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The spider assemblages (Araneae) of exposed riverine sediments in Scotland and northern England*

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Summary

A survey of spiders using pitfall traps on exposed riverine sediments (ERS) by rivers and tributaries in four catchments in Scotland and northern England yielded 105 species and lists from 149 sites. These data were analysed using ordination and classification techniques to identify the species assemblages present within and between catchments and the factors affecting the distribution of these assemblages. There were major differences between assemblages on ERS in highland and lowland catchments, but the major factor within catchments was the amount and type of vegetation. The distribution of sites within habitat groups tended to be related to site location within catchments, but sediment composition also had a limited effect on assemblage distribution. Few specialist ERS species were recorded, whilst a variety of species found on other habitats such as unmanaged and agricultural grasslands, wetlands and bare ground, were found on sediments throughout the four catchments. Fewer spider assemblages were identified on riverine sediments as compared with other invertebrate groups recorded from the same sites.

Introduction

Invertebrate research work on exposed riverine sediments (ERS) has tended to be concentrated on the distribution and habitat preferences of beetle species and assemblages (e.g. Eyre & Lott, 1997; Eyre *et al.*, 2001a,b) but there have also been a number of investigations of spider communities on ERS (Boumezzough, 1983; Bigot & Favel, 1985; Droschmeister, 1994; Smit *et al.*, 1997; Manderbach & Framenau, 2001) and some into ecology of single spider species on ERS (Albert & Albert, 1976; Framenau *et al.*, 1996). Sadler & Petts (2000) investigated the presence of a number of invertebrate groups on ERS, including both spiders and beetles, whilst other work has concentrated on other riparian habitats (Moring & Stewart, 1994; Greenwood *et al.*, 1995; Malt, 1995; Hendrickx *et al.*, 1998; Wenninger & Fagan, 2000).

Research on spider species assemblage distribution using epigeal species has been carried out on a number of different habitats. There are reports from grasslands of various types (e.g. Rushton & Eyre, 1992; Corey *et al.*, 1998; Pozzi *et al.*, 1998) and agricultural ecosystems (e.g. Rushton & Eyre, 1989; White & Hassall, 1994; Feber *et al.*, 1998), with some work on forests (e.g. Pajunen *et al.*, 1995). These studies were carried out using pitfall trapping as the sampling technique.

ERS are highly disturbed habitats by rivers with varying compositions and vegetation covers. Composition varies from boulder- and cobble-dominated sediments, found by fast-flowing stretches of rivers, to sediments of fine sand with silt found where both the river flow and sediment deposition are slow, while some sediments are a mixture of different particle sizes. Generally ERS tend to be unvegetated after winter, with the coarser sediments by the faster rivers remaining bare while sand and silt sediments acquire varying amounts of vegetation cover throughout the season. However, all sites are prone to disturbance at any time by river scouring, depending on flow conditions. In the present paper a standardised pitfall sampling approach (Luff, 1996) was applied to ERS in four catchments in Scotland and northern England to assess spider assemblage distribution and the variables influencing distribution.

Material and methods

Sites

Exposed riverine sediments (ERS) in the catchments of the Rivers Carron, Nith and Spey in Scotland and the Tweed, which straddles the Scotland-England border, were sampled in 1996 and 1997. The 10 km squares containing sites in the four catchments are shown in Fig. 1. The 1996 sampling was restricted to sites on the main rivers, whilst sampling was expanded in 1997 to

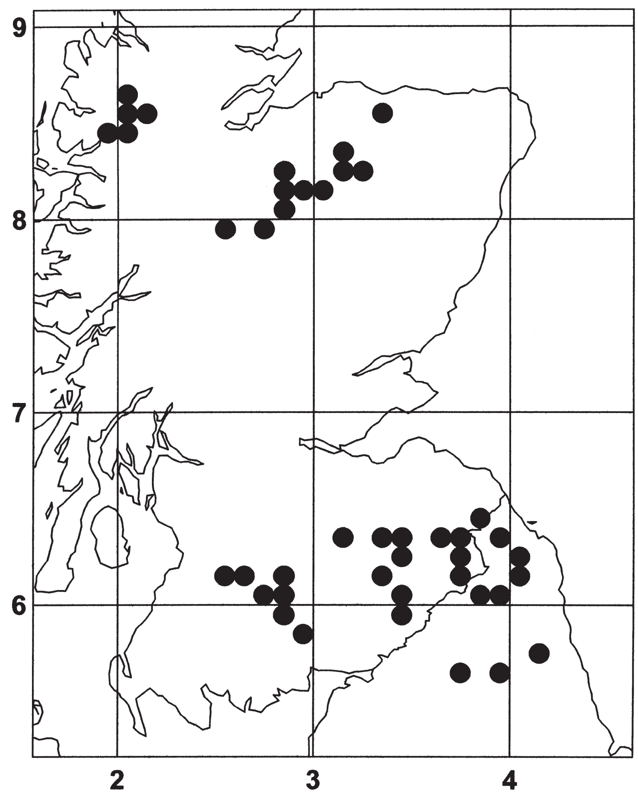

Fig. 1: Map showing the 10 km national grid squares in the Carron (northwest), Spey (northeast), Nith (southwest) and Tweed (southeast) catchments containing sites sampled in the survey.

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take in both the main rivers and their tributaries. A total of 149 sites were sampled, made up of 29 sites in the Carron, 26 in the Nith, 40 in the Spey and 54 in the Tweed catchments. The sampling rationale was to trap in the widest variety of ERS, covering differences in sediment particle size and vegetation cover with sites from all parts of the four catchments.

Sampling

Spiders were sampled using pitfall traps (8.5 cm diameter, 10 cm deep), partly filled with ethylene glycol. Ten traps were used at each site in a line at 1 m intervals, as outlined by Luff (1996). The traps were set in May of each year and sampling continued until August, with collections carried out at three-weekly intervals. There was some disruption of sampling caused by river spating but traps were reset as rapidly as possible. Samples from the ten traps in each collection were pooled and taken to the laboratory for sorting.

Analyses: ordination and classification

The multivariate techniques of ordination and classification have consistently been used to assess differences in invertebrate species assemblages, including in a number of spider investigations (e.g. Rushton & Eyre, 1989, 1992; Downie *et al*., 1995). These techniques produce results which can be interpreted in the light of known environmental variables and habitat types, and group together similar sites based on species assemblage composition.

In order to investigate the variation in the distribution of the spider species assemblages, the data were ordinated using detrended correspondence analysis (DECORANA — Hill, 1979). No transformation of the data was carried out and the number of segments used in the rescaling was 26. The presence/absence of species, in lists containing five or more species, was used in the ordinations, as in other work with spiders (e.g. Rushton & Eyre, 1989, 1992). Classification was carried out using fuzzy set clustering (Bezdek, 1981) based on the ordination, as in work on other invertebrate groups (e.g. Eyre *et al*., 2001a,b). The site scores on the first three axes of the ordination were used for the classification of sites in all catchments, but with the sites in individual catchments the scores from the first two axes were used because the third axis could not be explained.

In addition to the ordination by DECORANA, constrained ordination (CANOCO — Ter Braak, 1987) was also used with a number of environmental variables. Both DECORANA and CANOCO analyses were carried out using the CANOCO software. A sediment index was generated using a DECORANA ordination of an estimate of particle size at each ERS site. The particles and their approximate sizes were: silt (<0.2 mm), sand (0.2–2 mm), shingle (2–10 mm), pebbles (10–50 mm), cobbles (50–100 mm) and boulders (>100 mm). The percentage of each particle size was estimated, to the nearest 5%, as used by Eyre *et al.* (2001a,b). The axis 1 site ordination scores were used as the index, and the scores were generated for all sites together and for the sites in individual catchments. The index scores were small for silt/sand sediments and large for cobble/boulder sediments in all five examples. An estimate of river or stream size was made using bands of width in non-spate conditions. Each band was given a value: 1 = 1–5 m, 2 = 6–10 m, 3 = 11–15 m, 4 = 16–20 m, 5 = >20 m. The third variable was an estimate of vegetation cover on each site. Each vegetation cover type was assigned a value: 1 = bare, 2 = ruderal, 3 = rank, 4 = shrub cover, 5 = tree cover. For the analysis dealing with all the sites, categorical values were assigned to either highland catchments (Carron and Spey) or lowland catchments (Nith and Tweed). There was therefore differentiation between the northerly catchments, with base-poor, mainly igneous, geology and the southern catchments with more productive coal measures and sandstone geology.

Results

All catchments

A total of 105 spider species were recorded from the ERS sites and a full list, with the number of sites in each catchment from which each species was recorded, is given in the Appendix.

The variation along axis 1 (eigenvalue 0.377) of the ordination of all site lists was from ERS by the small tributaries of the Spey near the origin to sites by the downstream Tweed and Nith at the other end of the axis. The sites near the origin of axis 2 were open, dry, cobble-dominated sediments with little vegetation on the Nith, Carron and Tweed, whilst the sites at the other end were damp sand and shingle ERS with more vegetation. Sites shaded by trees by the streams of the Carron and the Nith were near the origin of axis 3, and open sites by the Nith and Tweed with sparse vegetation were at the other end.

Four groups were generated in the classification of all the sites in the four catchments, and the frequency of occurrence of species in the groups is shown in Table 1. Group 1 included 44 sites, 15 from the Carron, mainly by the upstream river and by streams, two from tributaries of the Nith, 16 from the upstream Spey and tributaries, and 11 from tributaries of the Tweed. These ERS had mixed particle sizes usually with sand, were mainly dry and had sparse vegetation. This group had the highest incidence of *Trochosa terricola* Thorell, *Drassodes cupreus* (Blackwall), *Alopecosa pulverulenta* (Clerck), *Xysticus cristatus* (Clerck) and *Pachygnatha degeeri* Sundevall. Group 2 included 38 sites, 11 from the Carron, four from the upstream Nith and tributaries, 16 from the Spey tributaries, and seven from the Tweed tributaries. These were bare sites on larger areas of mixed dry sediment than those in group 1, generally further down the catchments. They had the most *Oedothorax retusus* (Westring), but were otherwise similar in species occurrence to group 1 (e.g. *Pardosa agricola* (Thorell) and *P. pullata* (Clerck)) but with more *Oedothorax apicatus* (Blackwall). There were 37 sites in group 3, two from the downstream Carron, 14 from the

Species	Group 1	2	3	4
Haplodrassus signifer (C.L. Koch)	45	11	—	—
Xysticus cristatus (Clerck)	52	13	—	3
Drassodes cupreus (Blackwall)	70	53	8	3
Pardosa pullata (Clerck)	41	37	3	3
Robertus lividus (Blackwall)	39	11	—	3
Tiso vagans (Blackwall)	25	8	3	3
Alopecosa pulverulenta (Clerck)	59	39	14	7
Pirata piraticus (Clerck)	5	21	11	—
Trochosa terricola Thorell	73	53	19	20
Trochosa ruricola (De Geer)	30	3	8	17
Diplocephalus cristatus (Blackwall)	25	21	—	7
Pardosa agricola (Thorell)	75	79	62	13
Pachygnatha degeeri Sundevall	52	32	35	13
Walckenaeria acuminata Blackwall	25	21	—	17
Oedothorax retusus (Westring)	48	74	59	57
Erigone dentipalpis (Wider)	43	63	84	63
Pardosa amentata (Clerck)	84	97	92	73
Oedothorax apicatus (Blackwall)	27	58	97	63
Oedothorax fuscus (Blackwall)	14	26	27	33
Erigone atra Blackwall	25	53	86	73
Dicymbium tibiale (Blackwall)	9	3	—	27
Pachygnatha clercki Sundevall	16	16	49	80
Lepthyphantes zimmermanni Bertkau	7	—	3	47
Leptorhoptrum robustum (Westring)	2	5	8	50
Gongylidium rufipes (Linnaeus)	—	—	3	23
Bathyphantes gracilis (Blackwall)	—	5	5	33

Table 1: The frequency of occurrence (%) of spider species in the four groups generated from the classification of all site lists from the four catchments (minimum >20% in one group). The species order is as for the first axis of the ordination.

Nith, seven from the Spey, and 14 from the upstream Tweed. These ERS were a mixture of dry and damp particle sizes, and were by the main rivers with either ruderal or rank vegetation. There was the highest incidence of *Erigone dentipalpis* (Wider), *E. atra* Blackwall and *Oedothorax apicatus*, and few or no species in genera such as *Xysticus*, *Drassodes* and *Haplodrassus*. Group 4 included 30 sites, one by a stream of the Carron, six from the Nith, one from the Spey, and 22 from large tributaries and the downstream Tweed. These were either sand and shingle or sand and silt ERS, and were damp with either rank or shrub vegetation or were shaded by trees. The species in this assemblage were similar to those of group 3, but with the highest frequency of *Pachygnatha clercki* Sundevall, *Lepthyphantes zimmermanni* Bertkau and *Leptorhoptrum robustum* (Westring).

The constrained ordination biplot (Fig. 2) indicated that the major factor affecting spider assemblage distribution was differences in the catchment types, with the highland sites split from the lowland sites. The river width and vegetation cover variables had a similar amount of influence, but the sediment variable was less important. The sites in groups 1 and 2 were concentrated along the negative axis 1, with sites in group 1 spread along most of axis 2 and sites in group 2 generally limited to the negative axis 2. There was considerable overlap of sites in groups 1 and 2, and they were mainly highland sites in the catchments of the Carron and Spey. The sediment variable indicated larger particles in the sites of group 2, with these sites also being opposite the vegetation cover variable, indicating bare, open sediments. Group 3 and 4 sites were situated along the positive axis 1, with the lowland variable indicating sites in the Nith and Tweed catchments. The sites in group 3 were mainly downstream sites, as indicated by the width variable, whilst the sites in group 4 had the most vegetation, as shown by the cover variable.

Individual catchments

River Carron

The ordination of the Carron data produced an axis 1 (eigenvalue 0.442) with open, bare ERS by the downstream river near the origin and tree-shaded sediments by streams at the other end. Axis 2 also had the open, bare sediments near the origin, with the small, upstream river ERS next to moorland at the other end. The classification of the Carron data yielded three groups, and the frequency of occurrence of species in these groups, and in the groups generated by the classifications of the other catchments, is shown in Table 2. Group 1 included 10 sites, all by the upstream river. These small areas of sediment were open and dry, with mainly small particles, and were next to moorland. There was a high incidence of *Pardosa pullata*, *P. amentata* (Clerck), *Trochosa terricola* and *Oedothorax retusus*. There were 14 sites in group 2, 12 by the mid and downstream river and two by streams. These were mainly on large areas of sediment with a mixture of particle sizes, from boulders to sand, and were bare or with sparse vegetation. *Erigone dentipalpis*, *Pardosa agricola* and *P. amentata* were all numerous. Group 3 included five sites, all by streams with small particles, and all shaded by trees. There was the highest frequency of *Robertus lividus* (Blackwall) and *Walckenaeria acuminata* Blackwall, and several species, including *Lepthyphantes zimmermanni* and *Neriene clathrata* (Sundevall), were found only in this group.

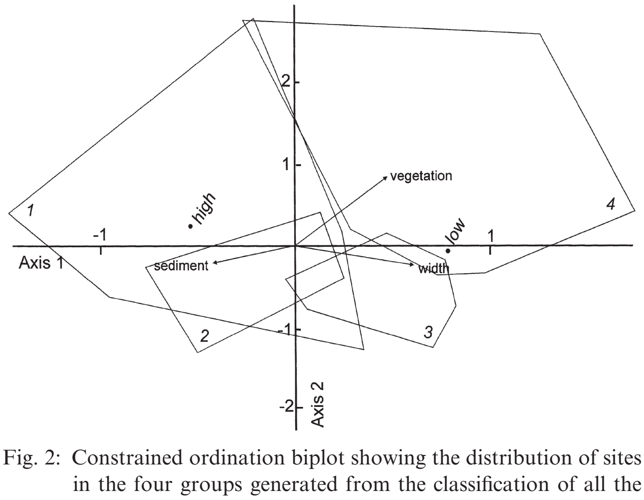

Fig. 2: Constrained ordination biplot showing the distribution of sites in the four groups generated from the classification of all the sites, the sediment index (sediment), river width (width) and vegetation cover (vegetation), shown by arrows, and the highland (high) and lowland (low) catchment variables, shown by dots. Polygons enclose the sites in each group, indicated by numbers in italics.

The constrained ordination biplot for the Carron sites, together with those of the other three catchments, is shown in Fig. 3. The most important variable was vegetation cover, with sites in group 3 by streams with tree shading having an assemblage distinct from the assemblages in the other two groups. River width and sediment had a similar influence on species assemblage distribution, with width related to the downstream sites in group 2 and the sediment variable related to sites in group 1.

River Nith

Axis 1 (eigenvalue 0.604) of the ordination of the Nith sites had sites with small particles and sparse vegetation by streams near the origin and downstream main river sites shaded by trees at the other end. Dry, open sediments with rank vegetation, by the main river and tributaries, were near the origin of axis 2. The sites at the other end of this axis were also main river and tributary ERS, but were damp with less dense vegetation. Only two groups were generated from the classification of the Nith sites. Group 1 included 19 sites, 15 by the main river and four by tributaries. There was a mixture of sediment types, from cobble-dominated to sand ERS, and the sites were bare or with sparse vegetation. There was a high incidence of *Oedothorax apicatus*, *Pardosa amentata*, *P. agricola* and *Erigone atra*, and a number of species occurred only in this group, including *Pachygnatha degeeri* and *Trochosa terricola*. There were seven sites in group 2, all by the main river. These were also composed of a mixture of particles, but had either rank vegetation or were shaded by trees. They had the most

Species	**Carron group**			**Nith group**		**Spey group**			**Tweed group**		
	1	**2**	**3**	**1**	**2**	**1**	**2**	**3**	**1**	**2**	**3**
Zelotes latreillei (Simon)						—	—	38			
Agyneta decora (O.P.-Cambr.)	—	21	—								
Steatoda phalerata (Panzer)						7	47	38			
Micaria pulicaria (Sundevall)						—	6	38			
Haplodrassus signifer (C.L. Koch)	40	14	40			7	41	63			
Clubiona comta C.L. Koch	—	—	40			—	12	38			
Antistea elegans (Blackwall)						—	—	25			
Xysticus cristatus (Clerck)						—	41	63	—	7	73
Drassodes cupreus (Blackwall)	—	43	20	26	—	20	76	100	—	20	93
Pardosa pullata (Clerck)	90	14	—			20	29	75	—	7	47
Robertus lividus (Blackwall)	60	7	100			—	18	50			
Tiso vagans (Blackwall)									4	20	60
Microlinyphia pusilla (Sundevall)	—	43	20								
Alopecosa pulverulenta (Clerck)	30	43	40	21	—	20	59	38	—	27	87
Pirata piraticus (Clerck)				32	—	—	6	25			
Agyneta olivacea (Emerton)	30	7	—								
Trochosa terricola Thorell	80	64	40	37	—	20	53	50	25	33	80
Trochosa ruricola (De Geer)									—	40	53
Diplocephalus cristatus (Blackwall)	—	36	60			—	29	—	8	7	27
Pardosa agricola (Thorell)	30	86	40	63	14	93	94	50	29	33	93
Pachygnatha degeeri Sundevall	50	14	60	58	—	13	24	25	21	40	80
Walckenaeria acuminata Blackwall	—	7	80			—	18	25	—	40	40
Walckenaeria nudipalpis (Westring)						—	—	38	4	33	7
Lepthyphantes tenuis (Blackwall)	14	40	20						—	27	13
Hypomma bituberculatum (Wider)	10	14	40						8	47	20
Oedothorax retusus (Westring)	90	50	60	74	29	53	71	—	58	73	53
Monocephalus fuscipes (Blackwall)	—	7	40						—	27	7
Clubiona reclusa O.P.-Cambr.									4	27	—
Neriene clathrata (Sundevall)	—	—	60	—	43	—	6	25			
Erigone dentipalpis (Wider)	30	79	40	74	43	67	29	13	88	80	73
Pardosa amentata (Clerck)	100	93	80	79	43	93	76	75	92	100	100
Oedothorax apicatus (Blackwall)	10	36	40	89	43	80	65	25	92	33	27
Oedothorax fuscus (Blackwall)	60	7	—	26	29				25	53	40
Erigone atra Blackwall	40	50	—	79	71	73	53	—	88	67	27
Dicymbium tibiale (Blackwall)									8	40	7
Troxochrus scabriculus (Westring)				—	43				4	33	20
Arctosa cinerea (Fabricius)				26	—						
Diplostyla concolor (Wider)	—	—	40								
Pachygnatha clercki Sundevall	30	7	—	37	100	40	6	—	67	80	13
Linyphia triangularis (Clerck)				—	29						
Lepthyphantes zimmermanni Bertkau	—	—	60	—	29				33	20	—
Leptorhoptrum robustum (Westring)									58	33	7
Gongylidium rufipes (Linnaeus)				5	43						
Bathyphantes gracilis (Blackwall)				11	43						
Diplocephalus latifrons (O.P.-Cambr.)				—	29						

Table 2: The frequency of occurrence (%) of spider species in the groups generated from the classifications of sites in the four individual catchments (minimum >20% in one group in each classification). The species order is as for the first axis of an ordination of the complete data.

Pachygnatha clercki and a lot of *Erigone atra*, as well as the presence of species associated with trees, e.g. *Neriene clathrata* and *Linyphia triangularis* (Clerck).

Vegetation cover was shown by the constrained ordination to be the most important variable affecting species assemblage composition, with the split between the two groups mainly dependent on this variable. River width and sediment composition had a limited influence on species assemblage distribution (Fig. 3).

River Spey

Axis 1 (eigenvalue 0.436) had sandy ERS with rank vegetation by the downstream main river near the origin, with stable sediments with short, patchy vegetation by small tributaries at the other end. Dry ERS by large tributaries with a mixture of sediment particles and sparse vegetation were near the origin of axis 2. The sites at the other end of this axis were the sandy main river sites with rank vegetation. Three groups were generated by the classification. Group 1 included 15 sites, nine by the main river, four by large tributaries and two by small tributaries. These were sites with a mixed composition, some sandy and some dominated by cobbles and pebbles, with most having either ruderal or rank vegetation. There was a high incidence of *Pardosa amentata*, *P. agricola* and *Erigone atra*, although this group had the fewest species. Group 2 included 17 sites, four by the upstream river, 12 by large tributaries and one by a small tributary. These sites also varied in sediment composition but were more open than those in group 1, with only sparse vegetation if any. They again had a lot of *Pardosa agricola* and the highest frequency of *Alopecosa pulverulenta* and *Oedothorax retusus*. There were eight sites in group 3, three by small streams and five by large tributaries. These were stable ERS with patchy, short vegetation. They had the most *Drassodes cupreus* and a high incidence of *Pardosa pullata* and *Xysticus cristatus*.

The constrained ordination of the Spey data showed that vegetation cover and river width had a similar amount of influence, with the sediment variable less important. The distribution of sites in the three species assemblage groups was less clear than with the other catchments, but sites in groups 1 and 3, with vegetation, were generally different from those in group 2, where there was little vegetation. The other main difference in assemblage distribution was between sites by the mainstream river and large tributaries in groups 1 and 2 on the one hand, and sites by smaller tributaries in group 3 on the other.

River Tweed

The ordination of the spider data from the Tweed catchment produced an axis 1 (eigenvalue 0.416) with downstream river sites with sand and silt ERS and considerable vegetation near the origin. The sites at the other end of this axis were by tributaries, with sand and shingle and sparse vegetation. Axis 2 had sand and shingle sites with rank vegetation by tributaries near the origin, and sites by the main river with mixed sediment composition and sparse vegetation at the other end. The classification of the Tweed sites produced three groups. Group 1 included 24 sites, 23 by the main river, occurring all the way down, and one by a tributary. There was

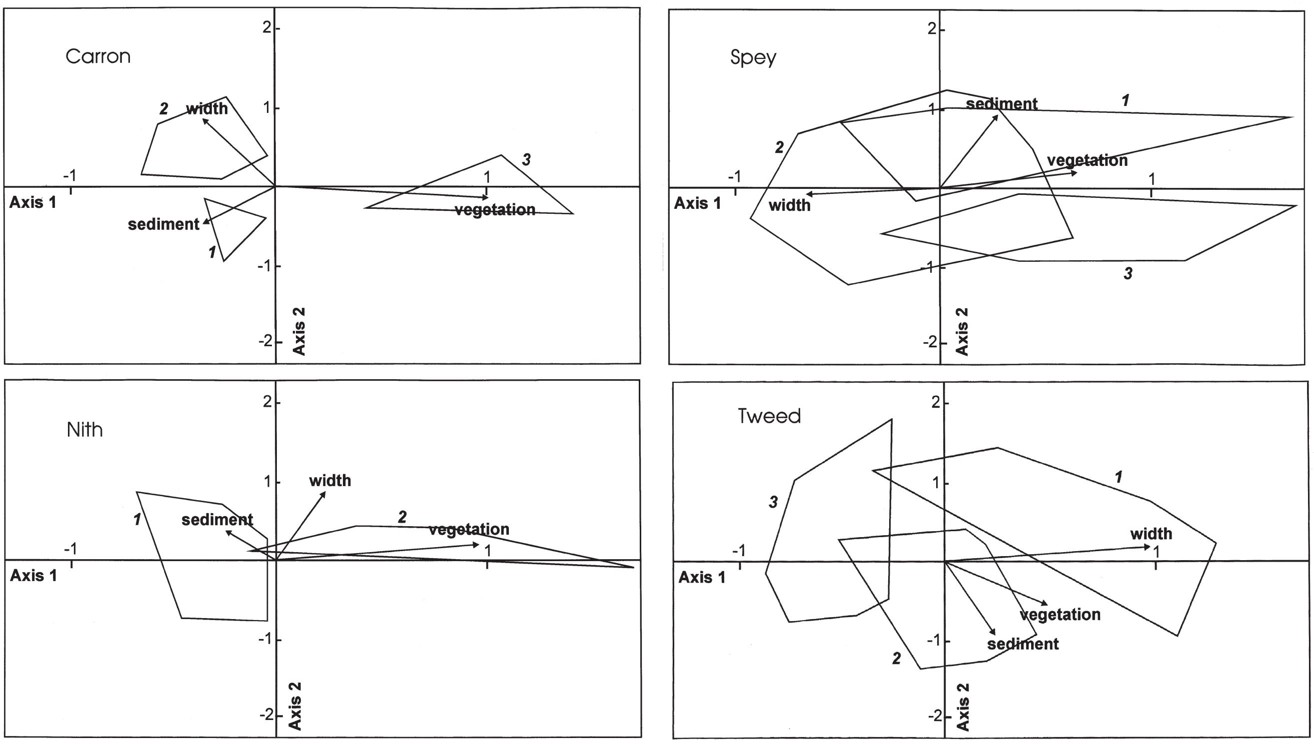

Fig. 3: Constrained ordination biplots showing the distribution of sites in the groups generated from the classification of sites in the four individual catchments, and the sediment index (sediment), river width (width) and vegetation cover (vegetation), shown by arrows. Polygons enclose the sites in each group, indicated by numbers in italics.

a mixture of sediment types, from cobble-dominated to sand and silt, most with sparse vegetation but some with rank vegetation. There was a high incidence of *Erigone atra*, *E. dentipalpis*, *Oedothorax apicatus* and *Pardosa amentata*. There were 15 sites in group 2, four by the main river, six by large tributaries and five by small tributaries. Most had sediments with small particles, especially sand, and were damp with rank vegetation. As well as *Pardosa amentata* at all these sites, they had the most *Pachygnatha clercki* and *Oedothorax retusus*. Group 3 included 15 sites, 14 by small tributaries and one by a large tributary. These were sand and shingle ERS, mainly dry, and either bare or with sparse vegetation. *Pardosa amentata* again occurred at all sites and there was the highest frequency of *Trochosa terricola*, *Pardosa agricola*, *Alopecosa pulverulenta*, *Drassodes cupreus* and *Xysticus cristatus*.

The constrained ordination of the Tweed data indicated that river width was the most important variable, with vegetation cover and sediment composition having less influence. This is in contrast to the other catchments where vegetation cover was more important. The distribution of species assemblages was primarily related to site location in the catchment, with sites in group 1 being mainly by the downstream main river, those in group 2 by the mid river and larger tributaries, and those in group 3 mainly by the smaller tributaries. There were some differences in vegetation cover, with more vegetation on the group 2 sites than on sites in groups 1 and 3.

Discussion

Whilst a considerable amount of previous work on spider species assemblages next to rivers has been concerned with various floodplain and other habitats (Greenwood *et al*., 1995; Gajdoš, 1996; Hendrickx *et al*., 1998; Bell *et al*., 1999), other recent work has concentrated on the spiders found on sediments (Smit *et al*., 1997, Sadler & Petts, 2000; Wenninger & Fagan, 2000). One aspect of the results presented here, and in other surveys such as that of Sadler & Petts (2000), is the large number of species recorded which are not specific to riverine sediments. *Pardosa agricola* was the only specialist ERS species (Albert & Albert, 1976) recorded from sites in all catchments, and the only other specialist ERS species in the UK, *Arctosa cinerea* (Fabricius), was recorded only from its usual habitat of dry, cobble-dominated ERS with some sand (Framenau *et al*., 1996), by the River Nith.

Species usually recorded from short and agricultural grasslands, such as *Erigone atra* and *E. dentipalpis* (Rushton & Eyre, 1989, 1992), were recorded frequently from sites in group 1 of the Nith, Spey and Tweed catchments, whilst those of unmanaged grasslands (e.g. *Pachygnatha clercki*) were found at a number of sites in group 1 of the Carron, Spey and Tweed and group 2 of the Nith classifications. The wetland species *Pirata piraticus* and *Leptorhoptrum robustum* were found at sites in group 1 of the Nith and Tweed respectively, and *P. piraticus* also in group 3 of the Spey, whilst species such as *Oedothorax apicatus* and *Trochosa terricola* which prefer dry, open and sandy substrates, including grasslands (Rushton & Eyre, 1992), were found in groups where sediments provided these conditions in all four catchments. These species of open, bare sites contrasted with those such as *Neriene clathrata* found on vegetated sediments in group 3 of the Carron and Spey and group 2 of the Nith catchments. Vegetation architecture has long been understood to be an important factor affecting spider species assemblage distribution (e.g. Rushton & Eyre, 1992; Downie *et al*., 1995). One obvious difference between the assemblages on ERS and those reported from grasslands and moorlands (Rushton & Eyre, 1989, 1992; Downie *et al*., 1995) was the paucity of species on ERS. These sediments appear to have considerably fewer species than less disturbed and more vegetated habitats, with Zulka *et al*. (1998) also recording only eight species from a gravel ERS.

There were major differences in the species assemblages between the highland and lowland catchment types, with two groups of the classification of all sites being dominated by highland ERS and two by lowland ERS. The secondary variation in the ordination of all-site data was mainly related to site position in the catchment, as reflected by river width, and the amount of vegetation on sites. The vegetation cover variable was the most influential factor in explaining the distribution of assemblages on ERS in the individual catchments of the Carron, Nith and Spey, whilst river width was most important in the Tweed catchment. Vegetation cover, or the lack of it, was shown to be a factor in all the classifications where the major differences between sites in the habitat groups tended to be reflected in a progression from bare sediment, through sparse and rank vegetation, to tree-shaded ERS. Sediment composition has been found to be an important variable affecting the distribution of ground beetles on ERS (Eyre & Lott, 1997) but it appears to be less important for spiders. The vegetation on ERS tends to be related to the position of the site in the catchment, with the distribution of sites in the habitat groups grouped in distinct bands limited to, for instance, tributaries or downstream main river stretches. However, it was interesting that the vegetated ERS in the Carron catchment were by the stream tributaries and the upstream river, whilst they were distributed on the mid and downstream stretches of the rivers of the other three catchments.

This survey shows that there were distinct spider assemblages present on ERS by rivers and tributaries in Scottish and northern English catchments. Other invertebrate assemblages, such as ground beetles and rove beetles (Eyre *et al*., 2001a,b), show similar patterns of distribution on ERS but it appears that numbers of both spider species and assemblages found on the Scottish and northern English sediments were smaller than for the beetle groups. There were also fewer habitat groups in a classification of spider grassland habitats in north-east England (Rushton & Eyre, 1992) than in a corresponding ground beetle classification (Luff *et al*., 1992). In surveys of epigeal invertebrates covering the same range of sites, it appears that different numbers of habitat types tend to be identified for different groups of invertebrates.

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Appendix

The spider species recorded from the survey of exposed riverine sediments, and the number of sites in each catchment at which they were found.

Family and species	Carron	Nith	Spey	Tweed
Gnaphosidae				
Drassodes cupreus (Blackwall)	7	5	24	17
Haplodrassus signifer (C.L. Koch)	8	—	13	3
Zelotes latreillei (Simon)	—	—	3	—
Micaria pulicaria (Sundevall)	—	1	4	3
Clubionidae				
Clubiona reclusa O.P.-Cambr.	4	1	1	4
Clubiona neglecta O.P.-Cambr.	—	—	1	—
Clubiona lutescens Westring	—	1	—	—
Clubiona comta C.L. Koch	2	—	5	1
Clubiona trivialis C.L. Koch	1	—	—	—
Clubiona subtilis L. Koch	—	—	1	—

Family and species	Carron	Nith	Spey	Tweed
Liocranidae				
Agroeca proxima (O.P.-Cambr.)	—	—	1	—
Zoridae				
Zora spinimana (Sundevall)	1	—	—	—
Thomisidae				
Xysticus cristatus (Clerck)	2	3	13	12
Xysticus bifasciatus C.L. Koch	—	—	2	—
Ozyptila trux (Blackwall)	1	1	3	4
Philodromidae				
Tibellus maritimus (Menge)	—	—	—	1
Salticidae				
Salticus scenicus (Clerck)	—	—	—	1
Heliophanus flavipes (Hahn)	—	—	1	—
Lycosidae				
Pardosa agricola (Thorell)	17	13	34	26
Pardosa palustris (Linnaeus)	—	—	1	3
Pardosa pullata (Clerck)	11	1	14	8
Pardosa amentata (Clerck)	27	18	33	52
Pardosa nigriceps (Thorell)	—	—	—	3
Alopecosa pulverulenta (Clerck)	11	4	16	17
Trochosa ruricola (De Geer)	1	3	4	14
Trochosa terricola Thorell	19	7	16	23
Arctosa perita (Latreille)	—	—	1	—
Arctosa leopardus (Sundevall)	—	1	—	—
Arctosa cinerea (Fabricius)	—	5	—	—
Pirata piraticus (Clerck)	2	6	3	3
Agelenidae				
Cryphoeca silvicola (C.L. Koch)	1	—	4	—
Hahniidae				
Antistea elegans (Blackwall)	1	—	2	3
Hahnia nava (Blackwall)	—	1	—	—
Mimetidae				
Ero furcata (Villers)	—	—	—	1
Theridiidae				
Steatoda phalerata (Panzer)	—	2	12	2
Steatoda bipunctata (Linnaeus)	—	1	—	—
Robertus lividus (Blackwall)	12	1	7	2
Nesticidae				
Nesticus cellulanus (Clerck)	—	—	1	—
Tetragnathidae				
Pachygnatha clercki Sundevall	4	14	7	30
Pachygnatha degeeri Sundevall	10	11	8	22
Metellina mengei (Blackwall)	1	1	1	1
Linyphiidae				
Ceratinella brevipes (Westring)	1	—	1	—
Ceratinella brevis (Wider)	2	—	—	1
Walckenaeria nudipalpis (Westring)	2	—	3	7
Walckenaeria vigilax (Blackwall)	—	1	—	—
Walckenaeria antica (Wider)	—	—	—	1
Walckenaeria cuspidata Blackwall	1	—	2	1
Walckenaeria unicornis O.P.-Cambr.	1	—	—	—

Family and species	Carron	Nith	Spey	Tweed
Walckenaeria kochi (O.P.-Cambr.)	—	—	—	1
Walckenaeria acuminata Blackwall	5	2	5	11
Dicymbium nigrum (Blackwall)	—	—	—	2
Dicymbium tibiale (Blackwall)	2	—	1	9
Gnathonarium dentatum (Wider)	—	2	1	1
Gongylidium rufipes (Linnaeus)	—	4	—	4
Dismodicus bifrons (Blackwall)	1	1	1	—
Hypomma bituberculatum (Wider)	5	2	2	12
Baryphyma pratense (Blackwall)	—	—	—	6
Baryphyma trifrons (O.P.-Cambr.)	—	—	—	1
Gonatium rubens (Blackwall)	1	—	—	2
Gonatium rubellum (Blackwall)	1	1	—	—
Pocadicnemis pumila (Blackwall)	1	—	—	1
Oedothorax gibbosus (Blackwall)	1	2	3	2
Oedothorax fuscus (Blackwall)	7	7	2	19
Oedothorax retusus (Westring)	19	16	19	33
Oedothorax apicatus (Blackwall)	8	20	25	31
Trichopterna thorelli (Westring)	—	—	—	3
Pelecopsis mengei (Simon)	—	—	—	1
Pelecopsis parallela (Wider)	1	—	2	—
Silometopus elegans (O.P.-Cambr.)	—	—	1	—
Tiso vagans (Blackwall)	1	1	1	13
Troxochrus scabriculus (Westring)	—	3	3	9
Monocephalus fuscipes (Blackwall)	3	—	1	5
Micrargus herbigradus (Blackwall)	2	—	—	3
Savignia frontata Blackwall	3	1	—	—
Diplocephalus cristatus (Blackwall)	8	1	4	7
Diplocephalus permixtus (O.P.-Cambr.)	1	—	—	—
Diplocephalus latifrons (O.P.-Cambr.)	—	2	—	2
Araeoncus crassiceps (Westring)	1	—	—	1
Milleriana inerrans (O.P.-Cambr.)	1	—	1	—
Erigone dentipalpis (Wider)	16	17	16	43
Erigone promiscua (O.P.-Cambr.	1	—	—	—
Erigone atra Blackwall	11	20	20	34
Leptorhoptrum robustum (Westring)	—	1	—	20
Hilaira excisa (O.P.-Cambr.)	1	—	—	—
Halorates distinctus (Simon)	—	1	—	4
Porrhomma convexum (Westring)	—	1	—	—
Agyneta subtilis (O.P.-Cambr.)	—	—	1	—
Agyneta decora (O.P.-Cambr.)	4	—	—	—
Agyneta olivacea (Emerton)	4	—	—	—
Meioneta saxatalis (Blackwall)	1	—	—	—
Centromerita concinna (Thorell)	—	—	1	1
Saaristoa abnormis (Blackwall)	2	—	—	—
Bathyphantes gracilis (Blackwall)	—	5	1	7
Bathyphantes parvulus (Westring)	—	—	—	4
Bathyphantes nigrinus (Westring)	—	1	—	—
Kaestneria pullata (O.P.-Cambr.)	—	1	—	1
Diplostyla concolor (Wider)	2	—	—	3
Stemonyphantes lineatus (Linnaeus)	—	—	1	—
Bolyphantes luteolus (Blackwall)	—	—	—	2
Lepthyphantes tenuis (Blackwall)	6	—	—	6
Lepthyphantes zimmermanni Bertkau	3	2	2	11
Lepthyphantes pallidus (O.P.-Cambr.)	—	—	—	2
Linyphia triangularis (Clerck)	1	2	2	1
Neriene clathrata (Sundevall)	3	3	3	5
Microlinyphia pusilla (Sundevall)	7	—	2	—