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1 **CATCHMENT-SCALE PEATLAND RESTORATION BENEFITS**
2 **STREAM ECOSYSTEM BIODIVERSITY**
3

4
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13 **Keywords:** Artificial drainage; drain-blocking; grip-blocking; macroinvertebrate;
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15

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18
19

20 **SUMMARY**

21 1. Drainage of peat-dominated catchments across the world has caused widespread
22 degradation of the ecosystem services provided by peat and freshwaters. In the UK, an
23 estimated £500 million has been spent over the last decade blocking drains to reverse
24 these changes. The practice raises water tables to induce rewetting and promote peat
25 aggradation. However, the potential benefits for impacted ecosystems such as streams
26 remain unknown.

27 2. This study examined stream physicochemistry and benthic macroinvertebrates
28 across peatland catchments with widespread artificial drainage networks, or drains
29 that have recently been blocked, and compared these with intact peatland sites having
30 no history of drainage.

31 3. Streams in artificially drained catchments were characterised by more benthic fine
32 particulate organic matter (FPOM), higher suspended sediment concentrations and
33 finer bed sediments (D_{50}) than in drain-blocked and intact catchments.

34 4. Drained sites had higher abundance of Diptera (Simuliidae, Chironomidae) larvae,
35 and lower abundance of Ephemeroptera, Plecoptera and Trichoptera larvae, than
36 drain-blocked sites. In contrast, streams in drain-blocked catchments had
37 macroinvertebrate communities broadly similar to intact sites in terms of taxon
38 richness, overall species composition and community structure. These changes were
39 associated with lower suspended sediment and FPOM concentrations following drain-
40 blocking.

41 5. *Synthesis and applications.* For the first time, this study has shown changes in the
42 structure of stream benthic macroinvertebrate assemblages linked to increases in
43 benthic POM and suspended sediment following peatland drainage. However, these
44 effects seem to be reversible following catchment-scale restoration by drain-blocking.

45 Drain-blocking therefore appears to benefit not only peatland soil, vegetation and
46 hydrological ecosystem services but also stream water quality and biodiversity. The
47 numerous agencies undertaking peatland restoration should consider implementing
48 detailed pre- and post-blocking monitoring of streams to: further improve our
49 understanding of the mechanisms through which peatland management affects stream
50 biodiversity and biological recovery dynamics, refine drain-blocking practices, and;
51 inform aquatic conservation and management strategies.

52

53 **INTRODUCTION**

54 River catchments worldwide have been altered significantly as a consequence of land-
55 use change (e.g. Harding *et al.*, 1998; Paul & Meyer, 2001; Allan, 2004). Peatland
56 covers around 500M ha globally but, historically, many countries such as the
57 Netherlands, Finland, Russia, Ireland, UK, New Zealand, Canada and Ecuador have
58 witnessed broad-scale artificial peatland drainage. However, the full catchment-scale
59 effects of these drainage practices have rarely been examined (Ramchunder *et al.*,
60 2009). In the UK, which is one of the most extensively drained lands in Europe
61 (Baldock *et al.*, 1984), some drainage predates Roman times (Darby, 1956) although
62 many peatlands were drained during the 1960s and 1970s to increase grouse, sheep
63 and timber production, provide peat for horticulture and fuel, and with the intention of
64 reducing downstream flooding (Holden *et al.*, 2004). At the time it was considered
65 that this management intervention would improve the ecosystem services provided by
66 upland moorland but, as Stewart and Lance (1983) noted, there was no evidence of
67 economic benefits from moorland drainage and little research was undertaken into the
68 wider environmental impacts.

69

70 Artificial drainage of peatland is now considered to impose a range of deleterious
71 effects including alterations to baseflow and stormflow runoff regimes with some
72 evidence of increased flow peaks and lower baseflows (e.g. Conway & Millar, 1960;
73 Holden *et al.*, 2006a). Impacts resulting from artificial drainage of peat have also
74 included: changes to soil chemistry leading to changes in solute (e.g. calcium,
75 magnesium, potassium) and nutrient (e.g. carbon-bound nitrogen and sulphur and
76 organically bound phosphorus) concentrations of streams (e.g. Ramchunder *et al.*,
77 2009), and erosion of exposed peat surfaces resulting in increased sediment delivery
78 to receiving waters (e.g. Holden *et al.*, 2007). In an attempt to restore peatlands
79 following such degradation, the practice of installing peat drain blocks or dams started
80 in the UK in the late 1980s (Armstrong *et al.*, 2009).

81 Drain-blocking has so far been implemented over >3200 ha of England alone
82 (Holden, 2009), with common practice being a series of dams rather than total
83 infilling. The principal aim of drain-blocking is to increase water table height,
84 encouraging re-vegetation by peat forming species such as *Sphagnum*. The restorative
85 capabilities of drain-blocking on terrestrial vegetation and soil structure/chemistry are
86 reviewed by Ramchunder *et al.* (2009) and the efficacy of different blocking methods
87 is detailed in Armstrong *et al.* (2009). Damming at intervals along each artificial drain
88 has reduced drain discharge in some places by over 70%, while alterations to the
89 hydrological routing of water have also been observed (Worrall *et al.*, 2007). Soil
90 water dissolved organic carbon concentrations have been shown to be less in drain
91 blocked peatland areas compared to where drains are still open (Wallage *et al.*, 2006).
92 However, questions remain as to whether catchment-scale restoration by drain-
93 blocking has any benefits for stream biodiversity. Therefore, further knowledge would
94 be useful given the general need to increase understanding of the ecological benefits

95 of catchment-scale remediation schemes (Boon, 1998; Hillman & Brierley, 2005),
96 which have received comparatively less attention than restoration schemes focused on
97 river sections or reaches (e.g. Bernhardt *et al.*, 2005; Palmer *et al.*, 2005).

98

99 This study investigated stream macroinvertebrate communities from nine headwater
100 (2-4 km²) peatland catchments (three intact, three with widespread artificial drainage
101 networks and three with blocked drains), on five occasions from 2007 to 2008. Based
102 on knowledge from hydrological studies of peatland drainage and drain-blocking, it
103 was hypothesised that: (1) stream systems in catchments that possess artificial
104 drainage networks would have higher suspended sediment concentrations, finer bed
105 sediments and more benthic fine particulate organic matter (FPOM) when compared
106 with stream systems from intact catchments (Prévost *et al.*, 1999; Holden *et al.*,
107 2007). These changes to the stream environment were expected to (2) lead to
108 macroinvertebrate communities containing taxa associated more with in-stream fine
109 sediment deposition and benthic POM (e.g. Ramchunder *et al.*, 2009) compared with
110 stream systems from intact catchments. In contrast, (3) drain-blocked stream
111 ecosystems were expected to be in a similar condition as those at intact sites, because
112 drain dams effectively reduce sediment flux to the stream network (Holden *et al.*,
113 2007), and restore hydrological and hydrochemical aspects of the terrestrial
114 ecosystem. The findings of this study are subsequently considered in the context of
115 more general literature discussing the effects of land management and catchment-
116 scale remediation schemes on stream ecosystems.

117

118 **METHODS**

119 *Study areas*

120 The study was undertaken at sites in the north Pennines and Yorkshire Dales, northern
121 England, specifically at Moor House Upper Teesdale National Nature Reserve,
122 Wensleydale, Wharfedale, Geltsdale and Weardale (Table 1). All sites have blanket
123 peat cover, with vegetation dominated by *Sphagnum* spp. (mosses), *Eriophorum* spp.
124 (cotton grasses) and *Calluna vulgaris* (heather) (Radley, 1962; Holden & Burt,
125 2003a). The climate of all sites is typical of the UK uplands and, although data are not
126 available for all nine locations, mean annual precipitation measurements of 2012 mm
127 (1951-1980 and 1991-2006) at Moor House (Holden & Rose, 2011) and 1817 mm
128 (1981-2008) at Oughtershaw Beck (Wallage *et al.*, 2006) can be considered broadly
129 representative. Mean annual air temperature at Moor House is 5.3°C (1931–2006;
130 Holden and Rose, 2011) and 6°C at Oughtershaw Beck (2007-2009, Brown *et al.*,
131 2010a).

132
133 Potential study sites were identified initially as those having second order streams
134 based on 1:25,000 Ordnance survey maps. Catchment (1.08–3.52 km²; Table 1) and
135 stream size were standardised as far as possible following Ramchunder *et al.* (2011)
136 who suggested catchment size (and thus stream order) can have a significant effect on
137 peatland stream macroinvertebrate community composition. Candidate drained and
138 drain-blocked (3-11 years post blocking) sites were identified from aerial photographs
139 and following discussions with local land managers. Sites were selected on the basis
140 of having no confounding effects of wildfire, rotational heather burning, mining,
141 major erosion or forest cover. At each catchment outlet, a representative 15 m reach
142 was selected randomly for detailed study with all subsequent sampling undertaken in
143 riffle areas of those reaches.

144
145 ***Field sampling***

146 Streams were sampled on a seasonal basis across two to four days per quarter (2007:
147 Sept. 03-07; Dec. 04-08; 2008: Mar. 05-09; June 04-08; Sept. 02-06). On each
148 sampling date, 16 stream environmental variables were measured (Table 2). Water
149 temperature, pH and electrical conductivity (EC) were measured using Mettler Toledo
150 MP120 and MP126 handheld probes (Mettler-Toledo, Ltd, Leicester, UK). Dissolved
151 oxygen (DO) concentration was measured using a Hanna Instruments HI9412 probe
152 (Hanna Instruments Ltd, Bedfordshire, UK). In addition, 120 ml of stream water were
153 passed through a 0.45 µm filter and subsequently analysed in the laboratory for major
154 anions (Cl, SO₄ and NO₃), dissolved organic carbon (DOC) and dissolved metals (Al
155 and Fe). A further 500 ml of unfiltered stream water was collected for determination
156 of suspended sediment concentration (SSC) by filtration. Streambed sediments were
157 characterised by measuring b-axis length and median grain size (D₅₀) of 100 randomly
158 sampled clasts. To provide a relative indication of flow differences between sites and
159 over time, flow velocity was measured at the time of sampling using a Valeport open
160 channel flow meter (Valeport Ltd, Devon, UK), with the channel cross-section
161 surveyed and stream discharge (Q) calculated using the velocity-area method.

162
163 Five replicate 0.05 m² benthic macroinvertebrate samples were collected from riffle
164 habitats using a modified Surber sampler with a 250 µm mesh net. Sediment was
165 disturbed to a depth of ~10 cm for approximately three minutes per sample. All
166 samples were preserved immediately in 70% ethanol then transported back to the
167 laboratory for sorting and identification. Where possible, macroinvertebrates were
168 identified to species level under a light microscope (x40 magnification) but other taxa
169 were identified to higher levels (e.g. Diptera [Family/Genus], Oligochaeta [Class])
170 using standard UK freshwater macroinvertebrate identification keys. Particulate

171 organic matter retained within the Surber samples was sorted into fine (<1 mm) and
172 coarse (>1 mm) fractions and ashed to determine ash free dry weight.

173

174 **Data Analysis**

175 Principal component analysis (PCA) was used to examine inter-relationships between
176 the 16 environmental variables across all sampling dates. Principal components (PCs)
177 with Eigenvalues >1 were retained and the % variance of each recorded. Repeated
178 Measures ANOVA (with season as the repeated measure) with Bonferroni correction
179 was used to determine whether there were significant differences in stream
180 environmental variables and PC scores as a function of site, land management type
181 and season. Site was included as a random factor in the model while land management
182 and season were fixed.

183

184 Prior to the analysis of macroinvertebrate data, the five replicate invertebrate samples
185 collected for each site/date were pooled (e.g. Brown *et al.*, 2007) to enable clearer
186 elucidation of the land management impacts as opposed to patch-scale variability.
187 Macroinvertebrate community structure was summarised using five measures: (1)
188 \log_{10} (total abundance +1) expressed as the total number of individuals per m²; (2)
189 taxonomic richness; (3) Relative abundance (%) of Ephemeroptera, Plecoptera,
190 Trichoptera, Chironomidae, Simuliidae and Other taxa; (4) 1/Simpson's diversity
191 index (1/S):

$$192 \quad 1/S = \frac{\sum n_i(n_i - 1)}{N(N - 1)}$$

193 where N is the total number of individuals in a sample, and n_i is the number of
194 individuals of taxon i ;

195 (5) Taxonomic dominance or evenness (D) estimated using the Berger-Parker index:

196 $D = N_{\max} / N$

197 where N_{\max} is the number of individuals in the most abundant species and N is the
198 total number of individuals collected.

199
200 RM-ANOVA was repeated for the macroinvertebrate summary measures using the
201 same methods as outlined above. All environmental and macroinvertebrate data sets
202 were tested for normality and, where necessary, \log_{10} , arcsin or square root
203 transformed to improve normality and homogeneity of variance prior to statistical
204 tests. All statistical tests were undertaken in SPSS v17.0 or Minitab v15 and
205 considered significant where $P < 0.05$.

206
207 Species-habitat relationships were assessed using multivariate ordination in
208 CANOCO v4.5. Macroinvertebrate data were $\log_{10}(x+1)$ transformed prior to
209 analysis. A preliminary Detrended Correspondence Analysis, showed axis 1 gradients
210 were 3.0SD, thus, subsequent analyses used direct gradient analysis (Redundancy
211 Analysis; RDA) to test for linear trends in species compositional change (Lepš &
212 Šmilauer, 2003). Forward selection was used to determine which of the
213 physicochemical variables accounted for a significant proportion of the species
214 variance. An initial RDA included a dummy variable 'Time' (no. days from start of
215 sampling) to determine whether there were significant temporal trends within the
216 stream macroinvertebrate communities. Thereafter, a partial RDA (p RDA) was
217 carried out to remove the variance accounted by Time, in an attempt to provide a
218 better indication of the spatial component of the dataset (Borcard *et al.*, 1992). One-
219 way analysis of similarity (ANOSIM) was employed to test the null hypothesis that
220 differences in stream macroinvertebrate taxa abundance between peatland
221 management types were not different to those within types. ANOSIM was undertaken

222 on all samples combined owing to the small number of replicates per quarterly sample
223 collection, and because spatial dynamics (linked to management type) were the key
224 focus of this analysis. ANOSIM was undertaken using both the Bray-Curtis (BC)
225 dissimilarity index (based on taxa relative abundance) and Jaccard's coefficient of
226 similarity (based on taxa presence-absence), with 10,000 permutations and Bonferroni
227 corrections using PAST 2.05 (Hammer *et al.*, 2001).

228

229 **RESULTS**

230 Mean SO₄, POM (fine and coarse), SSC and Al concentrations were all highest in
231 drained streams but mean DOC concentrations and D₅₀ were lowest (Table 2). EC and
232 pH were highest on average in the drain-blocked sites, although the highest recorded
233 pH was from an intact peatland stream. Cl, NO₃ and SO₄ concentrations were all
234 lowest on average at intact sites. The repeated measures ANOVA showed significant
235 differences in SSC, FPOM, D₅₀, and NO₃ (with seasonal interaction) between
236 peatland management types (Table 2).

237

238 The PCA generated five PCs with Eigenvalues >1 (Table 3 & Fig. 1). PC1 had strong
239 positive loadings (>0.5) of NO₃, EC, FPOM and POM and a strong negative loading
240 of Al. PC1 scores were significantly different between management types ($F_{(2, 44)} =$
241 6.3; $P = 0.004$). The Tukey's post-hoc test showed that PC1 scores were significantly
242 different between streams in intact and artificially drained catchments ($P = 0.003$).
243 Streams with artificial drainage were characterised by more negative PC1 scores but
244 they were not significantly different to those for drain-blocked streams ($P > 0.05$).
245 PC2 had strong positive loadings of coarse particulate organic matter (CPOM),
246 FPOM, POM and Fe, and strong negative loadings of pH and D₅₀. PC2 scores were
247 also significantly different between management types ($F_{(2, 44)} = 15.8$; $P < 0.001$). The

248 Tukey's post-hoc test showed that sites with artificial drainage were characterised by
249 more positive PC2 scores (Fig. 1), and there were significant differences between
250 intact and drain-blocked ($P = 0.022$), intact and artificially drained ($P = 0.018$), as
251 well as between drain-blocked and artificially drained sites ($P < 0.001$).

252

253 Mean abundance and richness were highest in drain-blocked and intact sites
254 respectively, while mean 1/S and dominance were highest in intact and drain-blocked
255 sites respectively. Lowest mean abundance, richness, 1/S and dominance were
256 documented in the drained sites (Table 4). The RM ANOVA revealed a borderline
257 significant difference in taxonomic richness between peatland management types
258 (Table 3 & Fig. 1). Ephemeroptera and Trichoptera relative abundance were typically
259 higher in the intact and drain-blocked sites when compared with the drained sites (Fig.
260 3), whereas Plecoptera and other taxa relative abundance were similar across the three
261 management types. The relative abundance of Chironomidae and Simuliidae were
262 typically highest in artificially drained systems (Fig. 3).

263

264 Axis 1 of the RDA accounted for a total of 16.2% of the total variance while the
265 second axis accounted for 7%. Taxa-environment correlations were 0.790 and 0.876
266 for axis 1 and 2, respectively. Time accounted for 10.1% of the species variance, thus
267 a *p*RDA was undertaken. Axis 1 and 2 accounted for a total of 17.0% and 7.2% of the
268 total variance while taxa-environment correlations were 0.791 and 0.853 for axis 1
269 and 2, respectively. Forward selection showed pH, SSC, Al, Fe, FPOM, SO₄ and
270 water temperature were associated with a significant proportion of the variance.

271

272 The analysis showed that the intact and drain-blocked sites were associated with low
273 suspended sediment, FPOM and SO₄ concentrations (Fig. 4a). The taxon-
274 environmental variables biplot showed some Ephemeroptera species (e.g. *Baetis*
275 *rhodani*, *Ecdyonurus torrentis*, *Ecdyonurus dispar* and *Rhithrogena semicolorata*),
276 Plecoptera (e.g. *Perlodes microcephala* and *Isoperla grammatica*) and caseless
277 Trichoptera larvae (e.g. *Polycentropus flavomaculatus* and *Hydropsyche pellucidula*)
278 were more abundant in streams from intact and drain-blocked catchments. In contrast,
279 some dipterans (e.g. Simuliidae and Chironomidae), the ephemeropteran *Ephemera*
280 *danica* and the cased Trichoptera larvae *Sericostoma personatum* were more strongly
281 associated with drained sites with higher SSC, FPOM and SO₄ concentrations (Fig.
282 4b). A diverse assemblage of Ephemeroptera species was found in the intact and
283 drain-blocked sites, while only *E. danica* was documented in the drained sites (Fig.
284 4b).

285

286 ANOSIM based on macroinvertebrate relative abundance data revealed significant
287 differences in community composition between land management types ($R^2 = 0.39$; P
288 <0.001), with pair-wise comparisons highlighting drained site macroinvertebrate
289 assemblages were different to those at intact and drain-blocked sites ($R^2 = 0.43$ and
290 0.65 , respectively; $P <0.001$ in both cases). Similarly, community composition at the
291 intact and drain-blocked streams was significantly different ($R^2 = 0.10$; $P = 0.032$).
292 ANOSIM based on presence-absence data also showed significant differences
293 between land management types ($R^2 = 0.36$; $P <0.001$), with pair-wise comparisons
294 showing macroinvertebrate communities were different at drained sites compared
295 with intact and drain-blocked sites ($R^2 = 0.43$ and 0.59 , respectively; $P <0.001$ in both

296 cases). In contrast to the relative abundance analysis, the intact and drain-blocked
297 streams were not significantly different ($R^2 = 0.07$; $P = 0.105$).

298

299 **DISCUSSION**

300 To the authors' knowledge, this study has provided the first detailed insight into the
301 spatial and temporal dynamics of stream physicochemical environmental variables
302 and macroinvertebrate communities in blanket peatland river systems influenced by
303 artificial drainage and drain-blocking. This discussion considers reasons for the
304 differences in: (1) physicochemical variables, and; (2) macroinvertebrate
305 communities, between streams influenced by different peatland catchment
306 management strategies. It then compares the results of this UK upland restoration case
307 study with catchment-scale restoration schemes from other parts of the world, to
308 identify commonalities that may be of relevance to future management interventions.

309

310 *Peatland management effects on stream environmental variables*

311 Artificial drainage of peatlands was linked to changes in several stream
312 physicochemical variables (e.g. increases in SSC and FPOM) allowing hypothesis 1 to
313 be supported. These findings are supported in part by evidence from other studies,
314 where 50-fold (Robinson & Blyth, 1982) and 12-fold (Ahtiainen & Huttunen, 1999)
315 increases in average stream sediment loads have been observed due to peat drainage.
316 The erosion of artificial drains can result in greater quantities of fine particulates
317 being deposited into nearby aquatic systems (Holden, 2006b; Holden *et al.*, 2007) and
318 this study showed significantly higher concentrations of FPOM in sites that were
319 artificially drained when compared with intact sites.

320

321 Stream benthic FPOM concentrations recorded from the drain-blocked catchment
322 streams were lower than those documented from artificially drained catchment
323 streams most likely because, even in poorly dammed drains, fine particulate erosion
324 and transport can be markedly lower when compared with unblocked drains (Holden
325 *et al.*, 2007). However, these previous studies investigated FPOM concentrations in
326 the drains as opposed to our study of receiving stream systems. Following drain-
327 blocking, the area of exposed bare peat, and the connectivity of bare areas with the
328 stream, is reduced (Holden *et al.*, 2007). Thus, peat erosion declines and less FPOM
329 reaches the stream and is deposited. Following drain-blocking, excess FPOM in
330 streambed sediments is likely to be removed during high flows at a greater rate than it
331 is re-supplied (e.g. Bilby & Likens, 1979), leading to a significantly lower
332 concentration over time. Further study is necessary to document the rapidity of this
333 likely recovery. However, we recognise that our samples were taken mainly during
334 baseflow conditions and further sampling is required across a range of flows to
335 properly characterise the suspended sediment and FPOM within the fluvial system.
336 Nevertheless, peat streams spend the majority of time at low flow (Holden & Burt,
337 2003b) and so baseflow conditions are an important component of stream habitat.

338

339 *Peatland management effects on stream macroinvertebrate communities*

340 The findings of this study supported the second hypothesis that there would be
341 significant differences in stream macroinvertebrate communities between intact,
342 drain-blocked and artificially drained catchments. The third hypothesis, that
343 macroinvertebrate communities in intact and drain-blocked sites would be similar
344 reflecting successful catchment-scale restoration, was also supported by the results.
345 Taxonomic richness was higher in intact and drain-blocked sites compared with the

346 drained sites, and the higher suspended sediment concentrations in the latter could
347 have led to greater deposition on benthic habitats and reduced macroinvertebrate
348 diversity. These inferences are supported by previous work by Vuori & Joensuu
349 (1996) and Vuori *et al.* (1998), who investigated forestry drainage in Finland and
350 observed a reduction in species richness linked to suspended and deposited sediment.
351 Deposited fine sediments can alter substrate composition and suitability (Richards &
352 Bacon, 1994), affect respiration by deposition on respiratory surfaces/appendages/nets
353 (Lemly, 1982), prevent feeding by grazers (Aldridge *et al.*, 1987) and reduce the
354 nutritional value and abundance of periphyton (Vuori *et al.*, 1998). Additionally,
355 reduced diversity and richness could be related to higher levels of benthic FPOM. The
356 usual consequence of increased FPOM is an increase in a few detritivorous species
357 with a decrease in overall richness and diversity (Moss, 1973; Perry & Sheldon, 1986)
358 because excess FPOM can alter the physical environment in a manner similar to fine
359 inorganic sediment.

360
361 The low relative abundances of Plecoptera and Trichoptera observed at the drain-
362 blocked sites could be due to prolonged effects of stream ecosystem stressors linked
363 to earlier artificial drainage. Historic land-use can continue to affect stream diversity
364 and communities over time scales spanning decades, thus long-term studies are often
365 required to quantify recovery (e.g. Harding *et al.*, 1998; Foster *et al.*, 2003). In this
366 study, stream biota were collected at sites where drain-blocking had been
367 implemented between three and 11 years prior to sampling, and therefore exact
368 recovery times/rates were not measured. Nonetheless, the low relative abundance of
369 Plecoptera and Trichoptera in drain-blocked sites suggests earlier drainage impacts
370 may continue. In contrast, relative abundance of Ephemeroptera was similar in drain-
371 blocked sites to intact streams. Ephemeroptera are often among the first

372 macroinvertebrates to recolonise stream habitats following disturbance, because adults
373 are relatively strong fliers and they have a propensity for drift as nymphs from any
374 undisturbed upstream populations (Williams, 1980). Recolonisation by drift seems
375 unlikely in these artificially drained peatland streams because drains covered the
376 entire catchment and so all parts of the stream network would likely have been
377 affected. Further research investigating pre-and post-blocking would help to establish
378 the role of dispersal constraints in the temporal sequence of drain-blocked peatland
379 stream recolonisation.

380
381 The ordination biplot indicated that several macroinvertebrate species found in the
382 intact sites were also documented in drain-blocked sites (e.g. *R. semicolorata*, *B.*
383 *rhodani*, *E. dispar*, *P. microcephala*, *I. grammatica*, *H. pellucidula* and *Hydroptila*
384 spp.) but not in artificially drained sites. These taxonomic differences were associated
385 with higher concentrations of suspended sediment and benthic FPOM. Most species
386 within the families Baetidae and Heptageniidae are algal scrapers/grazers, and so their
387 feeding could be quickly impaired on sediment smothered periphyton (Larsen &
388 Ormerod, 2010). Hydropsychiids (Trichoptera) are sensitive to increases in sediment
389 loads as their retreats and nets can become embedded under excess particles, thus
390 reducing oxygen levels in interstitial spaces (Runde & Hellenthal, 2000). Nets can
391 also clog, rip or be buried, resulting in decreased food acquisition (Strand & Merritt,
392 1997), interference with respiration (Lemly, 1982) and increased energy expenditure
393 due to net cleaning (Runde & Hellenthal, 2000). Furthermore, many predatory
394 Plecoptera such as Perlidae and Perlodidae are normally found living in coarse
395 sediments. Fine sediment can limit oxygen availability by reducing flow velocities in
396 clogged interstices, reduce interstitial water exchange and constrict the movement of
397 these invertebrates in the substrata (e.g. Beauger *et al.*, 2006; Bo *et al.*, 2007).

398
399 Higher abundance of the mayfly *E. danica* and the dipterans Chironomidae and
400 Simuliidae was recorded in drained peatland streams compared with intact and drain-
401 blocked sites. Previous work by Beisel *et al.* (2000) in northeast France found higher
402 abundance of *E. danica* in habitats with excess fine sediment, while Vuori & Joensuu
403 (1996) found Finnish forest drainage encouraged increased Chironomidae and
404 Simuliidae abundance. Simuliidae larvae filter FPOM effectively from the stream
405 water column (e.g. Vuori & Joensuu, 1996; Ciborowski *et al.*, 1997) which would
406 explain their increased abundance in streams from drained peatland catchments
407 characterised by higher suspended and deposited organic particulates.

408

409 The ANOSIM results further supported the finding that there were significant
410 community and taxonomic differences between the artificially drained catchment
411 streams and the intact and drain-blocked streams. The analysis based on Jaccard's co-
412 efficient of similarity indicated that taxa presence-absence was similar in drain-
413 blocked and intact streams, whereas there were significant differences between these
414 peatland management types in the analysis based upon BC distances. These results
415 suggest that drain-blocked sites have similar taxonomic composition but that there are
416 differences in relative abundance among constituent taxa. This could indicate that
417 drain-blocked streams have not completely recovered to an 'intact' state, or it may
418 represent the development of an alternative endpoint (e.g. Bradshaw, 1996; Ormerod,
419 2003) in the restored peatland streams.

420

421 *Catchment-scale restoration effects on stream ecosystems*

422 In many regions of the world, stream ecosystem services and biodiversity have been
423 compromised due to catchment degradation (Harding *et al.*, 1998; Paul & Meyer,

424 2001; Allan, 2004). In response, catchment-scale rehabilitation programmes have
425 become more common (see Hillman & Brierley, 2005) but there is growing
426 recognition that many schemes lack adequate pre- and post-restoration monitoring, a
427 problem similar to that for reach-scale river rehabilitation schemes (e.g. Bernhardt *et*
428 *al.*, 2005; Palmer *et al.*, 2005; Woolsey *et al.*, 2007). This study of peatland catchment
429 remediation and stream ecosystem response is one of only a few studies to consider
430 stream ecosystem responses to catchment-scale restoration. Stream ecosystems of
431 catchments where there was a recent drain-blocking intervention appeared to have
432 improved water quality, thus sustaining broadly similar macroinvertebrate
433 communities to those in catchments with no history of peat drainage. These findings
434 illustrate that such intervention may promote positive effects for in-stream
435 biodiversity. Importantly though, this progress is undoubtedly being missed by high
436 profile and costly monitoring schemes, such as those tracking attempts to improve
437 ecological status under the EU Water Framework Directive, because catchments
438 <10km² are rarely appraised (Logan & Furse, 2002). More detailed consideration of
439 small headwater systems that have been restored may be fruitful with regards to
440 improving estimates of the number of watercourses in 'good' or 'high' ecological
441 condition.

442

443 Conservation of stream biodiversity has received increasing recent attention as human
444 modification and disturbance of ecosystems increase (Harding *et al.*, 1998; Sponseller
445 *et al.*, 2008). Although, rapid recovery of biotic communities following short-term
446 catastrophic disturbances (e.g. short duration pulse disturbances) can often happen
447 due to immigration from nearby unimpacted streams (e.g. Doeg & Koehn, 1994),
448 impacts of sustained catchment-scale disturbances may profoundly affect all streams

449 in a catchment, eliminating local refugia and meaning that recovery following any
450 subsequent restoration may take a long time due to dispersal constraints (Harding *et*
451 *al.*, 1998). Although artificial drains studied here have only been blocked for a short
452 period of time (3 - 11 years), recolonisation of streams appears to have been relatively
453 rapid, perhaps as a result of the close proximity to intact peatland streams (cf.
454 Mackay, 1992). To ensure the quickest possible recovery of peatland stream
455 ecosystems following drain-blocking, land managers should consider the importance
456 of hydrological connectivity and proximity to potential sources of recolonisers when
457 planning future restoration schemes.

458

459 It is acknowledged that this study examined the spatiotemporal interactions between
460 physiochemical habitat variables and macroinvertebrate communities over only a
461 short period of time using a space-for-time substitution approach. This design was
462 necessitated by the lack of any pre- or post-restoration stream ecosystem data for
463 drain-blocked catchments, a common problem afflicting river rehabilitation schemes
464 more generally (Bernhardt *et al.*, 2005). In order to measure the efficacy of drain-
465 blocking and in-stream ecological recovery, detailed pre- and post-blocking stream
466 ecosystem monitoring is sorely needed. The importance of, and need for, long-term
467 monitoring to investigate impacts of past river system alterations cannot be
468 understated (Palmer *et al.*, 2005); such information would help deduce the level of
469 disturbance, post-restoration recovery times, and re-assembly mechanisms of biotic
470 communities following drain-blocking. To achieve such an aim there is a need to
471 improve knowledge exchange between upland stakeholders/government agencies
472 managers and freshwater scientists (e.g. Brown *et al.*, 2010b), particularly when
473 drain-blocking schemes are at the planning stage. Overcoming these issues will be

474 necessary to establish true baselines against which to judge the response of stream
475 ecosystems to future peatland restoration.

476

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483

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651

Table 1. Summary information for the nine stream study sites

Stream name	Management type	Soil types	Catchment area (km ²) ¹	Grid reference
Moss Burn	Intact	Blanket peat	2.15	54°41'1''N 2°27'0''W
Snaizeholme Beck	Intact	Blanket peat, stagnogley, stagnohumic gley, humic gley, fine loam, alluvial gley	2.23	54°15'7''N 2°16'1''W
Unnamed 2 nd order tributary of the River Tees	Intact	Blanket peat, alluvial floodplain	1.12	54°41'8''N 2°26'8''W
Crook Burn	Drain-blocked	Blanket peat, alluvial floodplain	2.98	54°42'2''N 2°20'5''W
South Tyne	Drain-blocked	Blanket peat, alluvial floodplain	3.52	54°43'6''N 2°22'8''W
Blea Gill	Drain-blocked	Blanket peat, humic gley, humic loam,	1.61	54°14'2''N 2°13'9''W
Cam Beck	Drained	Blanket peat, stagnohumic gley, seasonally waterlogged loam with peaty surface	2.91	54°13'9''N 2°16'1''
Old Water	Drained	Blanket peat, stagnohumic gley, seasonally waterlogged loam with peaty surface	1.29	54°52'4''N 2°37'9''W
Unnamed 2 nd order tributary of Killhope Burn	Drained	Blanket peat, slowly permeable loam over clay, stagnohumic gley	1.08	54°46'7''N 2°17'2''W

¹ Catchment area was measured using the hydrology tool in ArcGIS

Table 2. Descriptive statistics and RM-ANOVA results for the stream environmental variables

	Cl (mg l ⁻¹)	NO ₃ (mg l ⁻¹)	SO ₄ (mg l ⁻¹)	Al (mg l ⁻¹)	Fe (mg l ⁻¹)	DOC (mg l ⁻¹)	DO (mg l ⁻¹)	EC (µS cm ⁻¹)	pH	SSC (mg l ⁻¹)	D ₅₀ (cm)	CPOM (mg l ⁻¹)	FPOM (mg l ⁻¹)	POM (mg l ⁻¹)	Water temperature (°C)	Discharge (m ³ s ⁻¹)
<i>All streams</i>																
Mean	8.33	0.56	3.70	0.05	0.47	13.28	11.3	116.64	5.43	6.95	3.9	0.50	0.72	1.21	9.0	0.09
Min	0.11	< 0.01	0.53	< 0.01	< 0.01	0.09	5.8	18.00	4.29	0.20	1.0	0.02	0.03	0.07	0.6	0.01
Max	53.13	1.69	12.94	0.31	1.84	67.31	19.3	390.00	8.65	28.60	6.9	2.31	6.75	7.62	18.5	0.47
<i>Intact</i>																
Mean	3.75	0.36	2.29	0.05	0.49	14.01	11.1	76.72	4.99	4.61	5.0	0.31	0.41	0.70	8.8	0.08
Min	0.11	< 0.01	0.53	< 0.01	0.06	0.09	5.8	18.00	4.29	1.00	4.0	0.02	0.04	0.07	0.6	0.01
Max	9.35	1.26	5.65	0.18	1.33	67.31	19.3	191.40	8.65	12.80	6.9	1.52	3.48	4.07	18.5	0.25
<i>Drain-blocked</i>																
Mean	12.19	0.66	4.37	0.04	0.36	13.65	11.9	148.06	7.67	3.57	5.4	0.40	0.12	0.51	9.9	0.16
Min	0.84	< 0.01	0.83	< 0.01	< 0.01	1.92	6.20	23.25	6.98	0.20	5.3	0.02	0.03	0.07	1.1	0.01
Max	53.13	1.34	12.94	0.12	0.99	55.15	19.0	390.00	8.53	16.60	5.5	2.31	0.28	2.54	17.5	0.47
<i>Artificially drained</i>																
Mean	9.04	0.66	4.45	0.07	0.56	12.19	11.0	120.05	5.89	12.65	1.2	0.77	1.63	2.40	8.4	0.04
Min	2.27	< 0.01	2.22	< 0.01	< 0.01	1.76	6.3	30.70	4.77	0.80	1.0	0.02	0.18	0.31	0.9	0.01
Max	27.19	1.69	8.62	0.31	1.84	38.31	19.2	248.00	7.78	28.60	1.5	2.11	6.75	7.62	14.0	0.16
Stream (F _{6,44})	F = 3.62 P = 0.011	F = 8.96 P < 0.001	F = 10.23 P < 0.001	F = 2.38 P = 0.081	F = 1.33 P = 0.283	F = 3.44 P = 0.014	F = 0.74 P = 0.622	F = 6.35 P = 0.001	F = 15.42 P < 0.001	F = 5.17 P = 0.002	No replicates	F = 4.37 P = 0.004	F = 11.87 P < 0.001	F = 6.50 P < 0.001	F = 1.45 P = 0.239	F = 4.61 P = 0.004
Season (F _{4,44})	F = 5.18 P = 0.004	F = 54.51 P < 0.001	F = 16.46 P < 0.001	F = 6.74 P = 0.002	F = 3.75 P = 0.017	F = 2.34 P = 0.084	F = 18.41 P < 0.001	F = 6.10 P = 0.002	F = 4.83 P = 0.005	F = 2.21 P = 0.098	No replicates	F = 1.07 P = 0.395	F = 5.09 P = 0.004	F = 2.93 P = 0.042	F = 21.45 P < 0.001	F = 5.02 P = 0.005
Land management (F _{2,44})	F = 2.12 P = 0.201	F = 1.69 P = 0.261	F = 2.79 P = 0.139	F = 0.15 P = 0.868	F = 1.10 P = 0.392	F = 0.18 P = 0.836	F = 1.12 P = 0.384	F = 0.64 P = 0.560	F = 1.00 P = 0.423	F = 5.73 P = 0.041	F = 47.05 P < 0.001	F = 0.28 P = 0.768	F = 5.23 P = 0.048	F = 2.75 P = 0.142	F = 0.94 P = 0.443	F = 1.70 P = 0.260
Season*Land management (F _{8,44})	F = 0.79 P = 0.614	F = 4.20 P = 0.003	F = 2.19 P = 0.066	F = 1.19 P = 0.366	F = 1.78 P = 0.131	F = 1.43 P = 0.236	F = 0.23 P = 0.982	F = 1.13 P = 0.384	F = 0.52 P = 0.829	F = 1.65 P = 0.164	No replicates	F = 1.07 P = 0.420	F = 1.89 P = 0.110	F = 1.03 P = 0.439	F = 0.91 P = 0.522	F = 0.42 P = 0.896

Table 3. Loading scores, Eigenvalues and % variance explained for the five principle components produced from the environmental variables dataset. Values greater than 0.5 or less than -0.5 are highlighted in bold font to aid interpretation

Variable	Principle component				
	1	2	3	4	5
Cl	0.284	-0.141	0.102	0.577	0.392
NO ₃	0.795	-0.310	-0.251	0.165	-0.017
SO ₄	0.365	-0.451	0.535	0.023	-0.397
EC	0.529	-0.416	0.377	0.089	0.283
Water temperature	-0.338	-0.080	0.822	-0.262	0.005
pH	0.293	-0.636	0.404	-0.134	0.311
DO	0.308	-0.180	-0.723	0.338	0.194
SSC	0.453	0.409	0.336	0.381	-0.076
DOC	-0.377	0.147	-0.061	0.379	-0.062
CPOM	0.422	0.526	0.064	-0.342	0.399
FPOM	0.641	0.534	-0.046	-0.225	-0.130
POM	0.671	0.618	-0.014	-0.305	0.040
Q	-0.131	-0.146	-0.580	-0.494	0.053
Al	-0.625	0.484	0.071	0.322	0.105
Fe	-0.343	0.524	0.274	-0.028	0.520
D ₅₀	-0.341	-0.726	-0.187	-0.274	0.301
Eigenvalue	3.43	3.13	2.44	1.54	1.09
% variance explained	21.4	19.5	15.2	6.9	6.8

Table 4. Descriptive statistics and RM-ANOVA results for the macroinvertebrate community metrics

	Log₁₀ (total abundance +1) (per m²)	Richness	Simpson's Diversity (1/S)	Dominance (D)
<i>All streams</i>				
Mean	3.38	25	5.01	41.4
Min	2.54	10	1.54	18.1
Max	4.11	42	11.05	79.9
<i>Intact</i>				
Mean	3.39	30	6.10	37.7
Min	2.99	16	1.74	18.1
Max	3.66	41	11.05	75.3
<i>Drain-blocked</i>				
Mean	3.45	29	5.43	38.5
Min	2.98	15	1.54	19.1
Max	3.86	42	9.15	79.9
<i>Artificially drained</i>				
Mean	3.30	17	3.59	47.3
Min	2.54	10	1.60	26.5
Max	4.11	39	6.88	78.0
Stream (F _{6,44})	F = 6.67 P < 0.001	F = 9.92 P < 0.001	F = 7.34 P < 0.001	F = 6.78 P < 0.001
Season (F _{4,44})	F = 4.61 P = 0.007	F = 3.42 P = 0.024	F = 1.17 P = 0.351	F = 1.40 P = 0.264
Land management (F _{2,44})	F = 0.42 P = 0.676	F = 5.03 P = 0.05	F = 1.11 P = 0.390	F = 0.71 P = 0.530
Season*Land management (F _{8,44})	F = 1.15 P = 0.365	F = 1.66 P = 0.159	F = 2.02 P = 0.088	F = 2.01 P = 0.089

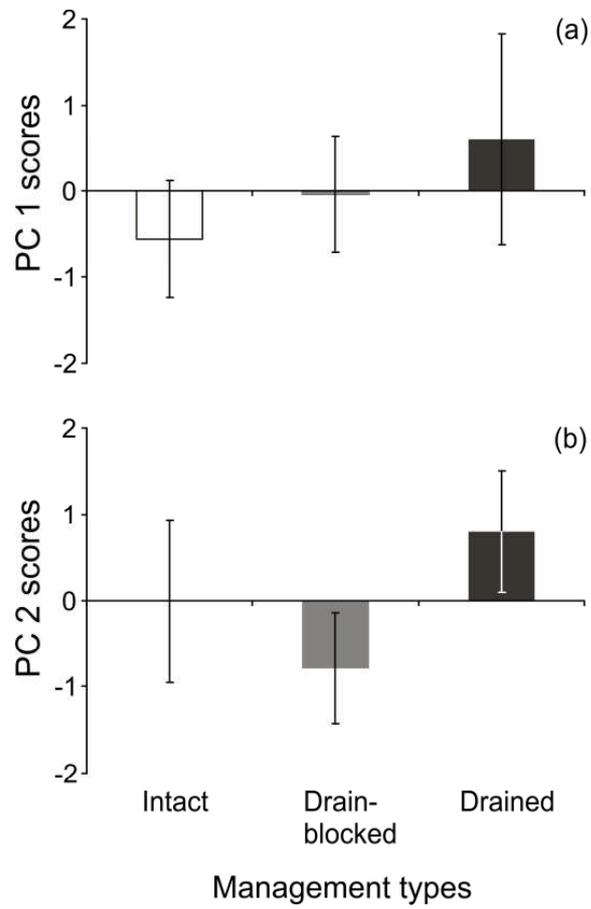


Fig. 1. PC scores for (a) axis 1 and (b) axis 2, for the three peatland management types [Error bars show $\pm 1SD$ from the mean]. See Table 1 for individual variable loadings, Eigenvalues and % variance of each PC

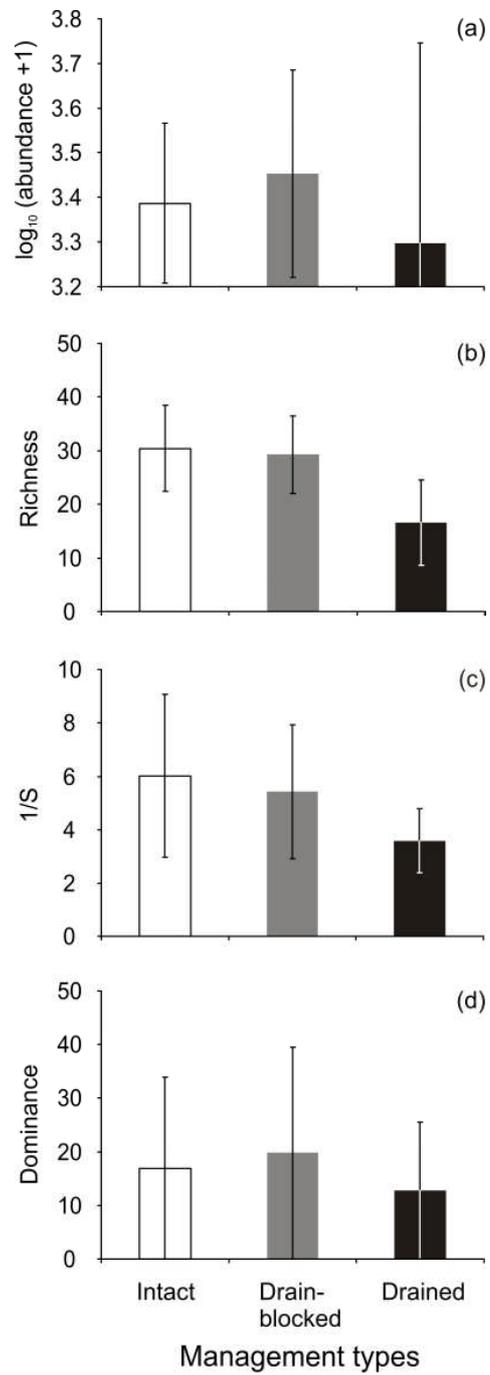


Fig. 2. Effects of management for (a) $\log_{10}(\text{abundance} + 1)$; (b) Richness; (c) 1/S; and (d) Dominance. [Error bars show $\pm 1\text{SD}$ from the mean]

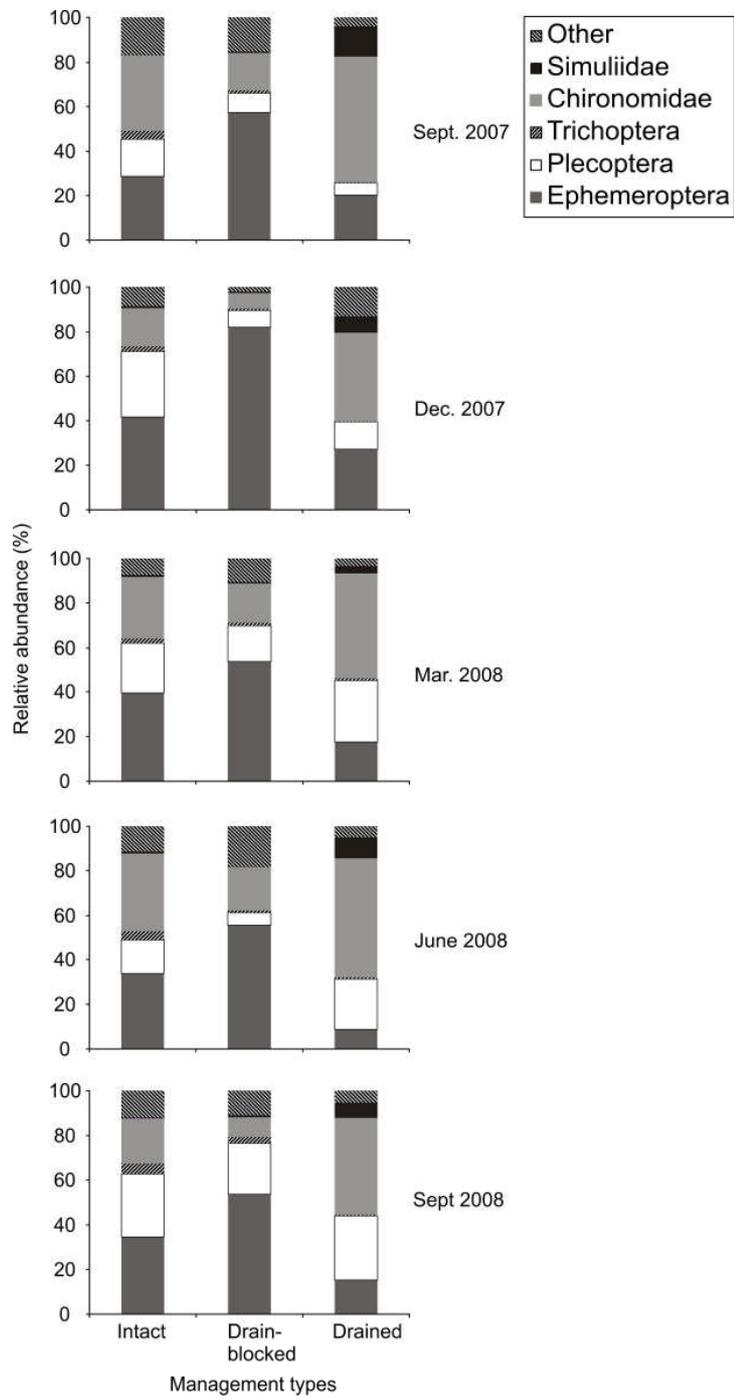


Fig. 3. Seasonal changes in the mean relative abundance of Ephemeroptera, Plecoptera, Trichoptera, Chironomidae, Simuliidae and Other taxa in relation to management types

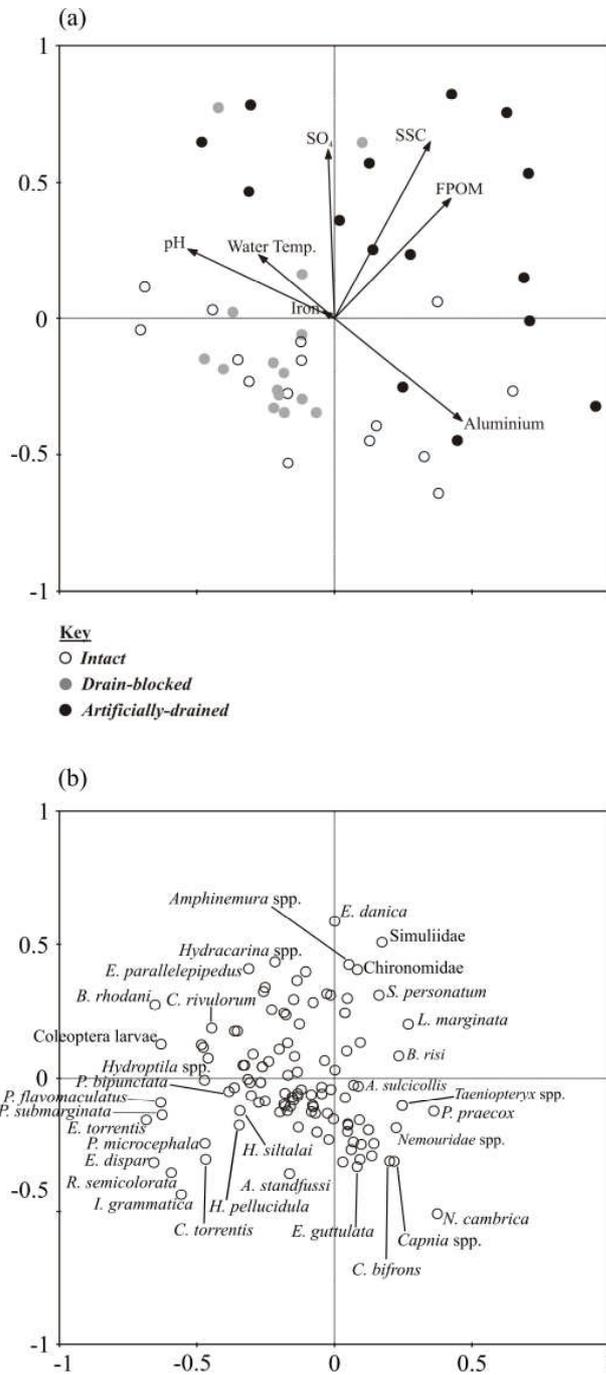


Fig. 4. Redundancy Analysis (RDA) ordination diagrams of (a) management types and environmental variables, and; (b) macroinvertebrate taxa (with selected taxa highlighted). Species abbreviations follow those provided in the main text