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The influence of riparian management on the habitat structure and macroinvertebrate communities of upland streams draining plantation forests

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Summary

1. Habitat features and macroinvertebrate communities were surveyed in 66 predominantly upland streams throughout Wales and Scotland to assess the efficacy of riparian management (as 'buffer strips') in protecting stream resources during commercial forestry.

2. Habitat data were reduced by principal components analysis (PCA). Macroinvertebrates in the stream margins and riffles were considered separately, and ordination of the community data was by DECORANA.

3. Habitat gradients recognized between the streams from PCA included trends in size, ionic strength, acidity, substratum type, and in the characteristics of marginal habitats. The latter represented a change from margins dominated by 'soft' vegetation features to margins composed of 'hard' features such as tree roots, rock and stones.

4. Marginal habitat characteristics differed between streams with different riparian management. Streams with 'harder' margins occurred where the banks were covered with either conifers or broadleaves. Streams with 'softer' margins occurred in seminatural moorland, and where a 'buffer strip' of moorland vegetation had been retained along the stream at the planting stage. Streams in conifer forest in which a riparian buffer strip had been cleared retrospectively were intermediate.

5. For any given pH, aluminium concentrations were significantly higher in streams draining conifer catchments than in streams draining whole catchments of moorland or deciduous woodland. This effect occurred irrespective of buffer strips in conifer catchments.

6. The taxon richnesses of Ephemeroptera, Plecoptera, Trichoptera and all taxa combined, in both riffles and margins, declined significantly with increasing acidity and aluminium concentration. Primary ordination axes from both habitats correlated with taxon richness, and hence also with pH and aluminium. However, there were significant effects on the ordination scores by riparian management, due mostly to reduced taxon richnesses in conifer sites without buffer strips. Significant effects remained even after accounting for increased aluminium concentration at conifer sites.

7. We conclude that gradients related to acidity are dominant correlates with the composition of invertebrate communities in upland British streams. However, riparian management can influence stream habitat structure and, to some extent, the macroinvertebrate fauna in the stream margins. Buffer strips consisting of broadleaf trees and moorland/grassland vegetation have different effects on taxonomic composition and abundance. They are most effective when implemented at the planting stage, though further data are required to assess succession with time where buffer strips have been cleared retrospectively.

Key-words: aquatic invertebrates, forestry, habitat, acidification, riparian management.

Introduction

Throughout the World, water catchments are used, often intensively, for purposes unconnected with the management of the rivers which drain them. Yet, because of the strong linkages which exist between rivers and their catchments (Hynes 1975), influences on river ecosystems almost inevitably arise. Such influences can involve chemical, energetic and physical pathways with a variety of biological consequences. In some cases, however, management strategies are adopted which aim to modify the extent to which rivers are affected by catchment land use, often by some form of riparian feature such as the 'buffer strip' (Mills 1986).

In Britain, plantation forestry has been perceived as a widespread example of an effect of catchment land use on river ecology (Mills 1986). Plantations involving predominantly exotic softwoods now occupy around 11% of the land area of Britain, mostly at the higher elevations where many of Britain's major rivers originate. Postulated consequences for rivers include acidification through the increased scavenging of air pollutants, altered hydrology, enhanced erosion and sedimentation, alterations in stream habitat structure, and alterations in energy inputs from heat, light and tree products (Ormerod, Mawle & Edwards 1986). However, recent joint initiatives between forestry, water and conservation bodies have led to the development and implementation of methods of riparian management in forests, the aim being to minimize some of the effects perceived as adverse for river ecology (Forestry Commission 1988). Predominantly, they involve riparian buffer strips of broadleaf trees and/or moorland vegetation either left at the time of planting, or created retrospectively by the removal of streamside conifers. So far, however, the efficacy of these techniques is largely unappraised, either in terms of the habitat conditions they create in streams, or the faunal communities which result. This lack of information is unfortunate not only in managerial terms; if available, it would provide an opportunity to assess how stream communities might be affected by such fundamental factors as their physical structure and riparian canopy, hence their energy base (Behmer & Hawkins 1986).

In this paper, we assess the effects of several methods of riparian management on the habitat structure of 66 streams throughout the uplands of Wales and Scotland. We also assess the effect of management on their macroinvertebrate communities because of the role of these organisms in the stream ecosystem, and because they are valuable indicators of wider conditions (e.g. Rutt, Weatherley & Ormerod 1990).

Methods and study locations

Sites for the study were chosen with the collaboration of the UK Forestry Commission, 66 streams of orders 1–3 (Strahler 1957) being selected throughout the uplands of Wales and Scotland (Fig. 1, Table 1). They reflected six different types of riparian management (= management groups) involving: (i) streams in catchments wholly of conifer forest, planted up to, and over, the stream banks (CON sites); (ii) conifer forest with a riparian buffer strip in which forest had been cleared 1–7 (mean 2·8) years ago to a width of 5–20 m on both banks of the stream, natural vegetation being allowed to regenerate (CLR sites); (iii) conifer forest, in which a buffer strip of moorland/grassland vegetation had been left unplanted to a width of 5–20 m on both banks of the stream (BUF sites); (iv) conifer forest, in which a buffer strip of deciduous trees and shrubs had been left *in situ*, or allowed to regenerate, to a width of 5–20 m on both banks of the stream (BRD sites); (v) streams, as far as possible, in catchments wholly consisting of semi-natural broadleaf woodland, with trees and shrubs present up to the stream banks (SNW sites); (vi) streams, as far as possible,

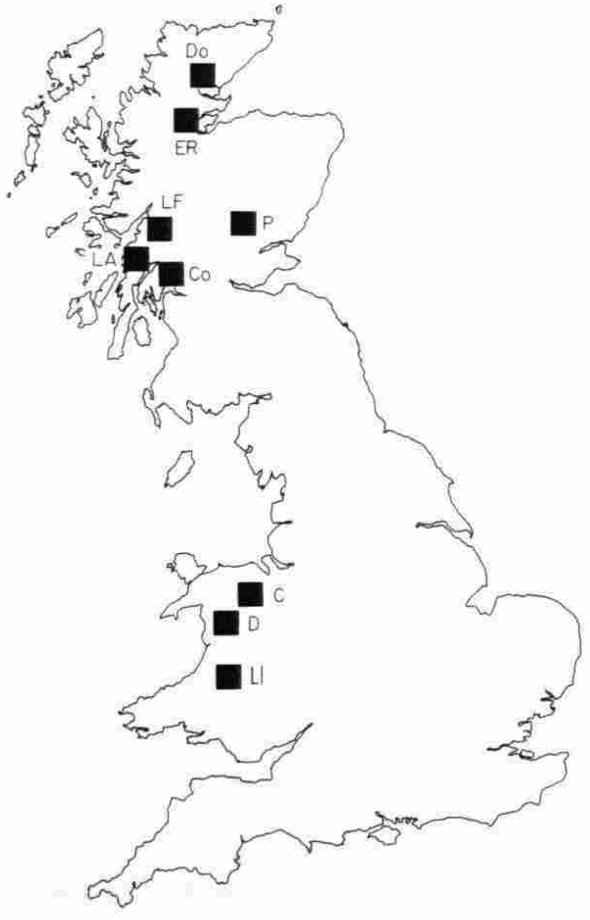

Fig. 1. The location of the sampling sites, arranged by Forestry Commission District, in Wales and Scotland: Ll, Llandovery; D, Dolgellau; C, Clwyd; Co, Cowal; LA, Loch Awe; LF, Lorne Forest; P, Perthshire; ER, Easter Ross; Do, Dornoch.

Table 1. List of sites from nine Forestry Commission Districts in Scotland (nos 1–44) and Wales (nos 45–66). Map references and management categories (CAT) are given, along with values for pH and calcium (mg/l) (from spot samples)

	F.D. Area	OS Ref	CAT	pH	Calcium
1.	Cowal	NS171849	CLR	6·5	2·4
2.	Cowal	NS126993	CON	6·3	2·2
3.	Cowal	NS132985	MOR	6·0	1·3
4.	Cowal	NS127001	BUF	6·4	2·1
5.	Cowal	NS129007	MOR	5·7	0·8
6.	Cowal	NS132964	SUW	6·0	2·2
7.	Cowal	NS112942	BUF	5·5	0·9
8.	Cowal	NS111946	CON	5·2	0·8
9.	Cowal	NS112872	BRD	5·5	1·3
10.	Lorne Forest	NN244320	BRD	6·2	1·7
11.	Lorne Forest	NN252338	MOR	6·6	4·0
12.	Lorne Forest	NN242318	BRD	6·0	0·9
13.	Lorne Forest	NN258303	BUF	6·2	2·3
14.	Lorne Forest	NN271308	CON	6·7	2·7
15.	Lorne Forest	NN264305	BUF	6·5	4·8
16.	Lofne Forest	NN229306	SNW	6·1	1·0
17.	Lorne Forest	NN235333	BRD	6·5	1·6
18.	Lorne Forest	NN155204	CON	5·4	0·6
19.	Lorne Forest	NN154502	SNW	5·9	0·5
20.	Lorne Forest	NN164509	CLR	5·9	0·6
21.	Easter Ross	NH564801	CON	4·8	1·0
22.	Easter Ross	NH562805	MOR	6·1	1·1
23.	Easter Ross	NH564802	BUF	4·7	0·6
24.	Easter Ross	NH607747	CLR	5·9	1·7
25.	Easter Ross	NH674767	BRD	4·6	1·0
26.	Dornoch	NH778944	CON	6·7	20·6
27.	Dornoch	NC591161	BUF	5·4	2·9
28.	Dornoch	NC538108	BRD	5·2	2·7
29.	Dornoch	NC548008	MOR	6·6	5·1
30.	Dornoch	NH665892	SNW	4·8	2·0
31.	Perthshire	NN991450	BRD	6·8	8·3
32.	Perthshire	NO114511	CLR	6·4	3·8
33.	Perthshire	NO134512	CON	6·0	4·4
34.	Perthshire	NN743607	BRD	6·2	3·5
35.	Perthshire	NN712622	MOR	6·5	5·5
36.	Perthshire	NN651576	SNW	6·4	3·4
37.	Perthshire	NN730232	SNW	6·9	7·4
38.	Loch Awe	NR868912	CLR	6·9	9·4
39.	Loch Awe	NR876906	CLR	6·1	4·4
40.	Loch Awe	NR886907	CLR	6·1	3·7
41.	Loch Awe	NR899914	BUF	6·2	6·3
42.	Loch Awe	NR867958	SNW	6·9	8·1
43.	Loch Awe	NR895947	CON	6·6	10·6
44.	Loch Awe	NR903932	BUF	5·2	1·6
45.	Loch Awe	NM908064	MOR	6·5	4·7
46.	Dollgellau	SH695321	CON	4·4	3·4
47.	Dollgellau	SH834268	CLR	5·9	2·0
48.	Dollgellau	SH722238	SNW	6·1	2·0
59.	Dollgellau	SH811368	BUF	6·5	3·6
50.	Dollgellau	SH808369	MOR	6·5	3·3
51.	Dollgellau	SH798403	MOR	6·0	1·8
52.	Clwyd	SH990518	CLR	5·1	5·1
53.	Clwyd	SH947547	BUF	4·2	2·8
54.	Clwyd	SH947545	CON	4·9	2·4
55.	Clwyd	SH962520	BUF	6·2	5·2
56.	Llandovery	SN811516	CLR	4·6	1·1
57.	Llandovery	SN821496	MOR	5·5	1·4
58.	Llandovery	SN815507	CLR	5·0	2·1
59.	Llandovery	SN816502	CON	6·3	4·7
60.	Llandovery	SN738466	SNW	6·1	2·0
61.	Llandovery	SN763574	MOR	5·9	2·4
62.	Llandovery	SN805487	BUF	4·7	1·2
63.	Llandovery	SN701489	MOR	5·2	0·8
64.	Llandovery	SN772568	MOR	5·0	1·1
65.	Llandovery	SN770564	MOR	4·6	0·5
66.	Llandovery	SN808530	CON	4·4	0·8

in catchments wholly consisting of semi-natural grassland and moorland (MOR). In all cases, conifers were beyond the phase of canopy closure, crops being at least 15–20 years old.

PHYSICOCHEMICAL SAMPLING AND ANALYSIS

Streams were visited once for biological and physicochemical sampling in October and November 1990. Physicochemical variables for habitat description were derived in four groups describing, respectively, characteristics of the streams' substratum, wetted margins, chemistry, location and size.

Substratum assessments and marginal characteristics were recorded on-site largely following the method of Rutt, Weatherley & Ormerod (1989). A $0·5 \times 0·5$ m quadrat, divided into 25 subquadrats of $0·1 \times 0·1$ m, was placed randomly on the stream bed to the left, right or mid-channel of 10 points located randomly over 100 m of each stream. The dominant substratum type in each submerged subquadrat was then recorded as tree roots, macroflora, bedrock, boulders (>256 mm), cobbles/pebbles (16–256 mm), gravel/sand (0·06–16 mm) and silt/clay (<0·06 mm). Adjacent to each of the 10 positions where substratum features were recorded, the dominant marginal habitat below the water surface was recorded in contiguous 0·1 m lengths on a random choice of either the left or right bank. Habitats recorded were rush and grass shoots and leaves, tree roots, grass roots, *Sphagnum*, other mosses, liverworts, leaf litter, soil, rock and stones. Since streams were mostly at base flow when sampled, these were liable to represent all the major habitats available in the banks under all except low flow conditions. The percentage of the stream overhung by trees and shrubs of all species was also estimated at each site.

For logistical reasons, chemical description was based on only one sample taken during the field visit. Conductivity and pH were measured in the laboratory by combination glass electrode. Colour was determined by air-segmented flow colorimeter at 400 nm, and metals were determined by inductively coupled plasma spectrophotometry, aliquots for metal analysis having been passed on-site through a 0·45 μm membrane filter into a 1% nitric acid fixative. Storage of samples between collection and measurements was at maximum 8 days, which might be expected to increase the pH of base-poor samples. However, investigation at Llyn Brianne showed that the resulting errors were small (0·2 pH units). Moreover, aluminium concentrations were largely unchanged by storage due to fixation, and aluminium often is a stronger correlate with biological status than pH.

To assess stream size, widths were measured on site at three equally spaced intervals along the survey reach. Altitudes, slopes (nominally from 1 km upstream to 1 km downstream of the study reach) and stream link magnitudes (Shreve 1966) were determined from 1:50 000 scale Ordinance Survey maps.

BIOLOGICAL SAMPLING

Macroinvertebrates were sampled separately in margins and riffles by kick-sweep samples (net mesh 900 μm) each of 2 min duration. Margins were defined as being within one net-width of the bank, and all microhabitats here were sampled roughly in proportion to their occurrence. The sampler always moved in an upstream direction to avoid cross-contamination of dislodged animals between habitats. Samples were preserved on site in 4% formaldehyde, and in the laboratory animals were sorted and identified, where possible, to species. In some cases, either due to taxonomic difficulty (e.g. Chironomidae, Simuliidae, Oligochaetes) or because early instars were frequently collected (e.g. Limnephilidae, Dytiscidae), identification was arrested at higher taxonomic levels.

STATISTICAL ANALYSIS

All variables requiring transformation to give approximate normality were logged prior to any further assessment. This applied to both physicochemical variables and animal abundances.

For analysis of physicochemical differences between sites, variables were grouped into those describing the stream substratum, stream margins, stream chemistry and those related to stream size and location (see Table 2). Within each of these groups, separate principal components analyses (PCA) were undertaken on the correlation matrices so that general physicochemical gradients between the sites could be identified. Scores on each principal component (PC) were then analysed for differences between management groups using ANOVAS. Initial analysis had shown that PCA involving all variables simultaneously provided principal components similar to those derived with variables grouped into the four categories, but the gradients in this larger analysis were weaker.

Ordination analysis of the macroinvertebrate data was by DECORANA (Hill 1979; Wright *et al.* 1984).

Table 2. Correlations (i.e. factor loadings) between each variable and the principal components from each of four analyses

	PC1	PC2
Margin		
Tree roots	0·45	−0·07
% Cover	0·39	−0·01
Rock	0·37	0·14
Stones	0.31	−0·33
Leaves	0·29	0·11
Gravel	0·16	0·06
Mosses/liverworts	0·02	0·48
Wood	0·01	−0·23
Herb/macrophytes	−0·04	0·29
Sand	−0·05	−0·29
Earth	−0·06	0·31
Grass roots	−0·21	−0·46
Sphagnum	−0·24	0·25
Grasses	−0·41	0·05
% variation explained	23·1	12·6
Substratum		
Boulders	0·48	0·36
Bedrock	0·43	−0·29
Tree roots	0·30	−0·24
Leaves	0·18	−0·15
Silt/mud	−0·23	−0·56
Moss	−0·28	0·08
Pebbles/cobbles	−0·34	0·54
Sand/gravel	−0·43	−0·28
% variation explained	23·6	21·2
Location		
Linkage	0·64	0·12
Width	0·62	0·17
Altitude	−0·03	−0·83
Slope	−0·45	0·50
% variation explained	46·5	29·1
Chemistry		
pH	−0·02	−0·64
Aluminium	−0·24	0·53
Colour	−0·38	0·19
Calcium	−0·40	−0·45
Conductivity	−0·45	0·02
Iron	−0·45	0·13
Magnesium	−0·46	−0·17
% variation explained	43·6	28·5

This technique arranges sites into an objective order, those with similar taxonomic composition occurring together. Scores for each site along the ordination axes can then be related to environmental variables.

Taxon richnesses and abundances for major macroinvertebrate groups were compared between management groups using ANOVA. DECORANA scores were related to forest management groups by ANOVA, and to physicochemical variables, including the PCs, using product−moment correlation.

Results

PHYSICOCHEMICAL CHARACTERISTICS

Sites ranged in altitude from 30 to 430 m OD, slopes were 10–400 m km^{-1}, width 0·5–3·5 m, calcium 0·5–20 mg l^{-1}, and pH 4·4–6·9, in general a combination representative of the locations and chemistry of forest streams throughout large areas of upland Britain (see Table 1).

PCA of the four principal groups of physicochemical variables indicated marked gradients between the sites, with the first two axes in each analysis explaining 35–73% of the total variance (Table 2). Trends along these gradients could be seen from the magnitude of the correlations between each variable and the PCs (i.e. factor loadings).

PCs describing stream location and chemistry were the strongest, and the gradients most straightforward. The first location gradient (PC1) described a trend predominantly from small to large size. On PC2, streams ranged from high to low altitude, although slopes tended to increase along this axis indicating that some steep streams could be found at lower altitudes. Chemical gradients reflected a trend from high to low ionic strength (= conductivity) on PC1, and a trend towards increasing acidity (i.e. decreasing pH), decreasing calcium and increasing aluminium concentration on PC2.

In general, gradients in the character of the stream margins (PC1) reflected a change from sites dominated by 'soft' features such as grasses, *Sphagnum* spp. and grass roots, to those dominated by 'hard' features such as tree roots, rock and stones. Trees overhanging the stream (i.e. % cover) and tree leaves also increased towards the 'harder' end of this gradient. PC2 represented a trend from margins dominated by grass roots to those dominated by mosses and liverworts.

Substratum gradients between the sites reflected a change along PC1 from those with larger amounts of sand and gravel to those predominantly with bedrock and boulders, the latter also showing a tendency for tree-roots to form part of the substratum. PC2 described a trend from streams with a muddy, silty substratum, to those with more pebbles and cobbles.

STREAM PHYSICOCHEMISTRY AND RIPARIAN MANAGEMENT

Several physicochemical features showed strong and highly significant differences between the riparian management groups. Those of greatest interest in relation to riparian management occurred along the first axis of the margin PC. This showed that there was greater development of grassy and emergent vegetation in the wetted stream margins of the BUF and MOR groups, but more 'hard' features such as tree roots and rock in the CON, BRD and SNW groups (Table 2, Fig. 2). CLR groups were intermediate as they had similar amounts of vegetation in the margins to the BUF and MOR groups, but similar amounts of rock and tree roots to the CON, BRD and SNW groups. Forest management group had no significant effect on Margin PC2.

Differences in substratum features between management groups were less marked, although BRD and SNW sites did tend to have substrata with more boulders and bedrock than elsewhere and so scored high on substratum PC1 (Fig. 2). Differences in size and location between groups occurred because CLR sites tended to be on larger streams, whereas MOR sites tended to be at lower altitudes.

No pronounced differences in scores on the chemical PCs could be detected between the six management groups. However, influences on chemistry due to general management could not be ruled out: both iron (geometric mean 0·19 mg l^{-1} × 0·55 SD vs. 0·08 mg l^{-1} × 0·69 SD, $F_{1,64} = 5{\cdot}07$, $P = 0{\cdot}03$ after log transformation) and aluminium concentrations (0·132 mg l^{-1} × 0·34 SD vs. 0·074 mg l^{-1} × 0·31 SD, $F_{1,64} = 8{\cdot}12$, $P = 0{\cdot}006$ after log transformation) were on average greater in all conifer streams (i.e. CON, CLR, BUF, BRD) than other types, irrespective of riparian management (Fig. 2). No other chemical variable showed a similar difference. Interestingly, pH explained 38% of the variance in the log concentration of aluminium, but residuals around this regression were strongly related to the presence of conifers ($F_{1,65} = 6{\cdot}07$, $P = 0{\cdot}016$). Thus, for any given pH, aluminium concentrations were, on average, 46 μg l^{-1} higher in streams draining forest catchments, irrespective of riparian management, than in other stream types.

STREAM MACROINVERTEBRATES: TAXON RICHNESS AND ABUNDANCE

In general, the macroinvertebrate communities recorded were typical of those across large areas of upland Britain, and dominated by the aquatic stages of the insect orders Ephemeroptera, Plecoptera and Trichoptera. Smaller numbers of coleopterans, dipterans and oligochaetes were also found. None of the sites was particularly diverse, the range of taxon richnesses in margins being 6–30, and that in riffles 4–30.

Both taxon richnesses and abundances for each of the major invertebrate groups were closely correlated between margins and riffles across sites (Table 3), indicating that generally similar trends were described by each type of sample. However, the occurrence of some taxa was significantly associated with one or other of the habitat types (Table 4). Data on macroinvertebrates from margins and riffles were thus analysed separately.

Some differences in the macroinvertebrates recorded could be related to riparian management, although in some cases effects occurred only at $P < 0{\cdot}1$. The clearest pattern was a reduction in the CON group of taxon richnesses for plecopterans, ephemeropterans and all groups combined (Table 5).

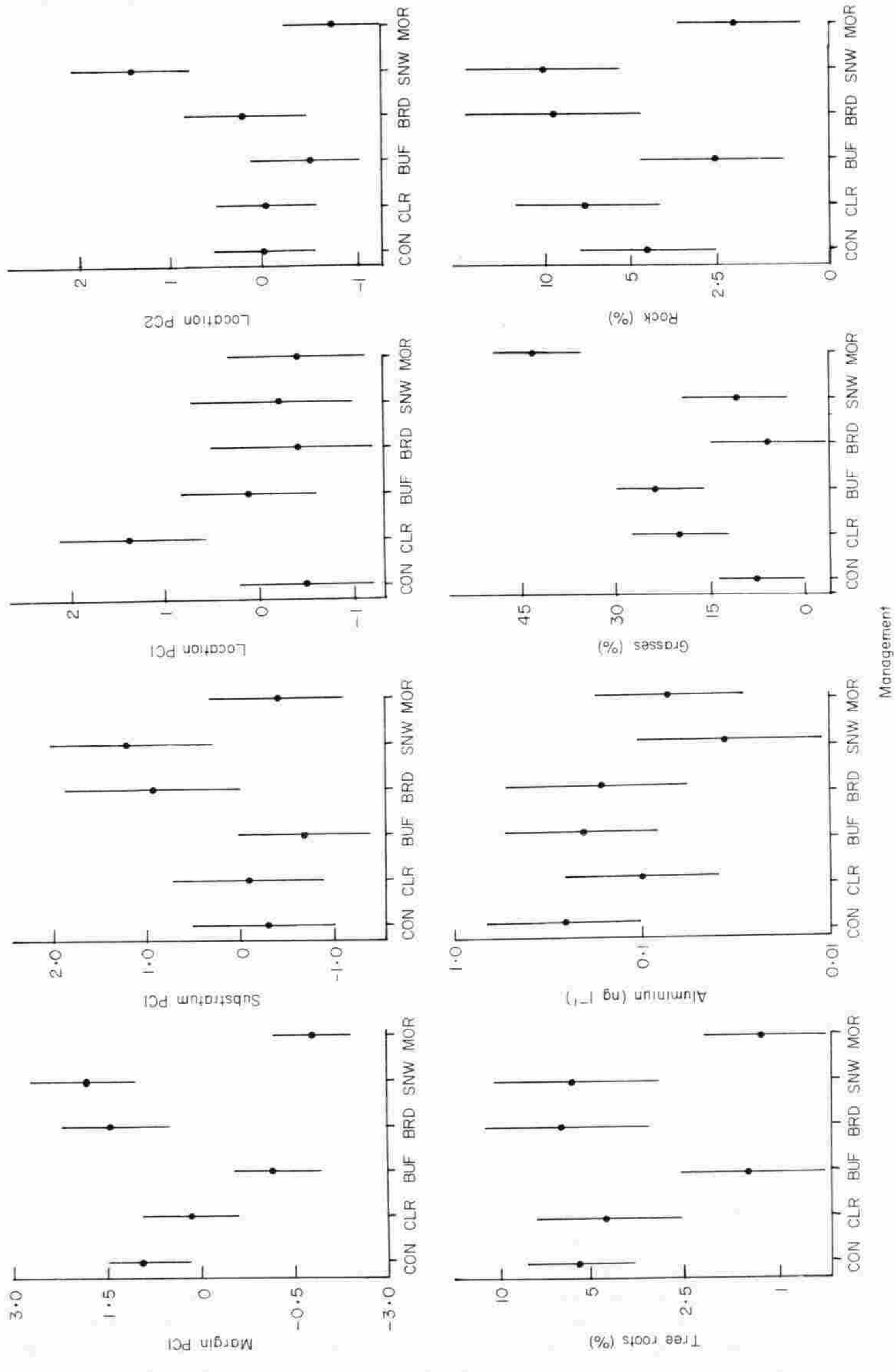

Fig. 2. Selected physicochemical differences between streams in upland Wales and Scotland subject to different forms of riparian management. Scores on principal components describing the marginal character, substratum and size/location of the sites are shown in the upper panel.

Table 3. Correlations across 66 streams in upland Wales and Scotland between the taxon richness and abundance of the principal macroinvertebrate groups found in riffles versus margins. All values are significant at $P = 0{\cdot}01-0{\cdot}001$. Correlations of abundance were determined after log transformation

	Taxon richness	Abundance
All groups	0·75	0·78
Ephemeroptera	0·72	0·56
Plecoptera	0·69	0·64
Trichoptera	0·64	0·78

Comparisons made *a posteriori* by one-way ANOVA between this management group and all others combined showed effects on taxon richness in both margins and riffles which were significant in every case ($F_{1,64} = 5{\cdot}1-9{\cdot}9$, $P = 0{\cdot}03-0{\cdot}003$) except for the Trichoptera. Abundances were related less clearly to management, and only for ephemeropterans in the margins was there a significant effect, nymphs being scarcest in CON streams.

Other physicochemical features were also important. In particular, the taxon richness, in both riffles and margins, of ephemeropterans, plecopterans, trichopterans and all groups combined correlated positively with stream pH ($r = 0{\cdot}26-0{\cdot}57$, $P = 0{\cdot}05-0{\cdot}001$) and negatively with aluminium concentration ($r = -0{\cdot}26$ to $-0{\cdot}50$, $P = 0{\cdot}05-0{\cdot}001$). However, the total taxon richness in margins also increased significantly with the amount of grassy vegetation in the stream margins ($r = 0{\cdot}34$, $P = 0{\cdot}01$).

Table 4. The occurrence of selected taxa in (1) riffles only, (2) margins only, (3) riffles and margins, in 66 streams in upland Wales and Scotland

Taxon	1	2	3	Chi sq.
Riffle taxa				
Perlodes microcephala	12	0	9	4·80*
Chloroperla tripuctata	12	2	3	5·00*
Rhyacophila dorsalis	20	3	14	5·67*
Margin taxa				
Limnephilidae	2	22	34	4·35*
Dytiscidae	4	25	11	8·65*
Generalist taxa				
Protonemura meyeri	12	4	33	0·78
Protonemura praecox	9	3	25	0·58
Nemoura cambrica	4	9	24	0·41
Nemurella picteti	5	3	13	0·12
Amphinemura sulcicollis	10	5	21	0·44
Leuctra hippopus	7	4	46	0·08
Leuctra nigra	5	14	14	1·72
Isoperla grammatica	7	5	28	0·06
Heptagenia lateralis	8	2	4	2·00
Rhithrogena semicolorata	7	0	11	1·69
Baetis rhodani	8	2	34	0·46
Hydropsyche siltalai	6	3	8	0·36
Diplectrona felix	3	0	3	1·00
Plectrocnemia conspersa	12	11	32	0·01
Philopotamus montanus	10	9	13	0·02
Wormaldia	9	5	1	1·00
Elminthidae	6	13	16	0·96
Helodidae	4	9	27	0·37
Dicranota	11	8	33	0·00
Simuliidae	9	3	49	0·33
Chironomidae	8	17	30	0·95
Oligochaeta	2	5	57	0·07

Table 5. The mean (with SD) abundance and taxon richness of major invertebrate groups in streams ($n = 8-12$ per group) draining catchments with different forms of management in upland Wales and Scotland. Abundance values were derived as geometric means by back-transformation from the log distribution: the SD is log scale.

	Forest management group CON	CLR	BUF	BRD	SNW	MOR	F
Species richness							
Riffle							
Plecopterans	4·2 (2·4)	5·7 (2·8)	6·7 (2·2)	7·3 (2·1)	6·4 (3·2)	5·9 (2·7)	1·8
Ephemeropterans	0·6 (1·0)	1·5 (1·5)	1·7 (1·4)	1·1 (0·8)	1·7 (1·4)	1·4 (1·2)	1·2
Trichopterans	2·7 (1·8)	2·5 (2·1)	3·3 (1·2)	3·6 (2·2)	4·6 (2·7)	3·9 (2·2)	1·5
Total invertebrates	12·2 (6·2)	14·4 (7·4)	17·3 (4·5)	16·6 (4·8)	18·8 (7·5)	16·9 (7·3)	1·5
Margin							
Plecopterans	3·7 (2·0)	4·4 (2·5)	5·3 (2·7)	6·3 (1·8)	5·6 (2·1)	5·7 (2·6)	1·8
Ephemeropterans	0·3 (0·7)	1·2 (1·1)	1·7 (1·6)	0·9 (0·8)	1·0 (1·2)	1·6 (1·1)	2·4*
Trichopterans	2·4 (0·8)	2·5 (1·7)	3·2 (1·3)	2·9 (1·4)	3·8 (1·2)	3·8 (1·5)	2·3
Total invertebrates	11·6 (3·3)	14·7 (6·2)	17·3 (5·1)	15·0 (3·9)	16·4 (4·1)	18·4 (5·8)	2·9*
Abundance							
Riffle							
Plecopterans	31·1 (1·6)	47·8 (1·4)	78·5 (0·9)	81·7 (0·7)	50·6 (0·7)	67·0 (1·1)	1·1
Ephemeropterans	2·0 (1·3)	7·3 (2·0)	7·9 (1·7)	5·7 (1·3)	8·7 (1·7)	6·9 (1·7)	1·3
Trichopterans	8·7 (1·0)	9·2 (1·4)	13·4 (0·7)	14·8 (1·1)	13·2 (1·1)	17·4 (1·4)	0·7
Total invertebrates	86·8 (1·0)	113·4 (1·1)	141·2 (0·8)	140·3 (0·6)	143·2 (0·6)	141·5 (1·1)	0·6
Margin							
Plecopterans	18·5 (1·4)	27·7 (1·2)	41·6 (1·0)	59·7 (0·8)	30·2 (0·7)	54·0 (0·9)	2·1
Ephemeropterans	1·5 (0·8)	4·5 (1·3)	6·2 (1·4)	2·4 (0·9)	2·9 (1·3)	7·8 (1·2)	3·3*
Trichopterans	9·1 (0·5)	7·6 (1·3)	16·0 (0·8)	11·1 (1·0)	13·9 (0·7)	20·4 (1·0)	2·1
Total invertebrates	74·4 (0·7)	83·1 (0·9)	119·6 (0·7)	116·7 (0·7)	97·9 (0·7)	149·8 (0·9)	1·4

This effect was not shown significantly in any individual invertebrate group, but is of importance in view of the effect of forest management on this variable (see Fig. 2).

Amongst abundance values only ephemeropterans increased significantly in numbers with pH ($r = 0{\cdot}35$, $P < 0{\cdot}01$ in margins; $r = 0{\cdot}53$, $P < 0{\cdot}001$ in riffles), decreasing significantly with aluminium ($r = -0{\cdot}31$, $P < 0{\cdot}05$ for margins; $r = -0{\cdot}47$, $P < 0{\cdot}001$ for riffles). The combined abundances of all groups increased with the amount of grassy vegetation in the margins ($r = 0{\cdot}44$, $P < 0{\cdot}001$ for margins; $r = 0{\cdot}35$, $P < 0{\cdot}01$ for riffles), similar results being shown by Plecoptera and Trichoptera. However, there was no correlation between these abundances and any of the PCs.

STREAM MACROINVERTEBRATES: COMMUNITY PATTERNS

DECORANA on margin and riffle data produced two strong axes which in both data sets explained around 70% of the total variance in ordination space. Ordinations from riffles and margins were similar on their first axes ($r = 0{\cdot}78$, $P < 0{\cdot}001$), and similar to the gradients shown by taxon richness; diversity generally decreased along axis 1 in both cases (Table 6). As expected from this pattern, stream pH and aluminium concentration again provided many of the dominant correlates with the ordination scores; there were also moderate effects by stream size (Table 7). In no case were there strong correlations between ordination scores and factors influenced by riparian management (e.g. margin PC1). However, sites scores on DECORANA axis I of the riffle data did differ significantly between management groups ($F_{5,60} = 3{\cdot}07$, $P < 0{\cdot}016$), due mostly to ordination scores at CON sites which were significantly higher than elsewhere. Moreover, with management groups combined *a posteriori* into categories from streams lined by broadleaves (BRD + SNW), and by grasses and moorland (CLR + BUF + MOR) this significant difference in ordination scores from CON sites was enhanced (Table 8). Residuals around the significant regression of ordination scores on aluminium ($r^2 = 0{\cdot}21$, $F_{2,62} = 17{\cdot}19$, $P < 0{\cdot}001$) still differed between management groups, due mostly to CON sites ($F_{2,64} = 3{\cdot}53$, $P < 0{\cdot}03$); conifers thus had an effect on ordination even after accounting for their effect on aluminium concentrations.

Discussion

In outline, the results of this study indicate that riparian management along forest streams can influence habitat features beneath the wetted perimeter of the stream margins. Such effects would be important if they had any major influence on the stream community. However, stream acidity and aluminium concentrations provided the single strongest correlates with taxon richnesses, and with ordination scores particularly among the riffle fauna. We cannot exclude the possibility that forest presence contributed to this pattern, because aluminium concentrations were elevated in all categories of forest stream irrespective of riparian management. Nevertheless, riparian areas of pure conifer appeared to have significant effects on faunal communities even after accounting for higher aluminium concentrations at forest sites, indicating that some of the effects by forestry were non-chemical. Additionally, streams bordered purely by conifer had taxon richnesses and ordination scores significantly different from other types of stream, suggesting that riparian management was effective in preventing similar patterns at other types of conifer site. On this evidence, riparian management may have some influence on communities of aquatic animals in the margins of upland British streams, but any effect operates within a much stronger trend related to stream acidity and aluminium concentration.

Table 6. Correlations between the taxon richness and abundance of principal invertebrate groups, and the first and second ordination axes from riffles and marginal habitats at 66 streams in upland Wales and Scotland

	DECORANA axis Riffle 1	Riffle 2	Margin 1	Margin 2
Species richness				
Plecoptera	−0·51***	0·10	−0·34**	−0·32**
Ephemeroptera	−0·69***	0·11	−0·48***	0·07
Trichoptera	−0·23	−0·02	−0·33**	0·03
Total invertebrates	−0·43***	0·05	−0·42***	−0·12
Abundance				
Plecoptera	−0·08	0·09	−0·08	−0·43***
Ephemeroptera	−0·61***	0·04	−0·34***	0·16
Trichoptera	−0·11	−0·06	−0·09	−0·08
Total invertebrates	−0·09	−0·09	−0·12	−0·11

Table 7. Correlations between DECORANA axes from margins and riffles and physicochemical variables measured at 66 sites in upland Wales and Scotland

	Riffle		Margin	
	Axis 1	Axis 2	Axis 1	Axis 2
PC scores				
Margin PC1	−0·13	−0·04	−0·16	0·03
Margin PC2	0·17	−0·32**	0·01	0·05
Substratum PC1	−0·21	−0·09	−0·34*	−0·01
Substratum PC2	−0·34**	0·24	−0·18	−0·07
Chemistry PC1	−0·18	0·00	−0·30*	−0·09
Chemistry PC2	0·49***	0·31*	0·59***	−0·33*
Location PC1	−0·38**	0·02	−0·03	0·14
Location PC2	−0·26*	−0·06	−0·32*	−0·06
Margin variables				
Stones	−0·31*	0·25*	−0·17	−0·06
Gravel	−0·24*	0·02	−0·20	0·04
Tree roots	−0·18	−0·11	−0·18	0·13
Herbs/macrophytes	−0·03	0·04	0·01	−0·05
Grasses	0·00	−0·04	−0·04	0·05
Grass roots	−0·14	0·36**	−0·01	−0·06
Earth	0·22	−0·01	0·33*	0·05
Rock	−0·16	0·01	−0·15	−0·18
Sphagnum	0·14	0·05	0·17	−0·13
Moss/liverworts	0·29*	−0·26*	0·17	0·12
Leaves	0·04	−0·19	−0·08	0·13
% Cover	0·09	0·08	0·03	0·02
Substratum variables				
Sand/gravel	0·28*	−0·05	0·35**	0·06
Silt/Mud	0·36**	−0·16	0·24	0·03
Pebbles/boulders	−0·14	0·18	−0·00	−0·06
Boulders	−0·21	0·04	−0·20	−0·00
Bedrock	−0·13	−0·02	−0·23	−0·07
Leaves	0·23	−0·19	0·07	0·17
Moss	0·07	0·18	0·28*	0·07
Tree roots	0·03	−0·17	0·01	0·06
Chemical variables				
pH	−0·55***	−0·31*	−0·66***	0·32*
Conductivity	0·22	−0·04	0·32**	0·08
Colour	0·17	0·07	0·25*	−0·21
Magnesium	0·08	−0·05	0·19	0·16
Calcium	−0·12	−0·23	−0·09	0·34**
Aluminium	0·46***	0·17	0·58***	−0·07
Iron	0·12	0·15	0·26*	−0·00
Location variables				
Width	−0·45***	0·04	−0·16	0·09
Altitude	0·14	0·09	0·17	0·19
Slope	−0·06	0·01	−0·31*	0·07
Linkage	−0·41***	0·01	−0·12	0·27

CHEMICAL PATTERNS

The marked dominance of acidity and aluminium as correlates with the composition and diversity of invertebrate assemblages has now been shown repeatedly in upland British streams (see Sutcliffe & Hildrew 1989; Rutt, Weatherley & Ormerod 1990). Moreover, there is a marked consistency between data sets in the species and trophic guilds (Rundle, Lloyd & Ormerod, in press) which show preference for certain chemical conditions, and experimental evidence that the relationships are causal (e.g. Ormerod *et al.* 1987, 1990). One important feature of such strong chemical gradients in the context of this study is that they may limit the array of species which can colonize streams whose banks are managed to enhance diversity.

Given such strong chemical influences on stream communities, a further important question arises over the extent to which forestry contributes to chemical change. Several features combine to influence the chemistry of streams, including the acidity and base-paucity of soils and bedrock, particularly in conjunction with anthropogenic features such as

Table 8. Differences in site scores on DECORANA axis 1 from the ordination of aquatic macroinvertebrates in the riffles and margins of 66 upland streams in Wales and Scotland in relation to selected categories of riparian management. Standard deviation and sample size are given in parentheses. Note that sites scoring low tended to have more diverse communities for most groups (see Table 6)

Riparian management	Mean ordination score on	
	Riffle axis 1	*Margin axis 1*
Conifer only (= CON)	235 (78,12)	160 (70,12)
Moorland/grassland (= CLR + BUF + MOR)	156 (76,37)	109 (71,37)
Broadleaves (= BRD + SNW)	156 (75,17)	92 (60,17)
ANOVA $F_{2,63}$	5·30**	3·66*

acid deposition (UKAWRG 1988). Conifer forests are thought to exacerbate acidification and several mechanisms have been suggested to explain this effect, although the major pathway is probably through the scavenging of airborne pollutants (Department of the Environment & Forestry Commission 1991). This mechanism is an enhancement of that thought partly responsible for the release of aluminium to surface waters, and aluminium concentrations in streams draining forest on base-poor soils are often elevated by comparison with adjacent moorland (Ormerod, Donald & Brown 1989). Our data from a large area of Wales and Scotland add further support to the role of conifers in increasing stream aluminium concentrations, in this case irrespective of riparian management. Buffer strips usually cover only a limited area of any catchment, and hence contribute only a minority of stream run-off. Riparian strips are also liable to be breached by soil pipes, drainage channels, and overland flow, so that chemical effects from the major part of the catchment may still dominate stream quality. Examples from mid-Wales show, for example, that bankside liming in forest streams had no measurable effect on stream chemistry for similar reasons (Edwards, Stoner & Gee 1990). So far, no straightforward method of managing the effects of surface water acidification on invertebrates has been devised, given the artificial, limited and sometimes negative response which results from liming (e.g. Ormerod *et al.* 1990; Weatherley & Ormerod 1990).

EFFECTS OF BUFFER STRIPS

Amongst the potential influences by forestry on aquatic ecosystems, buffer strips are most likely to modify those mediated wholly or partly through bankside processes, such as the physical (e.g. habitat structure) and energetic (e.g. inputs of heat, light and allochthonous litter). Our data show the potential value of buffer strips in influencing the former during afforestation with exotic conifers; hitherto this feature has been demonstrated largely with respect to seminatural vegetation left alongside streams when catchments have been logged of native timber (e.g. Barton, Taylor & Biette 1985).

Effects on habitat physiography are likely to have biological consequences, because many invertebrate species show strong associations with certain kinds of habitat. Forestry in the UK has been implicated in the past in effects of this type, but mostly through negative influences in instances which preceded the incorporation of buffer strips into forest design (e.g. Rutt, Weatherley & Ormerod 1989; Ormerod, Weatherley & Merrett 1990). The results of this study show that management can be used positively to influence stream communities. While such strategies have the proviso that other factors such as increased aluminium concentration or acidity may limit potential fauna, differences in faunal composition between pure conifer and other stream types were apparent even at acid sites. Interesting possibilities arise where different types of management have contrasting results. For example, in this study, buffer strips of broadleaves and moorland probably had different effects on habitat structure and stream communities. Groups preferring streams with riparian broadleaves included odontocerid, philopotamid and psychomiid caddis; those preferring the 'softer' edges found in acid streams with moorland buffer strips included dytiscid and hydrophilid beetles, and leptophlebid mayflies (Rundle, Lloyd & Ormerod, in press, Weatherley *et al.* in press). These different management techniques will also have contrasting influences on other conservation resources such as dragonflies and riparian birds (e.g. Ormerod, Weatherley & Merrett 1990; Ormerod & Tyler 1991). Some blend of riparian management, as advocated by the Forestry Commission (1988), would thus be one possible means of increasing diversity, although data on the habitat structure and stream fauna resulting from this strategy are unavailable. Forest managers may also have to choose whether buffer strips should be cleared from streams currently bordered by conifer. On our evidence, buffer strips were most effective when implemented at the planting stage, because retrospectively cleared strips still showed some of the physical characteristics of forest streams. However, further data are required to assess the succession of habitats and communities where buffer strips have been cleared in this way.

In part, some understanding of the effects of riparian management on stream communities depends on understanding how the stream's energy base and trophic structure is affected. Richardson (1991) has shown experimentally that some stream invertebrates, notably leaf-shredders, increased in density when the standing crop of broadleaf litter was also increased, although an important requirement was that the allochthonous litter should be retained by the stream's physical structure (Dobson & Hildrew 1992). In our study, shredders were the dominant functional group at all sites irrespective of bankside management, although their abundance was not increased in any management category (Rundle, Lloyd & Ormerod, in press). While leaves were more evident on the bed of streams bordered by broadleaves, 'harder' edges at these sites may also render them less retentive (Fig. 2, Table 2). By contrast, taxa whose abundances increased in the 'soft' margins of streams with moorland buffer strips were predominantly collectors of fine particulate organic matter; the same group increased in streams with sandy substrata where there was evidence of deposition rather than erosion (Rundle, Lloyd & Ormerod, in press). Together, these features suggest that successful riparian management in forest streams may thus have to take account of complex interactions between altered energy inputs, stream physical structure and stream chemistry. These will be the subject of a separate paper.

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