

1 **Working title:** Temporal effects of enhanced fine sediment loading on
2 macroinvertebrate community structure and functional traits

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4 Kate L. Mathers*, Stephen P. Rice and Paul J. Wood

5 Department of Geography, Centre for Hydrological and Ecosystem Science,

6 Loughborough University, Loughborough, UK

7 **Author for Correspondence**

8 Kate Mathers

9 Centre for Hydrological and Ecosystem Science

10 Department of Geography

11 Loughborough University

12 Loughborough Leicestershire

13 LE11 3TU

14 UK

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16 Email:- k.mathers@lboro.ac.uk

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30 **Temporal effects of enhanced fine sediment loading on macroinvertebrate**
31 **community structure and functional traits**

32 **Mathers, K.L, Rice, S.P. and Wood, P.J.**

33

34 **Abstract**

35 Deposition of fine sediment that fills interstitial spaces in streambed substrates is
36 widely acknowledged to have significant negative effects on macroinvertebrate
37 communities, but the temporal consistency of clogging effects is less well known. In
38 this study the effects of experimentally enhanced fine sediment content on aquatic
39 invertebrates were examined over 126 days in two lowland UK streams. Taxonomic
40 approaches indicated significant differences in macroinvertebrate community
41 structure associated with sediment treatment (clean or sedimented substrates),
42 although the effects were variable on some occasions. The degree of separation
43 between clean and sedimented communities was strong within 7 of the 9 sampling
44 periods with significant differences in community composition being evident. EPT
45 taxa and taxon characterised as sensitive to fine sediment demonstrated strong
46 responses to enhanced fine sediment loading. In marked contrast, faunal traits did
47 not facilitate the detection of enhanced fine sediment loading. More widely, the study
48 highlights the temporal dynamics of sedimentation effects upon macroinvertebrate
49 communities and the need to consider faunal life histories when examining the
50 effects of fine sediment loading pressures on lotic ecosystems.

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54 **Keywords:** colmation, sedimentation, sediment clogging, community composition,
55 life-history traits, colonisation.

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63 **1. Introduction**

64 Increased instream fine sediment loading is widely regarded as a global threat to
65 ecological integrity and lotic ecosystem health, often leading to reduced
66 macroinvertebrate diversity through direct exclusion of taxa, enhanced drift or
67 reductions in the availability of suitable trophic resources and habitat (Larsen and
68 Ormerod, 2010; Jones et al., 2012; Wood et al., 2016). The infiltration of fine
69 sediment into the river (colmation / clogging) has been reported to modify benthic
70 macroinvertebrate community structure and functioning (Descloux et al., 2013).
71 Substrates characterised by a high proportion of fine sediment are frequently
72 dominated by taxa with low dissolved oxygen requirements (Angradi, 1999; Zweig
73 and Rabeini, 2001) and exhibit an absence of taxa vulnerable to fine sediment due to
74 impairment or damage of filter-feeding apparatus or delicate gills (Wood and
75 Armitage, 1997; Larson et al., 2009). In addition, some taxa may be excluded and
76 unable to colonise habitats where excessive fine sediment is present, for example
77 due to the absence of suitable materials for case building by caddisfly larvae (Higler,
78 1975; Urbanič et al., 2005). Some functional feeding groups may also be
79 disadvantaged by enhanced fine sediment loading, due to reduced food quality or
80 impaired access to food resources, notably for algal scrapers and filter feeders
81 (Rabeni et al., 2005; Kreutzweiser et al., 2005). This may lead to shifts in community
82 structure towards those dominated by deposit feeders (Relyea et al., 2000).

83 Some fauna respond to fine sediment deposition pressures as a function of their
84 morphological characteristics and functional traits (Lamouroux et al., 2004; Bona et
85 al., 2016; Doretto et al., 2017). Recently there has been a growing focus on the
86 incorporation of faunal traits within biomonitoring tools to elucidate on the changes
87 that occur to invertebrate community structure in freshwater ecosystems (Menezes
88 et al., 2010; Göthe et al., 2016; Pilière et al., 2016). Biological traits are based on the
89 habitat model concept (Southwood, 1977), and therefore community traits may
90 reflect spatial and temporal variations in environmental factors (Townsend and
91 Hildrew, 1994). Trait composition can also be used to identify sources of
92 environmental impairment associated with anthropogenic and natural stressors
93 which act as 'filters', selecting taxa with relevant adaptive traits. Consequently, some
94 traits may be particularly sensitive to environmental pressures and it is this possibility
95 that has led to the increasing application of biological traits within biomonitoring tools

96 (Statzner et al., 2004; Friberg. 2014; Turley et al., 2016). However, relatively little
97 information exists regarding how macroinvertebrate faunal traits respond to instream
98 fine sediment loading and the limited studies in this area to date have yielded
99 variable results (e.g. Buendia et al., 2013; Descloux et al., 2014).

100 The majority of studies conducted on sedimentation to date have focussed on
101 artificial enhanced fine sediment loads (Suren and Jowett, 2001; Larsen et al., 2011)
102 or have been associated with heavily sedimented river beds (Matthaei et al., 2010;
103 Wagenhoff et al., 2012). A small number of studies have experimentally manipulated
104 the volume of fine sediment within the substrate directly through the application of
105 faunal colonisation devices, but these studies have typically examined the effects at
106 a single point in time (Bo et al., 2007; Larsen et al., 2011; Pacioglu et al., 2012;
107 Descloux et al., 2013; 2014). There is an absence of research that considers the
108 temporal variability of fine sediment effects on macroinvertebrate communities and
109 the value of life history traits for understanding and monitoring these effects.

110 Species phenology within a community affects the composition of
111 macroinvertebrates observed at differing times of the year (Delucchi and Peckarsky,
112 1989; Murphy and Giller, 2000), and may confound biomonitoring assessments if not
113 acknowledged (Clarke, 2013; Carlson et al., 2013). Temporal and spatial
114 heterogeneity of hydrological regimes is also a fundamental process in shaping
115 riverine macroinvertebrate communities (Dewson et al., 2007; Monk et al., 2008).
116 Natural streams are typically characterised by stable baseflow conditions punctuated
117 periodically by flow disturbances. These flow disturbances have important
118 implications for fine sediment dynamics, initiating entrainment of fine material stored
119 in the channel and increasing suspended sediment concentrations (Leopold et al.,
120 1964; Bond and Downes, 2003). The interaction between flow and fine sediment
121 dynamics (entrainment, suspension and depositional processes) has been identified
122 as a primary factor which influences the turnover of taxa within macroinvertebrate
123 communities (Rempel et al., 2000; Buendia et al., 2014; Jones et al., 2015).
124 Consequently, as a result of temporal variability in flow and species assemblages, it
125 follows that it is important to consider the effects of sediment loading over time.

126 This study is the first to specifically consider the temporal variability of experimentally
127 manipulated fine sediment loading on macroinvertebrate communities at a fine
128 temporal resolution (weeks). The following research questions were addressed:

- 129 (i) Is the effect of increased fine sediment loading on macroinvertebrate
130 communities consistent temporally?
- 131 (ii) Which taxa and functional traits are associated with enhanced fine
132 sediment loading?
- 133 (iii) Are the observed effects of enhanced fine sediment loading on
134 macroinvertebrate communities evident and consistent for both taxonomic
135 and faunal trait compositions?

136 **2. Materials and methods**

137 **2.1 Field sites**

138 The study took place on two small lowland rivers in Rutland, UK; the River Gwash
139 (52°38' N, 00°44'W) and the River Chater (52°37' N, 00° 44'W). Sites were selected
140 to be as broadly comparable in physical characteristics (channel size, water
141 chemistry, altitude and geology) as possible. Both river channels were characterised
142 by a riffle – pool morphology (channel width 2.9 – 6.5m). Catchment geology was
143 dominated by Jurassic mudstones and sandstones (British Geological Survey, 2008)
144 and study sites were located in arable farmland. Close to the catchment outlets,
145 mean daily flows were $0.18 \text{ m}^3 \text{ s}^{-1}$ and $0.52 \text{ m}^3 \text{ s}^{-1}$ for the River Gwash and Chater
146 respectively (record 1978-2015; NRFA, 2017). Subsurface bed material (based on
147 four pooled individual McNeil samples from two riffles per site, average sample
148 weight 20.01kg [McNeil and Ahnell, 1964]) indicated similar grain size distributions
149 (GSD) between sites; with both being naturally characterised by a moderate fine
150 sediment content (mass < 2mm; Gwash 20% and Chater 28.8%). Hydrological data
151 from local gauging stations indicated that the study coincided with periods of stable
152 flow punctuated by increased river stage associated with summer rainfall events
153 (Figure 1).

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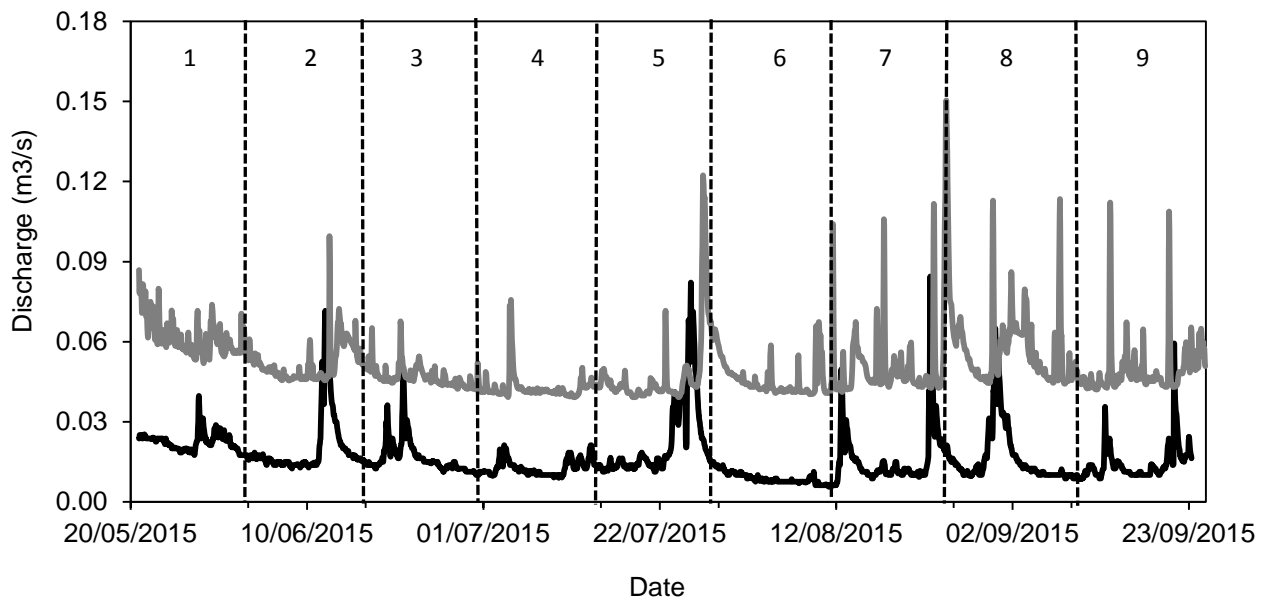
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166 **Figure 1.** River discharge (hourly average $\text{m}^3 \text{s}^{-1}$) for the River Gwash (black) and River
167 Chater (grey) Rutland, UK during the sampling campaign. Dashed lines indicate the two
168 week sampling periods (21st June - 24th September 2015).

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170 **2.2 Colonisation columns**

171 Macroinvertebrate colonisation columns were installed at the two sample sites.

172 These comprised PVC cylinders (diameter 65 mm, height 200 mm) perforated with

173 twelve horizontal holes (diameter 6 mm) to permit horizontal and vertical exchange

174 of water and the free movement of macroinvertebrates and fine sediment (Fraser et

175 al; 1996; Pacioglu et al., 2012; Descloux et al; 2013; Mathers and Wood, 2016). All

176 columns were filled with a pre-washed gravel framework collected from each of the

177 respective sample sites (truncated at 8 mm). This substrate was enclosed in a net

178 bag (7 mm aperture) within each column. Columns were assigned to one of two

179 treatments; a) clean substrates which were free from fines upon installation or; b)

180 heavily sedimented substrates comprising gravel and 250g of fine sand (63 – 2000

181 μm). Preliminary tests indicated that this volume of sand filled 100% of interstitial

182 volume. For the sedimented columns, a circular disk (64 mm diameter) was attached

183 to the mesh bag to effectively seal the base of the column and reduce the loss of fine

184 sediment vertically into the riverbed.

185 Columns were inserted into the river bed by placing the PVC cylinders onto a steel
186 pipe (35 mm diameter) that was driven into the river bed sediments until a sufficient
187 depth was obtained to insert it flush with the substrate surface (200 mm). The
188 surrounding stream bed remained unchanged and consisted of non-uniform cobbles
189 and gravel. Columns were left *in-situ* for the entire sampling campaign, but every 14
190 days the gravel netting bag was removed and replaced without disturbing the
191 surrounding gravel framework. At the end of each 14-day sampling period, the net
192 bag (containing the substrate and macroinvertebrates) was carefully removed,
193 placed in a sample bag and preserved in 10% formaldehyde for subsequent
194 processing in the laboratory. Empty columns were then replaced immediately with
195 the corresponding gravel bag treatment (clean or sedimented).

196 Colonisation columns were installed every 14 days between 21st May and 24th
197 September 2015 providing a 126 day record (9 sample sets). A time period of
198 14days was adopted because preliminary tests indicated that this represented
199 sufficient time to allow for colonisation by macroinvertebrates whilst minimising the
200 amount of fine sediment lost during occasional high flows (See Supplementary
201 Material and Figure S1). At each riffle site (three on the Gwash and two on the
202 Chater; one until the fourth sampling set), four columns of each type (clean or
203 sedimented) were installed providing a total of 20 replicates (16 initially for three
204 sample sets) for each 14-day sampling period. In total 162 clean and 163
205 sedimented substrate samples were examined (6 clean and 5 sedimented samples
206 were lost or not retrieved during the field campaign). Two additional sampling
207 timeframes (ca one month: 28 days and ca two months: 56 days) were examined to
208 capture potential temporal variability in environmental conditions (i.e. rising or falling
209 discharge or suspended sediment concentrations) and to confirm the most
210 appropriate time-frame to consider in the main study and are presented in
211 Supplementary material (Figure S1).

212 **2.3 Laboratory procedures and statistical analysis**

213 Within the laboratory, the contents of the column bags were passed through a sieve
214 nest (4 and 2 mm sieves) to remove larger gravel clasts. The remaining material was
215 passed through a 250 µm sieve and processed for invertebrates. All
216 macroinvertebrates were identified to the lowest taxonomic level possible usually
217 species or genus with the exception of Oligiochetea (order), Diptera families

218 (including Ephydriidae, Ptychopteridae, Chironomidae, Psychodidae, Simuliidae,
219 Ceraptogonidae and Stratiomyidae), Sphaeriidae and Zonitidae (family) and
220 Ostracoda, Hydracarina and Collembola which were recorded as such.

221 Compositional differences in communities between the two sediment treatments
222 were examined via non-metric multidimensional scaling (NMDS) using Bray-Curtis
223 similarity coefficients for the entire data set and for each individual sampling period.
224 This approach enabled an examination consistency in the community effects or if
225 they varied over time as a function of environmental conditions (i.e. discharge over
226 the 14-day period). A One way ANOSIM (Analysis of Similarities) was used to
227 examine differences in the communities amongst sediment treatments for the overall
228 data set and for each individual sample set (1-9) using a random Monte Carlo
229 permutations test (999 permutations). Both P and R ANOSIM values were examined,
230 with R values >0.75 indicating strong separation amongst groups, $R = 0.75-0.25$
231 indicating separate groups with overlapping values and $R <0.25$ as barely
232 distinguishable groups (Clarke and Gorley, 2006). Taxa contributing to the
233 divergence of communities were identified through the application of the similarity
234 percentage (SIMPER). The top six taxa identified as driving dissimilarity between
235 clean and sedimented communities were selected for further detailed analysis of
236 their sensitivity to fine sediment.

237 The functional composition of macroinvertebrate communities was determined
238 through the assignment of fauna into 6 categories which were comprised of 44
239 biological traits from the Tachet et al., (2010) database (Table 1). Categories
240 represent grouping features including 'maximum body size' and 'functional feeding
241 group', whilst traits signify modalities residing within these such as 'shredder' or
242 'filter-feeder'. Traits were assigned based on a fuzzy-coding approach with scores
243 ranging from zero (indicating no affinity) to three or five (the strongest affinity based
244 on available literature; Chevene et al., 1994). Affinity scores were subsequently
245 rescaled as proportions for each category (sum = 1) for each taxon. Chironomidae
246 and all taxa recorded at a coarser resolution than family-level were excluded due to
247 the large species diversity within the groups. To produce a trait abundance matrix,
248 taxon-trait categories were multiplied by $\log(x+1)$ transformed abundances (Larsen
249 and Ormerod, 2010; Descloux et al., 2014; White et al., 2017).. Functional
250 compositional differences for each sampling set were visualised via NMDS plots. All

251 ordination analyses were performed in PRIMER Version 7.0.11 (PRIMER-E Ltd,
252 Plymouth, UK).

253 The macroinvertebrate communities of the two study streams represent distinct
254 community structures as a function of signal crayfish invasion within the River
255 Gwash in 1996 (global ANOSIM $p < 0.001$; Mathers et al. 2016). Following invasion,
256 signal crayfish typically have significant, long-term and persistent effects on
257 macroinvertebrate communities (McCarthy et al., 2006; Twardochleb et al., 2013). As
258 a result, preliminary analyses were conducted on the individual rivers to determine
259 whether the gross effects of sediment loading were comparable for the communities.
260 This analysis took the form of temporal group centroid (clean and sedimented)
261 NMDS plots using Bray-Curtis similarity coefficients. These results indicated that the
262 temporal trajectory of community change and sedimentation effects were
263 comparable for both community composition and biological traits. Taxonomic plots
264 determined a significant sediment treatment effect for both rivers (ANOSIM Gwash p
265 = 0.035; Chater p = 0.012; Figure S2) whilst biological traits indicated no divergence
266 in trait composition (ANOSIM Gwash p = 0.143; Chater p = 0.104). Consequently, as
267 both river communities reacted in a similar manner to sediment loading, the final
268 analyses outlined above were conducted on the combined datasets.

269 Community abundance, taxa richness and richness of Ephemeroptera, Plecoptera
270 and Trichoptera (EPT) taxa were derived from the raw data. Abundances of taxa
271 characterised as sensitive to sediment according to sensitivity weights provided in
272 the Empirically-weighted Proportion of Sediment-sensitive Invertebrates index (E-PSI;
273 Turley et al., 2016) were also calculated for each sample. To examine statistical
274 differences associated with sediment treatment for individual taxon abundances (as
275 previously selected from the global SIMPER), generalised linear mixed effects
276 models were employed (GLMMs). Models were fitted using the '*lme4*' package in R
277 version 3.2.2 using the '*glmer*' function (R development Core Team, 2015). To
278 examine differences associated with the volume of fine sediment, sediment
279 treatment was specified as a fixed factor and riffle was nested within site as a
280 random factor (based on columns at individual riffles and sites being less
281 independent of each other). Models were fitted using a Poisson error distribution and
282 log link structure. Linear mixed models were fitted to the functional traits and
283 community metrics using the '*nlme*' package and '*lme*' function. The same model

284 structure (outlined above) was employed and the models were fitted using the
 285 restricted maximum likelihood (REML) estimation function. A Bonferroni correction
 286 was applied to all models to account for the large number of models constructed.

287

Table 1. Macroinvertebrate functional traits examined within this study (taken from Tachet et al., 2010).

Category	Trait
Maximal potential size	< 0.25 cm
	> 0.25 - 0.5 cm
	> 0.5 - 1 cm
	> 1 - 2 cm
	> 2 - 4 cm
	> 4 - 8 cm
	> 8 cm
Reproduction	Ovoviviparity
	Isolated, free eggs
	Isolated eggs, cemented
	Clutches, cemented eggs
	Clutches, free
	Clutches, in vegetation
	Asexual
Respiration	Gill
	Plastron
	Spiracle
	Hydrostatic vesicle
	Tegument
Locomotion	Flier
	Surface swimmer
	Full water swimmer
	Crawler
	Burrower
	Interstitial
	Temporarily attached
	Permanently attached
Feeding group	Absorber
	Deposit feeder
	Shredder
	Scraper
	Filter-feeder
	Piercer
	Predator
Parasite	
Substrate preference	Coarse substrates
	Gravel
	Sand
	Silt
	Macrophytes
	Microphytes
	Twigs / roots
	Organic detritus
	Mud

288 3. Results

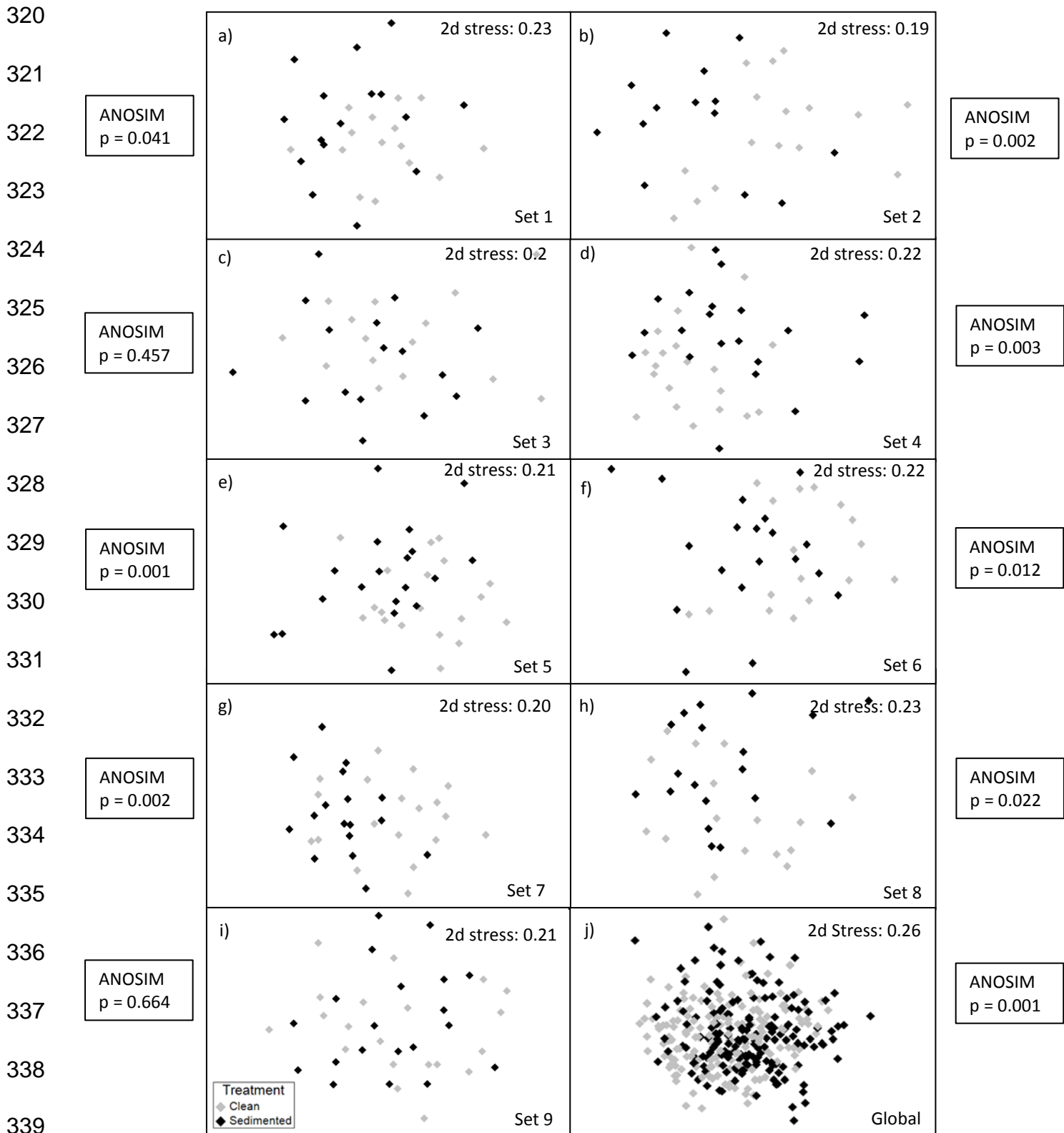
289 3.1 Community composition associated with sediment treatment

290 63 taxa were recorded in the clean sediment treatment (mean 6.79 taxa per sample,
291 range 2-13) and 58 taxa in the sedimented treatment (mean 6.94 taxa per sample,
292 range 1- 16). A total of 9,656 individuals were recorded in the clean sediment
293 samples (mean 59.98 individuals per sample, range 14-136) and 8,078 in the
294 sedimented samples (mean 49.86 individuals per sample, range 9-168).

295 Communities in the clean sediments were dominated by *Gammarus pulex* (67.68%
296 of total abundance), Chironomidae (9.67%) and *Potamopyrgus antipodarum* (6.73%).
297 The most abundant taxa within the sedimented substrates were *G. pulex* (53.50%),
298 Chironomidae (12.17%) and Oligochaeta (10.84%). A total of 11 taxa were unique to
299 clean sediments (3 Gastropoda, 2 Trichoptera, 2 Diptera, 1 Ephemeroptera, 1
300 Hirudinea, 1 Coleoptera and 1 Ostrococha) and 2 to the sedimented substrates (1
301 Tricladida, 1 Trichoptera) although these occurred at low abundances (constituting
302 29 and 2 individuals respectively).

303 Non-metric Multi-Dimensional Scaling (NMDS) ordination diagrams indicated distinct
304 clusters of macroinvertebrate communities associated with sediment treatment on
305 seven out of the nine sampling occasions (Figure 2). The degree of separation
306 between the groups varied over time with highly significant divergence in sets 2, 4, 5
307 and 7 (ANOSIM $p < 0.005$; Figure 2b,d,e & g), and moderate separation in set 1
308 (ANOSIM $p = 0.041$; Figure 2a), whilst a number of sets were less significantly
309 dispersed; sets 6 and 8 (ANOSIM $P < 0.05$; Figures 2f & h; Table 2). Two 14-day
310 periods, sets 3 and 9 (Figure 2c & i), demonstrated no significant differences in the
311 macroinvertebrate communities inhabiting the two substrate types. The global
312 dataset indicated some divergence of communities when all timeframes were
313 considered ($p < 0.0001$; ANOSIM) although analysis of the R value ($R = 0.083$),
314 indicated that the groups were barely distinguishable from each other (Figure 2j).
315 This low degree of separation reflects the varying stability of these patterns between
316 the individual sample sets. The top six taxa driving dissimilarity were Oligochaeta
317 (5.75% dissimilarity), Chironomidae (5.42%), *P. antipodarum* (5.12%), *G. pulex*
318 (4.49%), *Dicranata* sp. (3.10%) and *Habrophlebia fusca* (2.70%).

319



340 **Figure 2.** Non-metric multidimensional scaling (NMDS) of macroinvertebrate community
 341 data from the River Gwash and River Chater by sediment treatment using the Bray-Curtis
 342 similarities coefficients for cylinder sets 1 - 9 (panes a-i) and global dataset (pane j). Grey
 343 rhombus = clean cylinders and black rhombus = sedimented communities.

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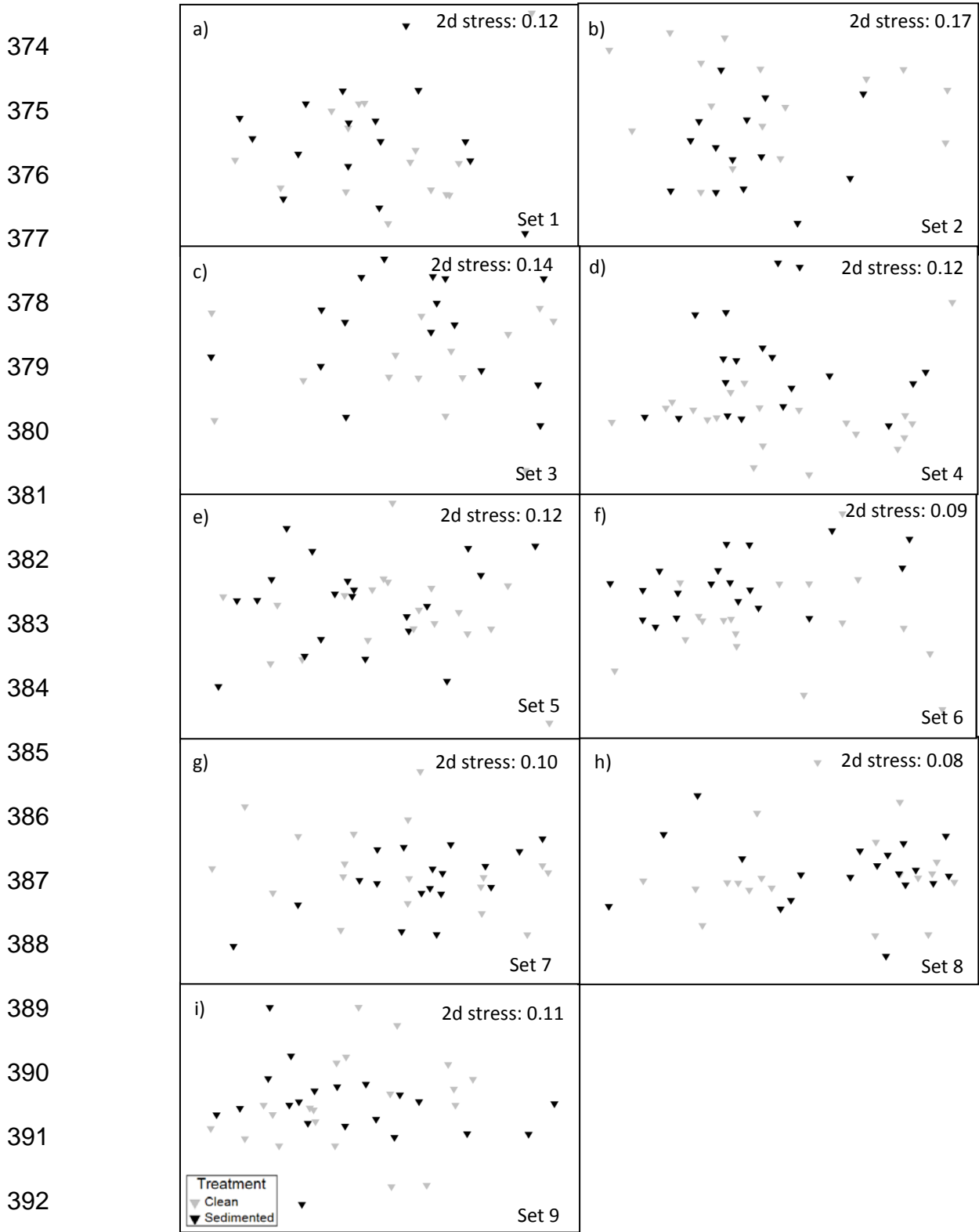
Table 2. Summary of ANOSIM values over time by sediment treatment .

Set	r value	p value
1	0.078	0.041
2	0.231	0.002
3	-0.003	0.457
4	0.107	0.003
5	0.127	0.001
6	0.096	0.012
7	0.166	0.002
8	0.082	0.022
9	-0.018	0.664

353 **3.2 Biological traits associated with sediment treatment**

354 NMDS ordination analysis indicated no clear and consistent differentiation between
355 sediment treatments over time when trait community composition was examined
356 (Figure 3). Trait based community composition demonstrated some degree of
357 separation in a number of instances (i.e. sample sets 3, 4, 6; Figures 3c, d & f), but
358 this was not consistent or clear for all sample sets (i.e. sample sets 1, 5; Figures 3a
359 & e). Divergence in communities was most marked during sample set 6 which also
360 corresponds to the only statistically significant difference in trait community
361 composition (ANOSIM $p = 0.037$; Figure 3f). When individual traits were considered,
362 eight trait modalities varied significantly as a function of sediment treatment. The trait
363 profile of locomotion was the most significant with individuals characterised as being
364 full water swimmers ($t_{10,320} = -4.53$, $p < 0.001$; LME), crawlers ($t_{20,310} = -3.224$, $p =$
365 0.001) or interstitial dwellers ($t_{10,320} = -4.93$, $p = < 0.001$) demonstrating significant
366 reductions for the sedimented treatment. Species demonstrating ovoviviparity ($t_{10,320}$
367 $= -4.51$, $p = < 0.001$), respiring via plastron ($t_{6,320} = -4.90$, $p = < 0.001$) or spiracles
368 ($t_{10,320} = -3.12$, $p = < 0.001$) and / or demonstrating shredder affinities ($t_{10,320} = -3.43$,
369 $p = < 0.001$) all demonstrated a reduction within sedimented substrates. Maximum
370 potential size of individuals also varied between treatments with a decline in larger
371 taxon characterised with a body size of 1-2 cm within the sedimented columns ($t_{10,320}$
372 $= -3.59$, $p = < 0.001$).

373



393 **Figure 3.** Non-metric multidimensional scaling (NMDS) of macroinvertebrate community
 394 functional traits from the River Gwash and River Chater by sediment treatment using the
 395 Bray-Curtis similarities coefficients for cylinder sets 1 - 9 (panes a-i). Grey rhombus = clean
 396 cylinders and black rhombus = clogged communities.

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399 **3.3 Community metrics and individual taxon abundances associated with**
400 **sediment treatment**

401 Community abundance, taxa richness and EPT richness did not vary by sediment
402 treatment (LME $p > 0.05$). Sediment sensitive taxa (as defined under E-PSI metric)
403 were recorded in significantly greater abundances in the clean sediments ($t_{10,310} = -$
404 2.94 , $p < 0.001$). The divergence of clean and sedimented substrates was not
405 apparent during Set 1, 3 and 9 with similar abundances of sensitive taxa in both
406 treatments whilst the greatest distinction between sediment treatments was during
407 sets 4-8 (Figure 4). When individual taxon abundances were considered, *Dicranota*
408 sp. and Oligochaeta were found in significantly greater abundances in sedimented
409 columns ($Z_{6,320} = 8.76$, $p < 0.001$ and $Z_{6,320} = 15.84$, $p < 0.001$; GLMM). Clean
410 sediment treatments were found to support greater abundances of the
411 ephemeropteran *H. fusca* ($z_{6,320} = -6.76$, $p < 0.001$) and the amphipod *G. pulex* ($Z_{6,320}$
412 $= -20.03$, $p < 0.001$). No significant sediment treatment differences were determined
413 for any other taxa ($p > 0.05$) although EPT richness demonstrated significant
414 variability over time within this study ($t_{10,320} = -3.45$, $p < 0.001$; LME; Figure 5).

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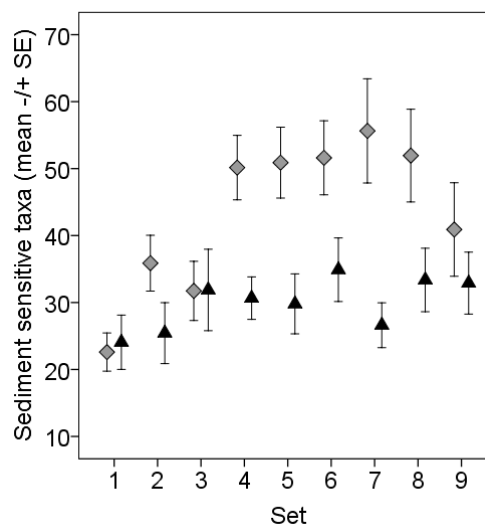
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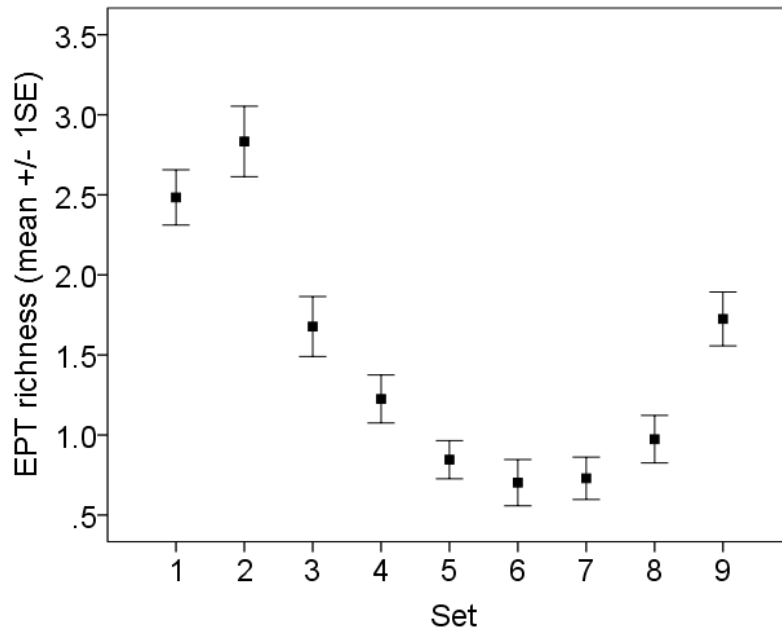


423 **Figure 4.** Mean abundances (+/- 1 SE) of sediment sensitive taxa (as defined under the E-
424 PSI index) over the nine sampling sets. Grey rhombus = clean substrates and; black triangle
425 = sedimented substrates.

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437 **Figure 5.** Mean abundances (+/- 1 SE) of EPT taxa over the nine sampling sets.
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439 **4. Discussion**

440 **4.1 Macroinvertebrate community composition**

441 This study sought to examine the temporal variability of experimentally enhanced
442 fine sediment loading on macroinvertebrates communities. The results indicate
443 colonisation by macroinvertebrates may be impeded as a result of enhanced fine
444 sediment loading but that the effects vary temporally. Analysis demonstrated a
445 significant difference in macroinvertebrate community composition associated with
446 sediment treatment during seven of the nine 14-day sampling periods. However, the
447 effects of sedimentation were not temporally consistent with differences between
448 community composition being stronger in some periods and breaking down
449 completely in others.

450 No evidence was found to suggest that spate periods affected the degree of
451 separation between communities within sedimented and clean substrates. A number
452 of sample sets experienced periods with high flows (e.g. sets 6 and 8) but this did
453 not appear to have any effect on the colonisation of the sediments. Similarly, sample
454 sets which demonstrated little separation did not correspond with periods of high flow
455 (i.e. sample set 3). It is likely that the variable responses to sedimentation reflects

456 the different life cycle characteristics and stages present in the river during the study
457 and therefore reflects natural temporal variability in the macroinvertebrate community
458 structure. The abundance of sediment sensitive taxa demonstrated a similar pattern
459 to that recorded for the taxonomic NMDS plots, with no differences in abundances
460 recorded for sets 1, 3 and 9. These changes in sediment sensitive taxa may be
461 driven by the life cycle of EPT taxa, which are particularly sensitive to fine sediment
462 within the substrate (Conroy et al . 2016) and which were temporally variable
463 abundance in richness during this study. EPT richness below a threshold of 2 taxa in
464 this study coincided with clear differences in community structure associated with the
465 sediment treatment.

466 Given the study took place during summer; discharges were naturally low and
467 favoured the deposition of fine sediments (Wood and Armitage, 1999). Consequently,
468 the dominant taxa recorded during this period are more likely to display affinities to
469 fine sediment such as the families of Caenidae and Chironomidae (Jowett, 1997;
470 Dewson et al., 2007). The presence of later instars of EPT taxa during the summer
471 months may be limited due to emergence patterns, but the majority (excluding
472 Caenidae) probably display a greater affinity for clean substrates (Sutherland et al.,
473 2012) and may account for the community patterns recorded in this study. As such,
474 the implications of fine sediment deposition will be most pronounced during summer
475 months. It is therefore vital to consider within-year temporal variation and taxon life
476 stages when assessing the implications of fine sediment deposition on aquatic
477 communities (Johnson et al., 2012).

478 Overall significant differences were recorded for the abundances of taxa classified as
479 sensitive to fine sediment (Turley et al., 2016). These results indicate that at the
480 patch scale, removal of fine sediments may enhance habitat complexity and thereby
481 increase the heterogeneity of instream communities. Micro-scale habitat
482 characteristics are critical in the regulation of macroinvertebrate diversity (Pardo and
483 Armitage, 1997; Lamouroux et al., 2004; Laini et al., 2014). Despite this, the majority
484 of studies conducted on fine sedimentation impacts often take a reach-scale
485 approach (e.g. Downes et al., 2006; Burdon et al., 2013) and therefore
486 understanding the importance of variable micro-scale habitat dynamics is limited.
487 Within this study clean substrates supported a greater number of unique taxa (11)

488 compared to sedimented substrates (2), highlighting the importance of micro-scale
489 habitat differences for biodiversity.

490 Taxa richness, community abundance and EPT richness did not demonstrate any
491 significant differences between sediment treatments. The documented effects of fine
492 sediment on taxa richness and community abundance are not consistent in the
493 literature with some studies documenting a reduction in taxa richness (Cline et al.,
494 1982; Rabeni et al., 2005) or community abundance (Armstrong et al., 2005; Larsen
495 et al., 2011) while others recorded no modification (Lenat et al., 1981; Kaller et al.,
496 2004; Downes et al., 2006); and in some instances abundances have been reported
497 to increase (Matthaei et al., 2006). Streams that are characterised by low fine
498 sediment content and support a greater proportion of fine sediment sensitive taxa,
499 are likely to be more heavily affected. In contrast, rivers that are species poor may
500 not display a marked response to an increase in fine sediment.

501 **4.2 Taxon specific responses to fine sedimentation**

502 A small number of associations were observed between individual taxa and fine
503 sediment treatments. Sedimented substrates were characterised by significantly
504 greater abundances of two taxa that typically burrow into fine substrates; *Dicranota*
505 sp. and Oligochaeta (Lenat et al., 1979; Fitter and Manuel, 1986). Even at the order
506 level, Oligochaeta are widely documented to be positively correlated with fine
507 sediment (Richards et al., 1993; Waters, 1995; Angradi, 1999; Descloux et al., 2013);
508 however, the experimental effects of fine sediment for *Dicranota* sp. have not been
509 widely documented. The reduction of pore space in heavily sedimented and clogged
510 substrates potentially favours taxa with small body sizes (Gayraud and Phillipe, 2001;
511 Duan et al., 2009; Xu et al., 2012). In marked contrast, two species demonstrated
512 strong affinities for clean substrates; the Ephemeropteran species, *Habrophlebia*
513 *fusca* which may be vulnerable to gill damage within fine bed material (Jones et al.,
514 2012) and *Gammarus pulex*, which although common in rivers with fine sediment
515 patches is a highly mobile taxon and may have actively sought clean sediments
516 (Wood et al., 2010; Mathers and Wood, 2016).

517 **4.3 Biological traits**

518 Several previous studies have suggested that macroinvertebrate community trait
519 profiles may alter as a function of habitat modifications; reflecting a filtering effect of

520 taxa with traits sensitive to fine sediment deposition (Usseglio-Polatera et al, 2000;
521 Larsen et al., 2011; Bona et al., 2016; Doretto et al., 2017). However, when the
522 functional composition of macroinvertebrate communities was examined in this study,
523 the effects of fine sediment were not as marked as those obtained using taxonomic
524 community composition data. Differences between functional trait composition
525 associated with sediment treatment were only observed on a very limited number of
526 sampling occasions. Despite the absence of a clear community effect, a number of
527 individual traits showed a significant response to fine sediment content.

528 Locomotion modalities were the most responsive to increased fine sediment loading
529 with crawlers, swimmers and interstitial dwellers all demonstrating a reduction in
530 occurrence within sedimented substrates. Habitat trait groups have been reported to
531 display significant responses to sedimentation, with fine sediment having the
532 potential to limit access to preferred habitats (Gayraud and Philippe, 2001; Rabeni et
533 al., 2005). Interstitial pore space is an important determinant in macroinvertebrate
534 colonisation and diversity, with fine sediment clogging limiting the ability of many
535 taxa to access subsurface habitats, in particular larger organisms that require larger
536 interstitial space (Larsen and Ormerod, 2010; Mathers et al., 2014). It is therefore not
537 surprising that the number of interstitial dwellers in combination with the maximal
538 size of organisms reduced within the sedimented columns (Buendia et al., 2013;
539 Descloux et al., 2014; Milesi et al., 2016). Similarly, crawlers have been widely
540 documented to be affected by increasing fine sediment content with some studies
541 citing their reduced locomotion as a factor in their reduced abundance (Bo et al.
542 2007; Buendia et al., 2013) whilst others link their decline to negative effects on
543 respiration modalities (Rabeni et al., 2005). In contrast, the habitat group of
544 swimmers demonstrated variable responses to enhanced sediment loading, with
545 some studies documenting a decrease in richness but no effect on density (Rabeni
546 et al., 2005), whilst others saw a reduction in abundance (Larsen et al., 2011) or
547 even a positive correlation (Buendia et al., 2013). Habitat complexity prior to
548 sedimentation probably influences the magnitude of the effects recorded on the
549 invertebrate assemblage. Rivers which are naturally more heterogeneous are likely
550 to display greater effects in response to instream stressors such as fine sediment
551 deposition.

552 Feeding modalities are often associated with fine sediment content, with increasing
553 fine sediment loads affecting the quality of trophic resources and thereby affecting
554 feeding activities (Jones et al., 2012). In contrast to the expectations of the wider
555 literature, the only taxa that demonstrated a reduction in abundance to increased fine
556 sediment content were those that displayed shredder feeding characteristics
557 (Descloux et al., 2014; Doretto et al., 2016). Similarly, respiration modalities are
558 often particularly sensitive to fine sediment with some respiratory structures being
559 significantly impaired or damaged by fine particles (Lemley, 1982; Townsend et al.,
560 2008). This study documented no significant associations with fine sediment content
561 and respiratory structures which were supported by the wider sedimentation
562 literature. Taxa which respire via plastron and spiracles demonstrated a reduction in
563 abundance in marked contrast to results reported by Logan (2007) and Archaimbault
564 et al., (2005). This biological response is primarily a function of increasing numbers
565 of the Diptera within the genus *Dicranota* sp. and may highlight a limitation of
566 biological trait analyses that only consider individual traits.

567 The application of biological traits in evaluating the effect of stressors has seen
568 increasing recognition, with many studies proposing that the application of trait
569 compositions may provide a better or comparable indicator for different types and
570 combinations of instream stressors than traditional taxonomic based metrics
571 (Menezes et al., 2010; White et al., 2016; Göthe et al., 2016). However, from the
572 results reported here and in a number of other studies, it is clear that further
573 research is required around the assignment of biological traits and caution should
574 therefore be applied when undertaking such analyses (Buendia et al., 2013;
575 Descloux et al., 2014). Further research is required to develop trait databases that
576 have greater applicability to the ecosystems being assessed. Currently the only
577 database available to European researchers is that by Tachet et al. (2010)
578 developed in French streams. Although applicable to other European streams, the
579 low taxonomic resolution of the database (family / genus) raises some questions
580 regarding the wider application of such an approach without some local modifications
581 as many families with multiple genus (e.g. Baetidae and Chironomidae) support
582 highly variable taxonomic responses (Monk et al., 2008). Traits are also unlikely to
583 act in isolation but rather a combination of traits will determine the response of an
584 individual species to a stressor (Pilière et al., 2016). Consequently, in future research,

585 traits should be assessed as interacting factors within a more fully developed
586 mechanistic understanding of the observed effects of fine sediment for
587 macroinvertebrates.

588 **5. Conclusion**

589 Understanding the mechanistic implications of fine sediment upon macroinvertebrate
590 communities still remains a significant challenge. This study indicates that the effect
591 of increased fine sediment loading upon macroinvertebrate assemblages is not
592 temporally consistent with a number of sampling periods displaying no discernible
593 effects of fine sediment loading. The implications of increased fine sediment loading
594 are likely to be heavily dependent on the timing of sedimentation events relative to
595 taxon life cycles. Future studies concerned with investigating the effects of fine
596 sediment should do so with a greater awareness of the temporal dynamics of the
597 communities they are studying. Despite the increasing application of biological trait
598 composition within biomonitoring efforts, community trait profiles displayed no
599 consistent effect to fine sediment on community structure in this study. Patch scale
600 responses to fine sediment were however evident, with the two substrate treatments
601 supporting distinct communities when taxonomic composition and individual trait
602 modalities were considered. The results from this study indicate the importance of
603 recognising micro-scale habitats within the context of maximising aquatic biodiversity.
604 Further research is required to fully understand the seasonal effects of fine sediment
605 deposition and dynamics on aquatic macroinvertebrate assemblage structure and
606 function.

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616

617 **List of Figures**

618 **Figure 1.** River discharge (hourly average $\text{m}^3 \text{s}^{-1}$) for the River Gwash (black) and
619 River Chater (grey) Rutland, UK during the sampling campaign. Dashed lines
620 indicate the two week sampling periods (21st June - 24th September 2015).

621 **Figure 2.** Non-metric multidimensional scaling (NMDS) of macroinvertebrate
622 community data from the River Gwash and River Chater by sediment treatment
623 using the Bray-Curtis similarities coefficients for cylinder sets 1 - 9 (panes a-i) and
624 global dataset (pane j). Grey rhombus = clean cylinders and black rhombus =
625 sedimented communities.

626 **Figure 3.** Non-metric multidimensional scaling (NMDS) of macroinvertebrate
627 community functional traits from the River Gwash and River Chater by sediment
628 treatment using the Bray-Curtis similarities coefficients for cylinder sets 1 - 9 (panes
629 a-i). Grey rhombus = clean cylinders and black rhombus = sedimented communities.

630 **Figure 4.** Mean abundances (± 1 SE) of sediment sensitive taxa (as defined under
631 the E-PSI index) over the nine sampling sets. Grey rhombus = clean substrates and;
632 black triangle = sedimented substrates.

633 **Figure 5.** Mean abundances (± 1 SE) of EPT taxa over the nine sampling sets.

634

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