beetles selecting habitat suitable for egg-laying and larval survival (Kleinwaechter and Rickfelder 2007), we considered the species represented to be ERS specialists. They were grouped as a single group (“larvae”) to confirm the presence of breeding ERS specialist species. (*Supplementary Material B*).

Environmental Data

To assess flow during the beetle surveys and to compare to conditions during preceding years, daily river discharge values on the River Usk were obtained for 2000-11 from the UK National River Flow Archive, using records from the closest available source at the Llandetty Gauging Station, 4 km downstream of the survey area at 51.87 N, 3.27 W.

For each site, ERS dimensions (length, width and area of exposed sediments) were measured at the start of each survey season. Following the methodology of previous studies (Bates *et al*. 2005; Bates *et al*. 2006; Sadler *et al*. 2006), at each beetle sampling location, the percentages of bare exposed sediment, ground cover, scrub and overhanging canopy were estimated and recorded. The physical profile at each location was estimated using the percentage of “flat” (low angle, low-lying ERS approximating 0^{o} to 5^{o}), “gentle” (more elevated angles approximating 5^{o} to 15^{o}, without avalanches at the bar edge) and “steep” (avalanche faces present, obvious steeper break of slope) sediment slopes within 50 m. The topographic variation of each site was scored as “simple” if there was no obvious break of slope within a uniformly flat area, “humped” if there were clear mounds or breaks in slope, and “complex” if there was a combination of slopes, humps, backwaters and flatter areas (Sadler *et al.* 2006). British Ordnance Survey grid references were recorded (± 6 m) for an approximate centroid at each sample location using a Garmin Etrex 12 Channel geographic positioning system (GPS). Habitat heterogeneity at each site was categorised on a scale ranging from 1 to 5 (low to high heterogeneity) using a matrix devised from the preceding environmental data (*Supplementary Material C*).

Statistical Analysis

Daily river discharge data were summarised to provide mean monthly discharge per year between 2000 and 2012. Both inter-annual and seasonal variation were then investigated using general linear models (GLM), using year and month as independent predictors.

Data on the distribution and abundance of beetles, species richness and habitat variables were summarised by year and sample location within sites, pooling abundance per species for each sample location. Species' abundances from all samples were ordinated using Principal Components Analysis (PCA) on the correlation matrix to identify major variations that represented the entire beetle assemblage, including rarities and singletons. Habitat data were similarly ordinated using PCA to provide variates that summarised habitat characteristics across years and sample locations.

Variation in the abundances of the main species was examined using GLM and least squares means (LSM), using year and site as independent predictors. Inter-annual variations in PCA variates describing habitat factors were investigated using GLM and LSM. Principal component variates describing species composition across samples were then related to principal habitat variates, as well as year and site, using GLM and LSM, treating year and site as independent predictors and principal habitat variables as sequential covariates. For succession analysis, species richness, abundance and MIB were investigated by GLM and LSM, using year and site as independent predictors. The best fitting general linear models explaining species responses were identified using Akaike's Information Criterion (AIC) (Akaike 1974).

With the exception of analyses of assemblage succession, any species occurring in less than 5% of samples were excluded to minimise chance associations. In this widely applied approach, excluding species occurring in less than 5% of samples reduces the stochastic detection of chance associations among singletons or scarcer taxa (Gauch 1982).

All abundance analyses were carried out on data transformed by log(n + 2) to normalise distributions. All statistical analyses were completed using Minitab 16®; with AIC calculations completed in Excel.

Results

River Discharge and Physical Habitat

During 2009-2011, seasonal river discharge varied and annual summer discharge (April to September) declined successively to some of the lowest values recorded during the preceding 12-year period ($F_{12, 77} = 1.73$, $p = 0.08$, R^2 adj' = 11.57%, *Figure 3a, b*). This mirrored the overall pattern between 2000 and 2011 when annual discharge varied ($F_{12, 155} = 1.93$, $p < 0.05$), with pronounced differences between winter and summer ($F_{11, 155} = 10.29$, $p < 0.001$, R^2 adj' = 42.46%, *Figure 3c, d*).

Principal components analysis of the habitat data revealed three major sources of variation, explaining 60.2% of the habitat pattern (*Figure 4*). The first principal component, PC1, reflected increasing site area, shore length, heterogeneity, and a shift from flat to gently sloping sediments. The second, PC2, reflected a trend from bare ground to vegetated cover on sloping and humped topography, while PC3 reflected a shift from steep or sloping, bare sediments to flatter ground exposed by retreating river discharge over which vegetation might colonise during low flow. Viewed on these axes, Sites 1 and 6 were characterised by their larger size, flatter profile and heterogeneity; Sites 3 and 4 were smaller with most bare ground; Site 5 varied most in vegetation cover, while Site 2 varied most in size of exposure under a combination of different discharge conditions and encroaching vegetation.

During the years of progressively retreating river levels, clear spatio-temporal variation in habitat character were maintained between sites ($F_{5, 131}$ = 1479.82, p < 0.001), but clear variations also emerged among years ($F_{2, 131}$ = 12.58, p < 0.001, R^2 adj' = 98.26%; *Figure 5*). In particular, ERS area fluctuated in response to the dynamic relationship between increasing ground cover as shoreline exposure increased at lower flow, accompanied by increasingly simple site topography.

Beetle Species

A total of 4,393 beetles was recorded over the period 2009-11, with 27 species and 11 ERS specialists identified (Fowles 2004). Seventeen species, over half of all those recorded, occurred in less than 5% of samples (*Supplementary Material D*), including four ERS specialists that occurred in low numbers or as singletons. Collectively, the four most abundant and frequently occurring species, also ERS' specialists, *Bembidion atrocaeruleum*, *B. prasinum*, *B. decorum* and *B. punctulatum*, contributed 89%, 77% and 86%, respectively, of total abundance in 2009, 2010 and 2011.

In response to habitat features, six species increased in abundance along Habitat PC1 (increasing shore length, ERS area and heterogeneity), including four ERS' specialists, *B. atrocaeruleum*, *B. decorum*, *B. monticola* and *B. tibiale*; and two riparian generalists, *B. tetracolum* and *Paranchus albipes*. *Bembidion prasinum*, by contrast, increased along Habitat PC2, where vegetation encroached and beetles tracked the fresh exposures revealed by the retreating river flow. Together with *B. prasinum*, *B. punctulatum* increased along Habitat PC3 (exposure of flatter ground) with the generalist species *B. tetracolum* and *Agonum muelleri* (*Table 1*). Inter-annual variations in abundance were revealed with *B. atrocaeruleum* declining between 2009 and 2011 ($F_{2, 78} = 2.85$, $p = 0.064$, R^2 adj' = 32.69%), whilst *B. prasinum*, *B. decorum* and *B. punctulatum* increased (*Figure 6*).

Beetle Assemblages in Relation to Habitat and Succession

There was no significant variation among years in species richness. Generalist species richness increased between 2009 and 2010, however ($F_{2, 236} = 3.62$, $p < 0.05$), while ERS' specialist species richness declined ($F_{2, 236} = 3.04$, $p < 0.05$; *Figure 7* and *Table 2*). This latter species richness also varied among sites ($F_{5, 236} = 2.54$, $p < 0.05$). Whole-assemblage abundance varied between sites ($F_{5, 236} = 3.75$, $p < 0.01$), but abundance values for generalist (but not specialist) ERS species also increased through time ($F_{2, 236} = 5.62$, $p < 0.01$).

Eleven species, of which seven were ERS specialists, were included in multivariate analyses with the environmental factors. Principal components' analysis revealed three components (*Figure 8*) explaining 47.3% of the spatio-temporal variation in beetle assemblage composition among samples. Most variations (PC1) reflected increasing abundance of all the *Bembidium* spp. (except *B. prasinum*), while PC2 reflected a shift from *B. prasinum* to *Agonum, Nebria* and larval-rich locations. Despite links between beetle assemblages and habitat character as revealed on these axes, assemblage variations between years were far stronger no matter what habitat measures were used as covariates (*Table 1*).

Mean Individual Biomass revealed an increase in body size accompanying increasing species richness among generalist species ($F_{2, 17} = 3.52$, $p = 0.07$). For both specialists and generalists, MIB varied among sites ($F_{5, 17} = 3.56$, $p < 0.05$ and $F_{5, 17} = 2.85$, $p = 0.075$, respectively). More striking was a sharp increase in MIB for all species and generalist species between 2009 and 2010 ($F_{2, 17} = 6.16$, $p < 0.05$ and $F_{2, 17} = 5.59$, $p < 0.05$, respectively), tracking the increasing representation of generalists. This was not accompanied by any inter-annual increase of ERS specialist abundance.

Discussion

During a period of reduced variation in successive summer river discharge, the riparian habitats in this study stabilised as a consequence of reduced re-sorting of sediments and more ground cover encroachment. These processes are likely to inhibit the dynamics and development of ERS (Bates *et al*. 2009; Henshall *et al.* 2011). During the three-year study period, habitat conditions changed significantly in ways that reflected terrestrialisation as catchment-scale flow patterns changed, local river flows retreated, and the dynamics of ERS and associated river bed features were arrested. Over the same time period, conditions appeared to favour generalist carabids over specialists. There was a lower overall specialist riparian Carabidae abundance in response to an apparent 'riparian squeeze' where encroaching vegetation and retreating river flow reduced the availability of suitable freshly disturbed ERS habitat (Strayer & Findlay 2010). Together, these outcomes supported both hypotheses tested.

Although there was significant inter-annual and inter-site variability in habitat character, principally the balance between exposed sediment and vegetation encroachment, no influence on species composition was apparent. This was despite the expectation that specialist life history traits should interact with habitat structure (Gerisch 2011; Gerisch *et al.* 2012). Following previous work on ERS (Sadler & Bell 2000; Sadler *et al.* 2006), variation in macro-habitat conditions were recorded based on the percentage cover, dimensions and heterogeneity of habitat features. It is possible that such an approach was too crude to detect finer-scale patterns, for example humidity, surface temperature and aquatic food subsidies (Desender 1989; Paetzold *et al.* 2005; Bates *et al*. 2007b), or precise sediment size, vegetation cover, shade and livestock trampling (e.g., Bates & Sadler 2005; Bates *et al.* 2007a; Lambeets *et al.* 2008; Henshall *et al*. 2011; Baiocchi *et al*. 2012). Regardless, the overall conclusion that ERS beetles were influenced by large-scale variations between years more than local habitat character is supported by experimental manipulations carried out at the same sites (P. Sinnadurai *et al*. unpublished data).

As well as changes in species composition, Mean Individual Biomass among carabids in the Usk system also changed during the study, responding to ERS homogenisation and flow stability. Over the three years, the transition from smaller specialist to larger generalist species was consistent with more stable flow conditions. These indicated a shift away from dynamic conditions more favourable to specialist species on regularly disturbed ERS. On such sites, naturally disturbed habitats would be expected to favour smaller r-strategists, rather than the larger K-strategists expected to characterise more stable conditions (Kotze *et al.* 2003). Changes of this nature, specifically increasing mean carabid body-size on ERS through time, have the potential to indicate ERS ecosystem change (Buchholz *et al.* 2013) from a more- to a less-regularly disturbed environment. Mean carabid body-size has been used to investigate changing environments; revealing, for example, progressively smaller individuals on stressed sites but larger individuals in stable locations (Braun *et al.* 2004). Several studies have recorded such trends along environmental gradients, from larger individuals at rural locations to smaller individuals with apparently greater dispersal ability at urban or human-disturbed locations (Gray 1989; Alaruikka *et al.* 2002; Ulrich *et al.* 2008).

At an autecological level, the persistent distribution of *B. prasinum* highlighted the association of the species with new exposures and freshly disturbed ERS. By contrast, the decline of the most abundant species, *B. atrocaeruleum*, an ubiquitous specialist of ERS (Bates *et al.* 2006), tracked overall declining ERS availability, whilst *B. prasinum* and *B. punctulatum* persisted probably at the interface between exposed river-bed and encroaching vegetation. Given the importance of ERS for dynamic interactions between terrestrial and aquatic habitats (Henshall *et al.* 2011), a decline in ERS extent within a river system is likely to affect species dependent on such interactions. Alterations in the balance between nutrient or energy flux, from terrestrial and aquatic energy, and nutrient exchanges, are likely under prolonged low flows (Collier *et al.* 2002; Ballinger & Lake 2006; Rolls et al. 2012). These, in turn, provide some clues about the possible effects of future climate change (Capon *et al.* 2013).

Conclusions and Management Implications

Other studies of riparian sediments in the UK have focussed either on relatively unmodified and unregulated rivers, or on particular stretches of rivers, improving the understanding of the distribution and habitat selection of specialist ERS species (e.g., Sadler *et al.* 2006; Bates *et al.* 2009; O'Callaghan *et al.* 2013). In contrast, the River Usk is regulated by impoundment, abstraction and entrainment, experiencing successive low summer discharge as typified by this study. Our within- and between-site investigations were intra- and inter-annual over a period without significant inundation events or sediment resorting. Such environmental perturbations are essential to the formation and maintenance of ERS. The resulting faunal responses to inter-annual flow stability indicated that large-scale factors influenced carabid assemblages more than local factors. In turn, specialist ERS beetles such as *B. prasinum* appeared to act as important indicators of trend and condition.

The conservation ramifications from our study are clear: any habitat management or restoration aimed at maintaining these organisms would ideally be executed at a reach or catchment scale, and over a prolonged timeframe. Localised management within sites would, at least on the evidence of this study, be less likely to retain the range and scale of environmental variables required for the favourable conservation status of ERS and their specialist fauna. We advocate further long-term studies of entire river catchments, and nested reaches within them, to determine whether the patterns seen in the regulated Usk are representative (e.g., Larsen *et al.* 2009; Clews *et al.* 2010). Other parallels from management and restoration in river ecosystems already exist, for example, where catchment-scale hydrology or geomorphology subsumes smaller-scale attempts at restoration (Ormerod 2004). Given current emphasis on wider catchment management for climate change adaptation, flood risk reduction and conservation, we strongly advocate that the conservation of specialist riparian organisms be included in current thinking.

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Figures and Tables

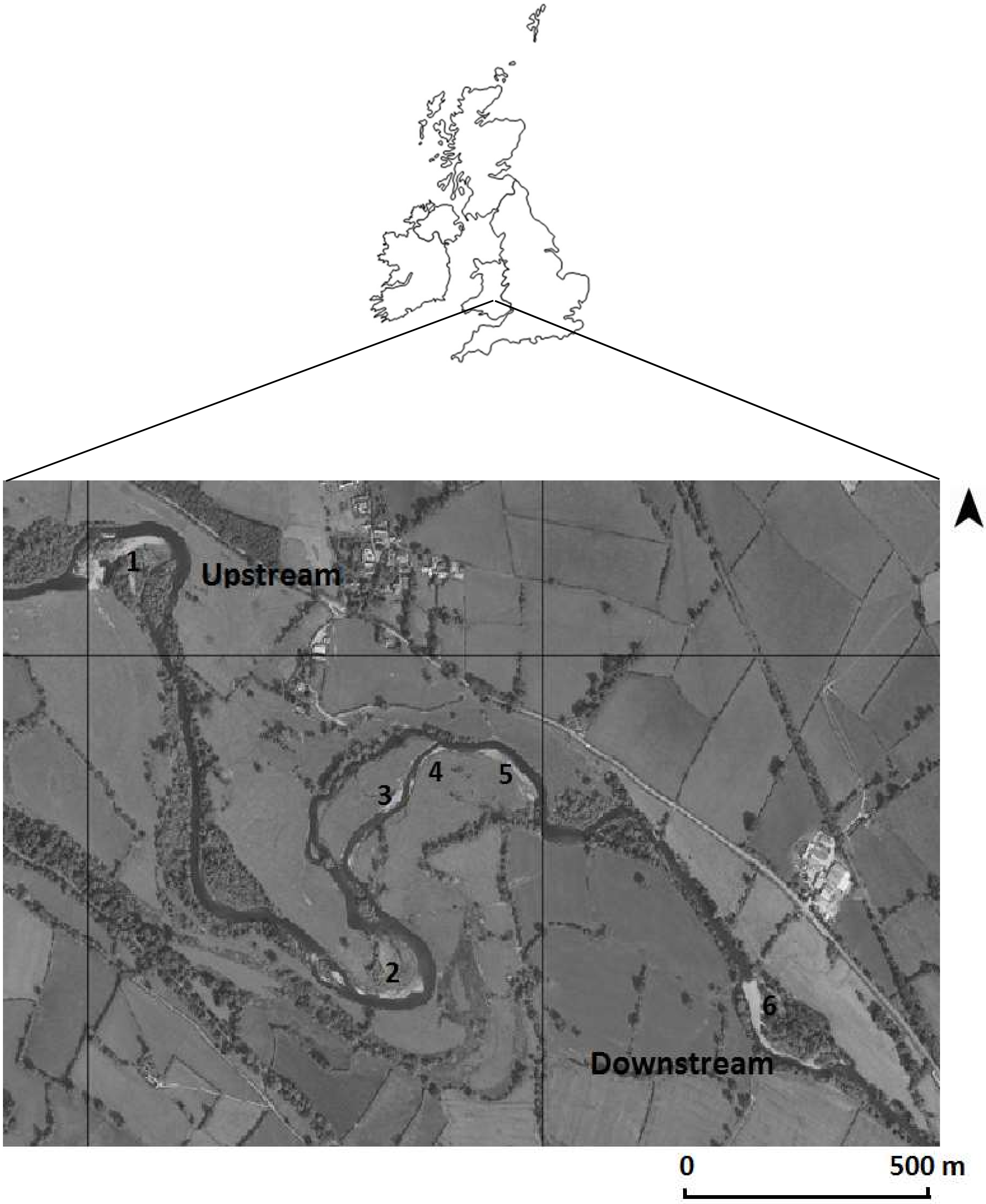


Fig 1 The study area situated on the River Usk Special Area of Conservation, within the Brecon Beacons National Park, Wales. Study Sites 1 – 6, illustrating upstream – downstream flow and 1 km grid. See detail in *Figure 2*

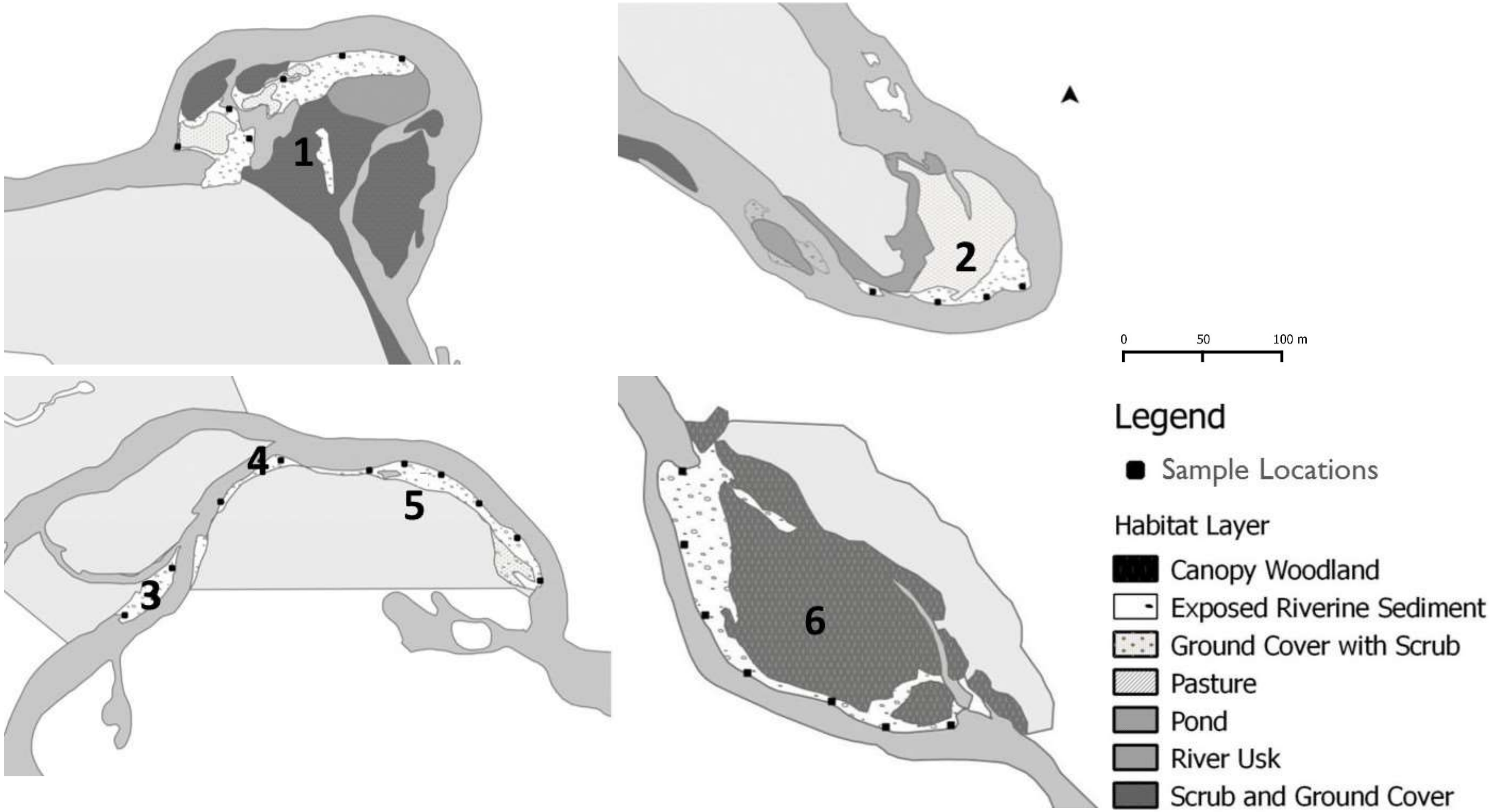


Fig 2 Location of ERS Study Sites 1 – 6 on the River Usk Special Area of Conservation, illustrating the approximate distribution of exposed sediments and recorded habitat features during three years 2009 to 2011

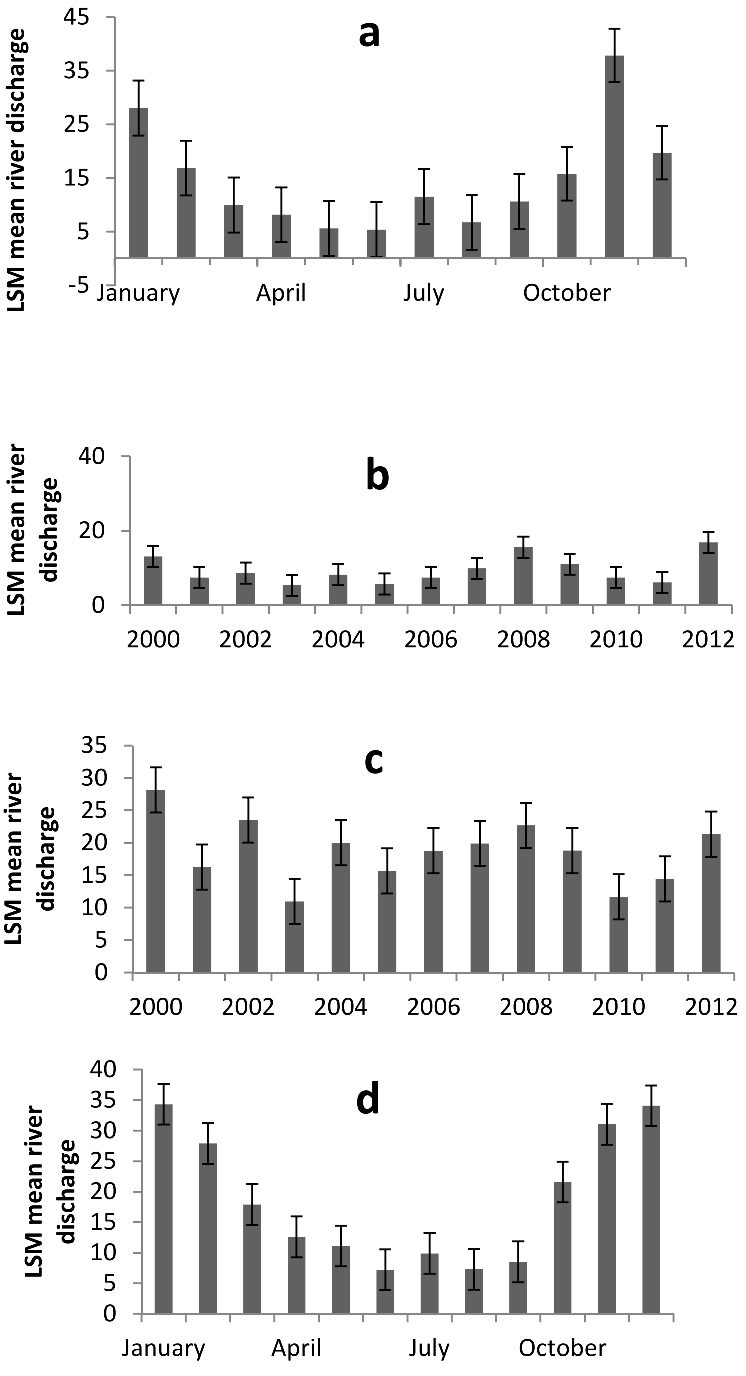
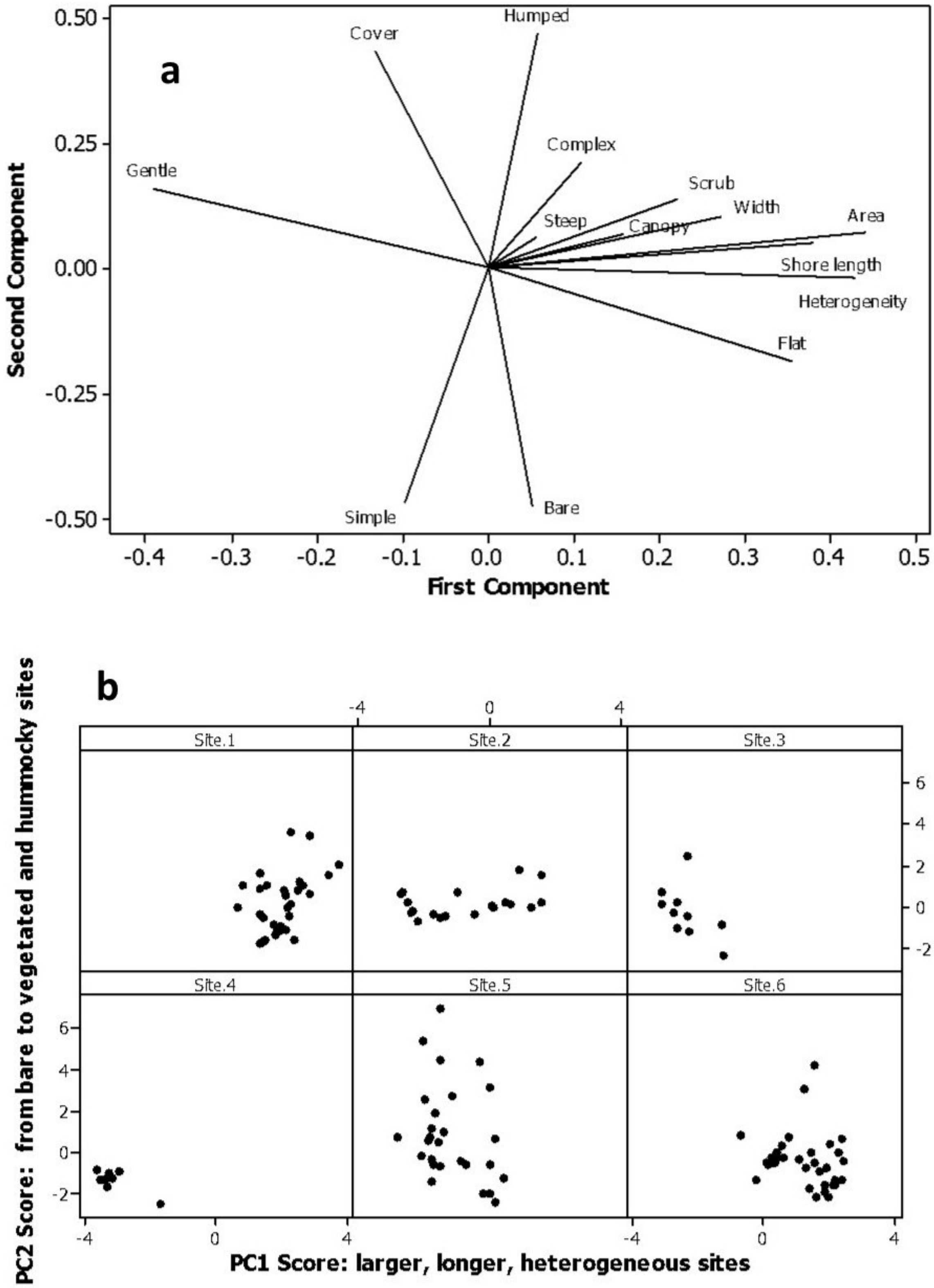


Fig 3 Discharge (cumecs, mean +/- s.e.) (least squares means - LSM) in the River Usk at Llandetty, SO126203, for 2000 to 2011. a) Monthly river discharge 2009 to 2011, illustrating winter:summer variation; and b) summer each year (April to September) 2000 to 2011; c) annual river discharge 2000 to 2011; d) monthly river discharge 2000 to 2011, illustrating winter:summer variation. Data from Environment Agency Wales



Minitab 16© **Fig 4** a) The position of samples from the six study sites on principal components describing habitat conditions over a three-year study in the Usk river system. b) Correlation between samples and habitat distribution on each site; Sites 1 and 6 were most coincident with the co-linear habitat variables

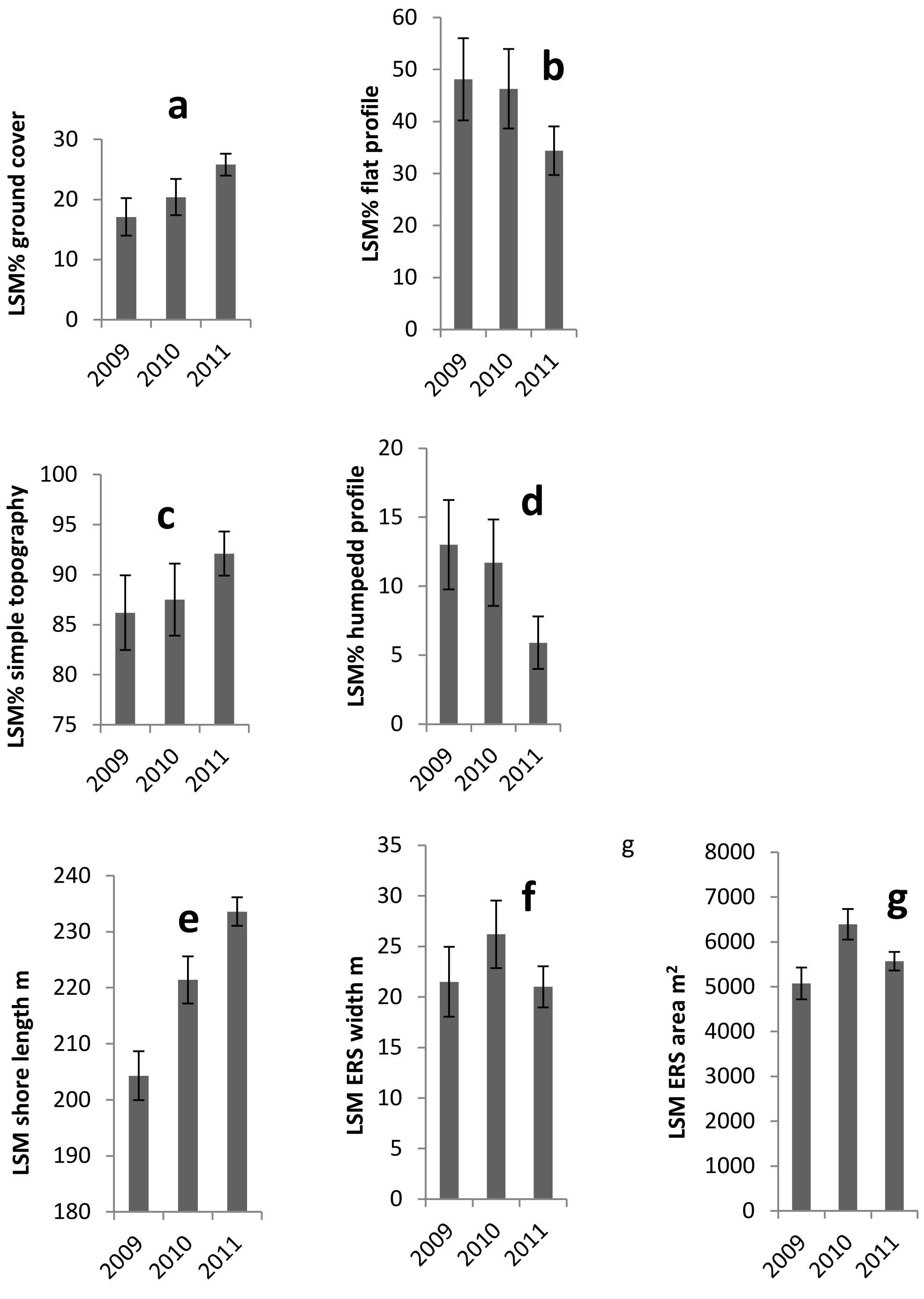


Fig 5 Annual distribution of the dominant habitat variables (as least squares means LSM +/- s.e.) within principal components. a) Ground cover; b) flat ERS profile; c) simple ERS topography; d) humped ERS topography; e) ERS shore length m; f) ERS width m; g) ERS area m^2

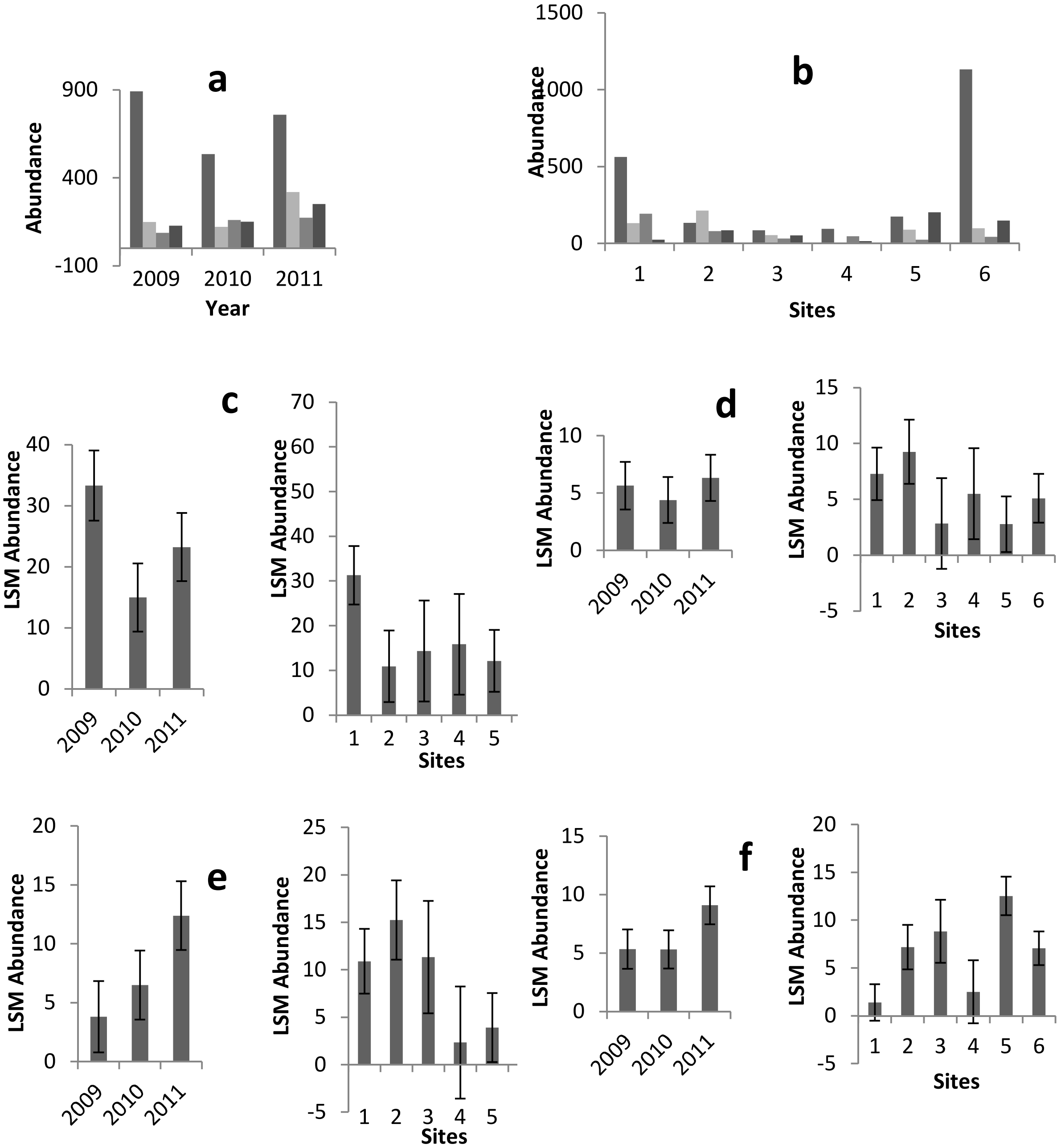


Fig 6 Contribution of four principal species to beetle assemblages on 6 ERS sites in the River Usk, 2009-2011 (LSM +/- s.e.): a) each year; b) each site over three years. ■ *Bembidion atrocaeruleum*, ■ *B. prasinum*, ■ *B. decorum*, ■ *B. punctulatum*. c) – f) LSM for these species each year and on each site over three years: c) *B. atrocaeruleum*, d) *B. prasinum*, e) *B. decorum* and f) *B. punctulatum*

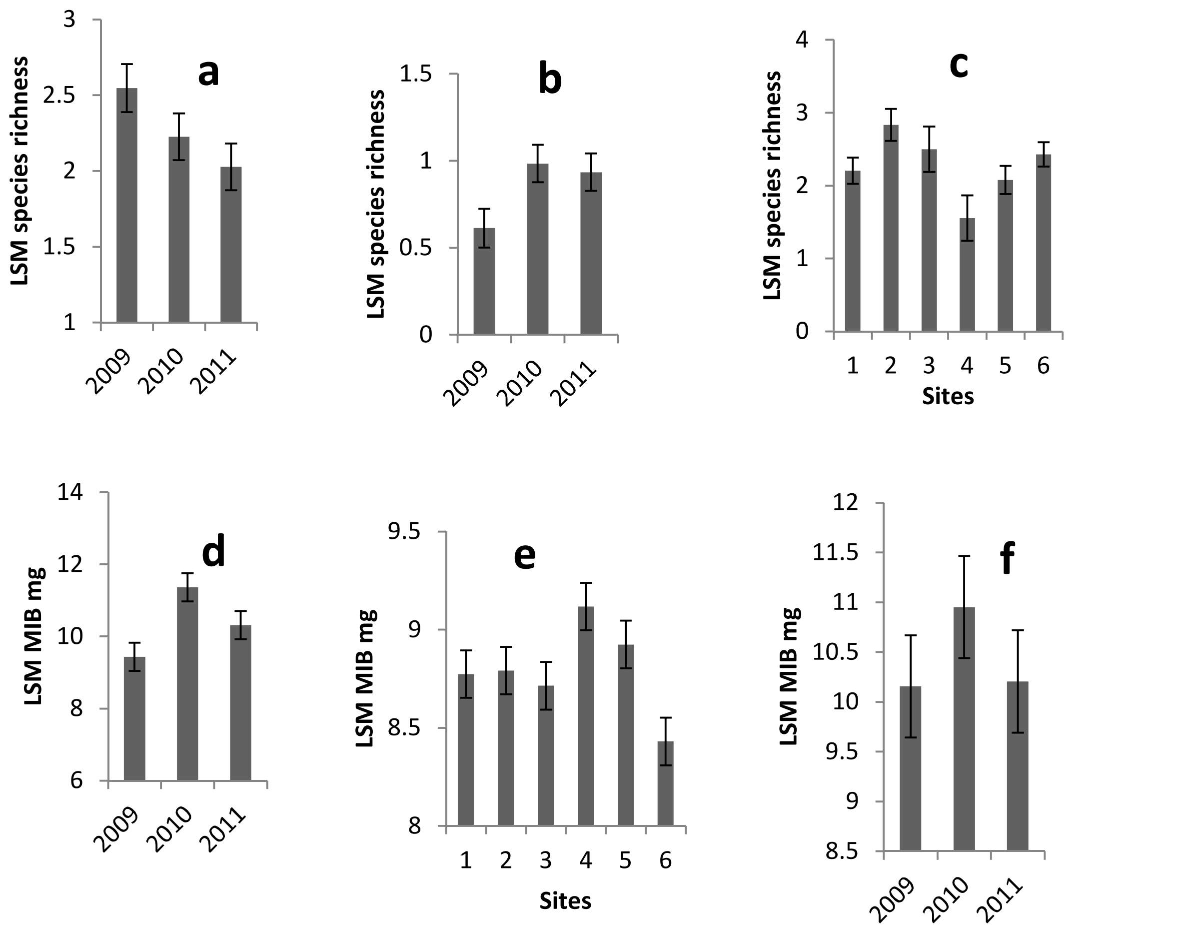
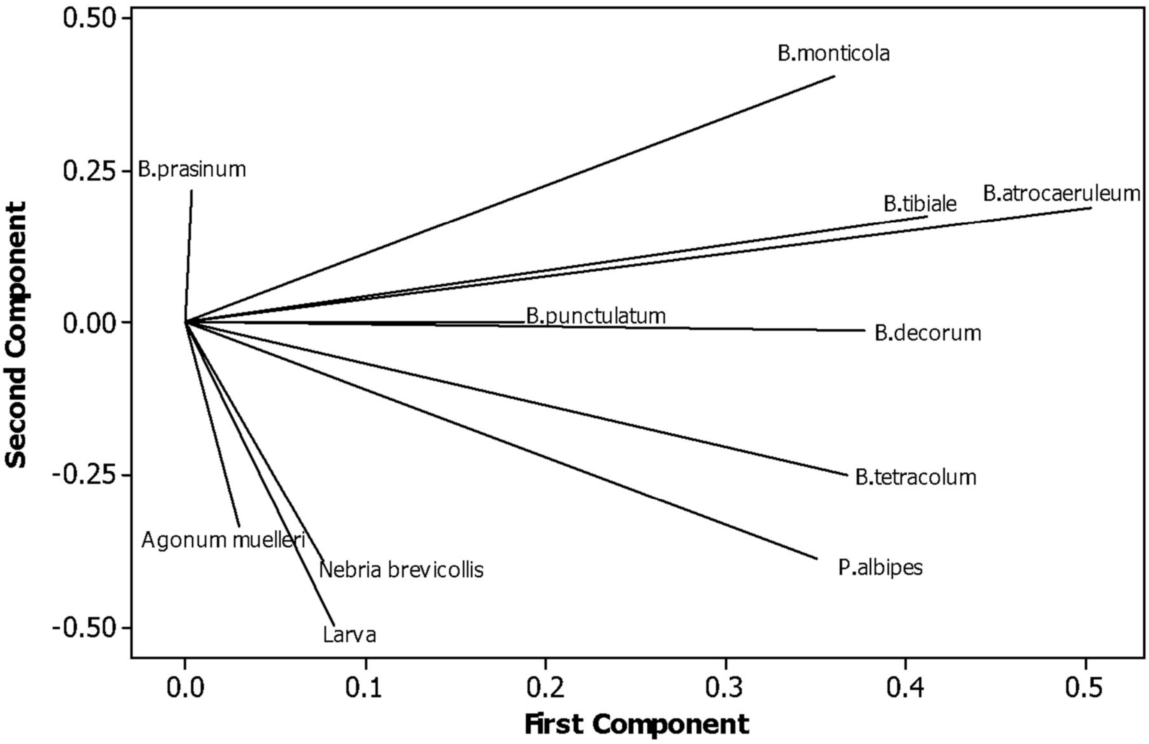


Fig 7 Inter-annual and inter-site gradients in species richness, beetle abundance and Mean Individual Biomass (MIB, mg live weight) (LSM +/-s.e.). Where gradients for all species and for those present in > 5% of samples were equivalent, only those for species in > 5% of samples are illustrated (see also *Tables 5.1* and *5.2* for GLM and AIC values). a) ERS specialist species richness > 5% of samples; b) generalist species richness > 5% of samples; these species showed a similar pattern for abundance; c) ERS specialist species richness > 5% of samples (inter-site variation); d) MIB all species, with generalist species dominating this pattern; e) MIB ERS specialists (inter-site variation); f) MIB generalist species (inter-site variation)



Minitab 16© **Fig 8** Species distribution on the first two principal components of beetle abundances over three years at six sites in the Usk river system, Wales

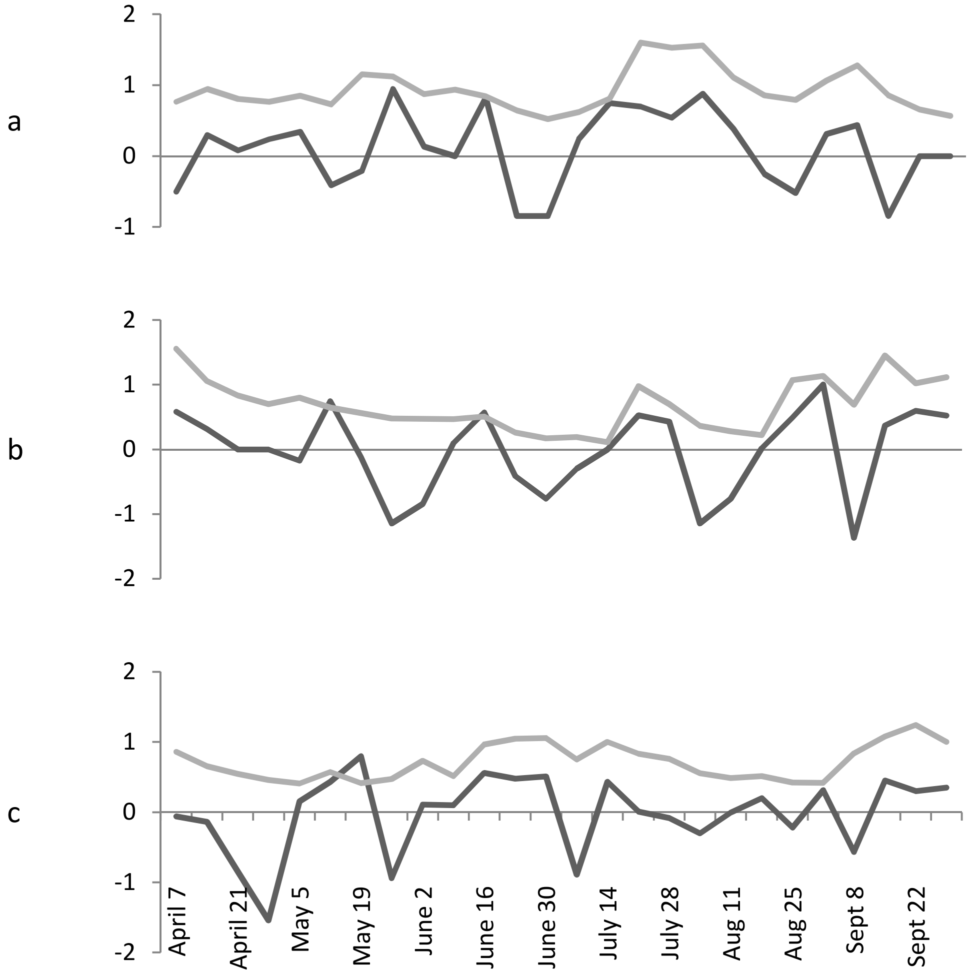
Table 1 Species responses to variations among years, between sites and within-sites during three years, based upon general linear models (log(n + 2) transformation) and Akaike's Information Criterion (AIC). AIC values ranked for a) species richness, b) abundance, c) four principal species and d) species principal components. Significance levels indicate * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$. See data displays in *Figures 3 - 6*

	GLM ranked by AIC values			
	Species Factor	**Model (* significance) and direction of change ↑ ↓**	**Habitat covariate (* significance)**	**AIC value**
a	Spp richness	Year(Site)*** ↑	HabPC1*	-482.80
	Spp richness	Year(Site)*** ↑	HabPC2	-481.26
	Spp richness	Year(Site)*** ↑	HabPC3	-479.49
b	Abundance	Year(Site)*** ↓	HabPC1*	-34.05
	Abundance	Year(Site)***	HabPC2	-26.10
	Abundance	Year(Site)***	HabPC3	29.46
c	*B. decorum*	Site*** ↓ downstream, Year(Site)** ↑	HabPC1	-367.65
	B. decorum	Site*** Year(Site)***	HabPC3	-367.65
	B. decorum	Site*** Year(Site)***	HabPC2	-367.61
		Site*** varied between sites	HabPC3	-324.88
	B. punctulatum			
	B. punctulatum	Site***	HabPC2	-323.08
	B. punctulatum	Site**	HabPC1	-322.92
	B. prasinum	Year(Site)* ↑	HabPC3***	-293.62
	B. prasinum	Site*** ↓ downstream, Year(Site)*	HabPC1***	-291.87
	B. prasinum	Site*	HabPC2	-275.73
		Year(Site)*** ↓	HabPC3*	-232.75
	B. atrocaeruleum			
	B. atrocaeruleum	Year(Site)***	HabPC1	-229.75
	B. atrocaeruleum	Site** varied between sites, Year(Site)***	HabPC2	-227.76
d	SpPC3	Site*** varied between sites	HabPC1*	-5.29
	SpPC3	Site**	HabPC3	-4.37
	SpPC3	Site***	HabPC2	-2.10
	SpPC2	Site*varied between sites, Year(Site)*** ↓↑	HabPC3**	1.18
	SpPC2	Year(Site)***	HabPC2*	6.18
	SpPC2	Year(Site)***	HabPC1	8.63
	SpPC1	Site* varied between sites, Year(Site)*** ↓		
	SpPC1	Year(Site)***	HabPC1	15.06
	SpPC1	Year(Site)***	HabPC2	15.17

Table 2 GLM results showing variations in carabid species richness, abundance and Mean Individual Biomass (MIB) following three years of sample visits across six sites visited three times per year. Significance levels indicate * p < 0.05 and ** p < 0.01; NS = not significant

Data subset		**Spp richness**	**Abundance**	**MIB**
All species	Year	NS	NS	*
	Site	NS	NS	NS
All ERS specialists	Year	p = 0.06	NS	NS
	Site	*	NS	*
All generalist species	Year	*	**	*
	Site	NS	NS	p = 0.075
Spp in >5% samples	Year	NS	NS	NS
	Site	NS	**	NS
ERS specialists in >5% samples	Year	*	NS	NS
	Site	*	NS	NS
Generalist species in >5% samples	Year	*	**	p = 0.07
	Site	NS	NS	NS

Supplementary appendices etc



MS Excel 2010 *Figure A1 Variations in river discharge and rainfall on the River Usk* during the study season April to September in a) 2009, b) 2010 and c) 2011. *Log$_{10}$ mean weekly river discharge* (cumecs) recorded at Llandetty (Ordnance Survey grid ref SO31262203) approximately 5 km downstream of the study area; and Log$_{10}$ total weekly rainfall (mm) recorded at the Natural Resources Wales weather station at Velindre, approximately 12 km north-east of the study area (SO31842367).

Table A2 Specialist profile of species recorded during three years across six ERS sites on the Usk river system, Wales, UK, summarising the ERS specialists and other early succession specialists (Fowles 2004). Where evidence was unavailable, an assumption of habitat preference has been made.

Species	Habitat preference	ERS specialist?[1]	Early succession habitat?	Reference
Amara aenea	Dry grasslands, waste	X	✓	Van Looy *et al.* 2007; Saska and Honek 2003); Jaskula and Soszynska-Maj 2011
Amara sp	Generally on sand, fine gravel	X	✓	Saska and Honek 2003;Jaskula and Soszynska-Maj 2011
Agonum lugens	Silt	X	✓	Bouchard *et al.* 1998;
A.muelleri	Grasslands, open woodland	X	x	Jaskula and Soszynska-Maj 2011
B.atrocaeruleum	Shingle	✓	✓	Van Looy *et al.* 2007
B.decorum	Sand and gravel	✓	✓	Van Looy *et al.* 2007
B.dentellum	Muds, marshes	✓	x	Assumption
B.guttala	Ubiquitous	X	x	Assumption
B.lunatum	Silty river banks	✓	x	Assumption
B.monticola	Gravel	✓	✓	Assumption
B.prasinum	Shingles and cobbles	✓	✓	Andersen 2011
B.properans	Dry, open clay soils	X	✓	Traugott 1998
B.punctulatum	Gravel and shingle	✓	✓	Van Looy *et al.* 2007)
B.tetracolum	Open damp soil	X	✓	Assumption
B.tibiale	Gravel and shingle	✓	✓	Assumption
Bracteon littorale	Sand, fine gravel	X	✓	Assumption
Chlaenius vestitus	Mud and clay cracks	✓	x	del Camino Pelaez and Salgado 2007
Clivina collaris	Clay, sand, silt	✓	✓	Assumption
Harpalus rufipes	Open dry soils	X	✓	Zhang *et al.* 1997
Nebria brevicollis	Ubiquitous	X	x	Noordhuis *et al.* 2001; Jaskula and Soszynska-Maj 2011
Paranchus albipes	Freshwater margins	X	x	Assumption
Patrobus atrorufus	Upland habitats and woodland	X	x	Assumption
Platynus assimilis	Woodland	X	x	Kivimagi *et al.* 2009
Pterostichus melanarius	Gardens, grassland, crops	X	x	Noordhuis *et al.* 2001; Jaskula and Soszynska-Maj 2011
P.nigrita	Most damp lowland habitats	X	x	Jaskula and Soszynska-Maj 2011
P.vernalis	Most damp lowland shaded habitats	X	x	Jaskula and Soszynska-Maj 2011
Trechus quadristriatus	Widespread	X	x	Jaskula and Soszynska-Maj 2011
Larvae	Gravel, shingle, cobbles	✓	✓	Assumption

Table A3 Matrix to assign habitat heterogeneity on ERS within the River Usk study area; a score of 1 indicates lower heterogeneity than a score of 5.

Habitat heterogeneity score		Uniformly flat	Bare	Some ground vegetation	More than 1 sediment size	Scrub and/or trees	Pools or backwaters	Breaks of slope	Eroding banks/ river cliffs
1 (low)	**At least 2 of:**	✓	✓	✓					
2	**At least 2 of:**		✓	✓	✓				
3	**At least 4 of:**		✓	✓	✓	✓	✓		
4	**All of:**		✓	✓	✓	✓	✓	✓	
5 (high)	**All of:**		✓	✓	✓	✓	✓	✓	✓

Table A4 The abundances of beetle species recorded during a three-year study of exposed riverine sediments in the Usk river system, Wales, a) identifying the species used in multivariate analyses and b) those excluded because they occurred in < 5% of samples.

	a	b	2009	2010	2011	Abundance	No. samples present	ERS specialist?
1.	*Bembidion atrocaeruleum*		✓	✓	✓	2185	91	✓
2.	*B.prasinum*		✓	✓	✓	589	59	✓
3.	*B.punctulatum*		✓	✓	✓	530	80	✓
4.	*B.decorum*		✓	✓	✓	420	83	✓
5.	*Paranchus albipes*		✓	✓	✓	205	65	
6.	*B.tetracolum*		✓	✓	✓	195	59	
7.	*Agonum muelleri*		✓	✓	✓	84	38	
8.	Larvae		✓	✓	✓	59	30	✓
9.	*B.tibiale*		✓	✓	✓	38	22	✓
10.	*B.monticola*		✓	✓	✓	29	16	✓
11.		*B.lunatum*		✓		10	5	✓
12.		*Bracteon littorale*	✓			10	1	
13.	*Nebria brevicollis*			✓	✓	8	7	
14.		*Clivina collaris*	✓		✓	6	3	✓
15.		*A.lugens*		✓	✓	4	4	
16.		*Platynus assimilis*	✓	✓	✓	3	3	
17.		*Pterostichus nigrita*		✓	✓	3	3	
18.		*Amara sp.*		✓		2	2	
19.		*B.guttala*	✓			2	1	
20.		*B.properans*			✓	2	2	
21.		*Chlaenius vestitus*			✓	2	2	✓
22.		*Amara aenea*		✓		1	1	
23.		*B.dentellum*	✓			1	1	✓
24.		*Harpalus rufipes*		✓		1	1	
25.		*Patrobus atrorufus*			✓	1	1	
26.		*Pterostichus melanarius*	✓			1	1	
27.		*Pterostichus vernalis*		✓		1	1	
28.		*Trechus quadristriatus*			✓	1	1	
		TOTAL	16	19	19	4393		11

Table A5 Ranked Akaike's Information Criterion (AIC) values for the GLM of variations in a) species richness, b) abundance and c) MIB. Smallest AIC values indicate the strongest effect.

a. spp richness	**AIC value**	**Factor**
All species	NA	
Spp in >5% samples	NA	
Generalist species in >5% samples	-37.13	year
All generalist species	10.23	year
ERS specialists in >5% samples	131.35	year
All ERS specialists	146.7	year, site
b. abundance	**AIC value**	**Factor**
All species	NA	
All ERS specialists	NA	
ERS specialists in >5% samples	NA	
Generalist species in >5% samples	-528.64	year
All generalist species	-501.49	year
Spp in >5% samples	-227.71	site
c. MIB	**AIC value**	**Factor**
Spp in >5% samples	NA	
ERS specialists in >5% samples	NA	
All ERS specialists	-60.79	Site
All species	6.33	Year
All generalist species	43.38	Year, site
Generalist species in >5% samples	58.04	Year

Table A6 Loading values of dominant habitat variables (shaded) onto three principal components (correlation matrix) describing habitat character at six ERS sites in the Usk river system over three years.

	HabPC1	HabPC2	HabPC3
Eigenvalues	**3.81**	**2.62**	**2.00**
Cumulative proportion	**27.20%**	**45.90%**	**60.20%**
Bare	0.052724	-0.47432	-0.39449
Ground Cover	-0.13158	0.433683	0.416832
Scrub	0.221948	0.138929	-0.00296
Canopy	0.157736	0.068475	-0.13141
Flat	0.355582	-0.1847	0.297586
Gentle	-0.39155	0.159116	-0.16899
Steep	0.055274	0.061033	-0.46405
Simple	-0.09684	-0.4677	0.290742
Humped	0.058947	0.467122	-0.27544
Complex	0.109715	0.211233	-0.08855
Shore length	0.380084	0.051153	-0.13799
Width	0.271463	0.101504	0.297119
Area	0.442246	0.069864	0.118705
Heterogeneity	0.42934	-0.02064	-0.17679

Table A7 Loading values of dominant beetle species (shaded) on three principal components derived from correlation among their abundances (see *Figure 7* for graphical display). ✓ indicates ERS specialist.

	PC1	PC2	PC3
Eigenvalues	**2.26**	**1.55**	**1.39**
Cumulative proportion	**20.60%**	**34.60%**	**47.30%**
Agonum muelleri	0.030036	-0.33395	0.418154
Bembidion atrocaeruleum✓	0.502376	0.189831	-0.17119
B.decorum✓	0.376347	-0.0121	-0.07917
B.monticola✓	0.360592	0.403301	-0.12208
B.prasinum✓	0.003631	0.215831	0.587354
B.punctulatum✓	0.187543	-0.0003	0.593352
B.tetracolum	0.36714	-0.25085	0.158478
B.tibiale✓	0.411238	0.175185	0.037873
Nebria brevicollis	0.076554	-0.39095	-0.21456
Paranchus albipes	0.351118	-0.38722	-0.05694
Larvae✓	0.082546	-0.49665	-0.04232