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**Article:**

Robertson, AL, Brown, LE, Klaar, MJ et al. (1 more author) (2015) Stream ecosystem responses to an extreme rainfall event across multiple catchments in southeast Alaska. *Freshwater Biology*, 60 (12). 2523 - 2534. ISSN 1365-2427

<https://doi.org/10.1111/fwb.12638>

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1 Stream ecosystem responses to an extreme rainfall event across multiple  
2 catchments in southeast Alaska

3

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13

14 Abbreviated title: Stream responses to extreme rainfall across multiple catchments

15

16 Keywords: Floods, climate change, glacial recession, channel geomorphology,  
17 invertebrates.

18

19 SUMMARY

- 20 1. Floods are a key component of the flow regime of many rivers and a major  
21 structuring force of stream communities. Climate change is predicted to  
22 increase the frequency of extreme rainfall (i.e. return intervals > 100 years)  
23 leading to extensive flooding, but the ecological effects of such events are not  
24 well understood. Comparative studies of flood impacts are scarce, despite the  
25 clear need to understand the potentially contingent responses of multiple  
26 independent stream systems to extreme weather occurring at meso- and  
27 synoptic spatial scales.
- 28 2. We describe the effect of an extreme rainfall event affecting an area >100,000  
29 km<sup>2</sup> that caused extensive flooding in SE Alaska. Responses of channel  
30 morphology and three key biological groups (meiofauna, macroinvertebrates  
31 and fish) were assessed in four separate and recently deglaciated stream  
32 catchments of contrasting age (38-180 years) by comparing samples taken  
33 before and after the event.
- 34 3. Ecological responses to the rainfall and subsequent flooding differed markedly  
35 across the four catchments in response to variations in rainfall intensity and to  
36 factors such as channel morphology, stream sediment composition and  
37 catchment vegetation type and cover, which were themselves related to  
38 stream age.
- 39 4. Our study demonstrates the value of considering multiple response variables  
40 when assessing the effects of extreme events, and highlights the potential for  
41 contrasting biological responses to extreme events across catchments. We  
42 advocate more comparative studies to understand how extreme rainfall and  
43 flooding affects ecosystem responses across multiple catchments.

45 **Introduction**

46 Floods are a significant feature of the flow regime of many rivers (Poff *et al.*, 1997),  
47 and a major force structuring stream communities (Lake, 2000; Jones, 2013).

48 Extensive precipitation and/or snow melt can cause floods, but flow responses can  
49 vary markedly in space and time depending on antecedent conditions, catchment  
50 characteristics such as geology and relief, and human activities. Pluvial floods vary  
51 in magnitude and predictability as a result of the natural variability of precipitation,  
52 both within and between years, but a changing climate is expected to alter the  
53 frequency, intensity, spatial extent, duration and timing of extreme weather events  
54 (IPCC, 2013), and may result in unprecedented effects on river flow and associated  
55 riverine communities. Extreme or great floods can be defined as having discharges  
56 exceeding 100-year return intervals (Milly *et al.*, 2002). As such events are  
57 infrequent and unpredictable, knowledge of their ecological effects is incomplete, yet  
58 there is a growing need to improve understanding of their impact on river  
59 ecosystems as the climate changes.

60 The response of stream communities to flooding has been researched extensively  
61 over the past three decades (Niemi *et al.*, 1990; Yount & Niemi, 1990; Stanley *et al.*,  
62 2010) yet there remain relatively few studies of extreme flooding. Floods can affect  
63 riverine ecosystems directly, as disturbance alters biodiversity, abundances and  
64 standing biomass, and indirectly, via changes to river channel and floodplain  
65 hydrology, geomorphology and biogeochemistry (Poff, 1997). Extreme floods may  
66 have particularly deleterious effects on stream benthic communities because they  
67 scour and redeposit sediments, and incise channels, potentially reducing habitat  
68 heterogeneity and the availability of flow refugia for biota (Death, 1997).

69 Responses to flooding may depend on channel morphology, sediment composition  
70 and habitat complexity (e.g. the presence of backwaters, pools and debris dams)  
71 which dictates the extent of in-stream refugia. These factors may vary between  
72 catchments, with those in earlier successional stages tending to have less complex,  
73 more unconsolidated glacial deposits than those that are older and/or less modified  
74 (Milner *et al.*, 2000, 2013). Thus stream communities in different catchments could  
75 vary in their responses to flooding. Flood responses may also be modulated by the  
76 precipitation history and nature of the catchment (e.g. vegetation type and cover)  
77 and the resultant hydrological history of the river because the flow regime is a major  
78 ecological filter (*sensu* Poff, 1997), influencing the composition of the local  
79 community and 'selecting' species with appropriate traits from the regional species  
80 pool.

81 In a typical flood, a large volume of fast-flowing water moves rapidly downstream,  
82 creating high channel shear stress. Organisms are dislodged, crushed by moving  
83 substrata or forced to migrate from the channel (Death, 2010). Invertebrate and fish  
84 communities often exhibit low resistance to floods and total abundance is usually  
85 reduced significantly (e.g. Vieira *et al.*, 2004; Kroon & Ludwig, 2010; McMullen &  
86 Lytle, 2012) but populations are frequently resilient and recover rapidly if pools of  
87 colonists remain within the system or in nearby areas (Milner *et al.*, 2013). Some  
88 individuals move actively or passively into high-flow refugia such as river margins,  
89 floodplains and possibly the hyporheic zone, returning to the main channel after flow  
90 recedes (e.g. Robertson *et al.*, 1995; Dole-Olivier, 2011; Sueyoshi *et al.*, 2014).

91 Thus, habitat heterogeneity and connectivity are important for assemblage resilience  
92 (Matthews, 1998). The response of river biota to flooding may be taxon-specific,  
93 although few studies have considered a wide range of organismal groups (but see

94 Milner *et al.* 2013). Species responses can also be age-specific, for example, floods  
95 remove fine sediment thereby favouring gravel-nesting fish (e.g. Kroon & Ludwig,  
96 2010; Matthews *et al.*, 2013), whereas , scouring and sediment deposition during  
97 floods can kill fish eggs. Additionally flood waters displace juvenile salmonids  
98 downstream unless they are able to find flow refuges (e.g. Harvey, 1987).

99 The impact of flooding on riverine communities is usually assessed within individual  
100 catchments (e.g. Olsen *et al.*, 2010; Stanley *et al.*, 2010; Mesa, 2010; Milner *et al.*,  
101 2013) and there is a notable paucity of studies comparing the effects of floods on  
102 aquatic invertebrates across rivers and catchments (Death, 2007) with the exception  
103 of some patch-scale experimental manipulations (e.g. Gjerløv *et al.*, 2003; Melo *et*  
104 *al.*, 2003). However, adjacent catchments may be expected to differ in vegetation  
105 extent and type, and the rivers within them to differ in channel morphology, sediment  
106 composition and the degree of habitat complexity. In turn these differences may  
107 modulate ecosystem responses to extreme rainfall and subsequent flooding,  
108 highlighting the need to understand how independent systems respond during broad-  
109 scale extreme events and emphasising the importance of incorporating multiple  
110 catchments into studies of high flow impacts. By doing so we can begin to unpick  
111 the myriad of factors influencing community responses (Olden *et al.*, 2014).

112 This paper focuses on the effect of an extreme climatic event which led to extensive  
113 flooding of streams of differing habitat complexities in Glacier Bay, southeast Alaska.  
114 Over 400mm of rain fell over a 4-day period (21<sup>st</sup> – 24<sup>th</sup> November 2005) including >  
115 130mm on a single day (Fig. 1). The intensity of the rainfall over 24 h indicated that  
116 this event had a return interval of > 100 years and its severity was compounded by  
117 the duration of the storm and extensive catchment snow cover (Milner *et al.*, 2013).  
118 Furthermore, rainfall intensity varied across the study area, being higher in the north

119 (170mm on 22<sup>nd</sup> November 2005) and lower in the south (110mm on 22<sup>nd</sup> November  
120 2005) (Fig. 1). We assessed ecosystem response to this extreme rain and flooding  
121 event using three biological groups (meiofauna, macroinvertebrates and fish) from  
122 four streams at differing stages of development following glacial recession in Glacier  
123 Bay.

124

125 Our primary aim was to examine the impact of an extreme rainfall event leading to  
126 extensive flooding on stream ecosystems in multiple catchments across an 11,000  
127 km<sup>2</sup> study area. We hypothesised that the flood event would have the following  
128 effects:

- 129 1. Stream geomorphology will be modified across the streams, with channel  
130 reconfiguration leading to reduced habitat heterogeneity.
- 131 2. Community total abundance will decline whereas taxon richness may increase  
132 or decrease depending on the habitat preferences of individual taxa. Stream  
133 communities will converge post-flood, as formerly contrasting communities  
134 'reset' to an earlier stage of development.
- 135 3. Streams subjected to the highest rainfall intensity, and greatest flooding,  
136 should exhibit the biggest shifts in invertebrate community structure.
- 137 4. Responses to flooding will differ among the three organismal groups  
138 (meiofauna, macroinvertebrates and fish) depending on traits and/or timing of  
139 the flood with respect to life cycle stage.

## 140 **Methods**

141 Glacier Bay National Park and Preserve (GBNP) is located west of Juneau in  
142 southeast Alaska (58° 10'- 59° 15'N; 135° 15'- 138° 10'W). Glacial recession has created

143 a deglaciaded landscape, with a temporal scale of 220 years and a spatial scale of  
144 11,000 km<sup>2</sup>. The climate of Glacier Bay is temperate maritime, with mean annual  
145 temperature of 5 °C (mean monthly range - 3 °C to 13 °C) and average annual  
146 precipitation of 1400 mm. A Neoglacial ice sheet once covered the majority of  
147 GBNP, reaching a maximum around AD 1700. A change in local climate c.250 years  
148 ago led to recession of the ice sheet (Chapin *et al.*, 1994). Detailed historical and  
149 geological information provides accurate information on the rate of glacial recession  
150 within GBNP, from which stream age can be estimated. Stream and catchment ages  
151 were defined as the time since ice recession from the stream mouth (Milner *et al.*,  
152 2000).

153 Four streams (Table 1) were selected to represent c.180 years of catchment  
154 development following glacial recession (Milner *et al.*, 2000). The catchments of the  
155 older streams (140 - 180 years) had extensive forest cover, while those of the  
156 younger streams (38 - 65 years) possessed more intermittent and less complex  
157 vegetation.

158 To determine changes in stream channel cross-sections following the flood,  
159 tachometry channel cross-section data were collected in 1997 using a Sokkia dumpy  
160 level (Topcon, Tokyo, Japan) with tripod and staff. Measurements were taken at two  
161 separate locations within each study reach, at a maximum of 100 m apart, and  
162 located a maximum of 1 km from the stream mouth, hereafter termed 'upper' and  
163 'lower' cross-sections. Annual observations demonstrated that these cross-sections  
164 did not change markedly prior to the extreme rain and flooding event in late 2005.  
165 GPS fixes at the floodplain terrace on both banks of the channel cross-sections  
166 facilitated re-surveying in 2006 to provide information on channel change. Floodplain  
167 area, bankfull width and detailed channel bed measurements were taken, allowing

168 entrenchment ratios (width of flood-prone area/ width at bankfull) to be estimated.  
169 Only the upper cross-section could be re-surveyed in 2006 at Stonefly Creek. The  
170 percentage of pools in the habitat was determined before (Milner et al. 2000) and  
171 after the flood (Klaar et al. 2009).

172 For macroinvertebrates, samples collected in the same summer month before (2005)  
173 and after (2006) the flood were compared, excepting Berg Bay South stream where  
174 samples collected in July 2005 were compared with September 2006. For  
175 meiofauna, comparisons were made between samples collected in summer 2004  
176 (before flood) and summer 2006 (after flood). For meiofauna four additional sets of  
177 samples (two in 2006 and two in 2007) were used to examine the recovery  
178 trajectory.

179 Meiofauna were collected in summer (June – August) from a representative  
180 sampling station located c. 0.5 - 1 km from the mouth of each stream using a Surber  
181 net (five replicates; 63 $\mu$ m mesh). Meiofauna are organisms which pass through a  
182 1 mm sieve but are retained by a 63 $\mu$ m sieve (Giere 1993) and usually incorporate  
183 the small instars of macroinvertebrates, as well as taxa such as copepods which  
184 remain in this size category throughout their life cycle. Macroinvertebrates were also  
185 collected from the same reaches using a Surber net (5 - 10 replicates; 330 $\mu$ m mesh).  
186 Both size fractions were preserved in 70% ethanol and later separated in the  
187 laboratory from detritus and inorganic matter before enumeration.

188 Macroinvertebrates were identified using Merritt *et al.* (2008). Meiofauna were  
189 identified using Thorp & Covich (2009) and Smith (2001). Macroinvertebrates < 1  
190 mm were typically identified to order because their immaturity precluded assignment  
191 to genus and/or species.

192

193 Numbers of adult pink salmon (*Oncorhynchus gorbuscha*) spawners were estimated  
194 using the average of counts by two observers walking the length of the stream, and  
195 juvenile coho salmon (*Oncorhynchus kisutch*) densities (Catch Per Unit Effort -  
196 CPUE) with minnow traps baited with salmon eggs soaked previously in Betadyne  
197 iodine and fished for 2h (Milner *et al.*, 2000).

## 198 **Data analysis**

199 Pre- and post-flood data (based on mean densities from replicate Surber samples in  
200 each stream) were ordinated using non-metric multidimensional scaling (NMDS)  
201 using Bray-Curtis dissimilarity matrices.. One-way ANOSIM tested the null  
202 hypothesis that the taxonomic composition of meiofaunal and macroinvertebrate  
203 communities were unaffected by the flood. ANOSIM was conducted on individual  
204 replicates using Bray-Curtis dissimilarity scores with 10,000 permutations and  
205 Bonferroni-corrected significance values. A similarity of percentages (SIMPER)  
206 routine was used to identify five taxa contributing most to community dissimilarity  
207 before and after the flood in each stream. One-way ANOVA was then used to  
208 determine the significance of these taxonomic differences. All analyses were  
209 conducted on  $\log_{10}(x+1)$  transformed data) and statistical tests were undertaken  
210 using SPSS v19. NMDS, ANOSIM and SIMPER were undertaken using PAST v3.0.

211

## 212 **Results**

213 The effect of the flooding on channel cross-sections varied markedly among the four  
214 study streams (Fig. 2; Table 2). At Stonefly Creek, infilling reduced channel width by  
215 21% whereas at Wolf Point Creek the flood scoured the bed and banks, and  
216 increased channel entrenchment. However, the highest degree of channel change

217 occurred at Ice Valley Stream, where depth (+17.2%) and width (+37.5%) increased  
218 and entrenchment decreased (Table 2). Channel migration was also evident in the  
219 lower transect profile (Fig. 2). The channel response at Berg Bay South Stream  
220 varied among transects, but generally, channel depth decreased as a result of  
221 infilling (47.5% and 3.4% decrease in channel depth post-flooding at the upper and  
222 lower transects respectively), and channel width increased. The occurrence of pool  
223 habitat - a measure of channel heterogeneity - was unaffected by the flood in  
224 Stonefly Creek and Ice Valley Stream, but declined in Wolf Point Creek, and  
225 increased in Berg Bay South Stream.

226 Flooding significantly reduced the taxon richness and total abundance of meiofauna  
227 in all streams except Ice Valley (Table 3). Declines in meiofaunal abundance ranged  
228 from 84 – 90% in Stonefly Creek, Wolf Point Creek and Berg Bay South. In Stonefly  
229 Creek, meiofaunal-sized Plecoptera and Ephemeroptera, Ostracoda and  
230 *Acanthocyclops vernalis* were absent from post-flood assemblages. In Wolf Point  
231 Creek absentees were Oligochaeta and *Cyclops scutifer*, and in Berg Bay South  
232 stream, these were meiofaunal-sized Plecoptera, Ephemeroptera and *Simulium* sp.,  
233 Tardigrada, *Chaetogaster* spp., other Oligochaeta, Ostracoda, *Bryocamptus*  
234 *zschokkei* and *Cyclops scutifer*. Despite the immediate post-flood decline,  
235 meiofaunal taxon richness in Stonefly Creek, Wolf Point Creek and Ice Valley  
236 recovered later in 2006 and 2007 to fall within the range of pre-flood taxon richness  
237 (Fig. 3). In Berg Bay South meiofaunal taxon richness in 2006 and 2007 remained  
238 lower than that in pre-flood samples, however, all taxa collected before the flood  
239 were found in at least one post-flood sample suggesting that pre-flood taxa persisted  
240 within the stream albeit at low levels of abundance.

241 ANOSIM indicated that meiofaunal community composition was significantly affected  
242 by the flood in Stonefly Creek (ANOSIM  $r^2 = 0.76$ ,  $P < 0.01$ ), Wolf Point Creek  
243 (ANOSIM  $r^2 = 0.99$ ,  $P < 0.01$ ) and Berg Bay South Stream (ANOSIM  $r^2 = 0.95$ ,  
244  $P < 0.01$ ) but not in Ice Valley. NMDS showed that Berg Bay South, Stonefly and Wolf  
245 Point Creek communities clustered together more closely post-flood, suggesting  
246 more similar meiofaunal communities in these disturbed streams (Fig. 5b).

247 SIMPER revealed that the identity of five taxa contributing most to pre- vs. post-flood  
248 community dissimilarity differed among streams, especially for meiofauna (Fig.  
249 4b, Table 5). Abundances of these key taxa largely declined following the flood,  
250 although the cyclopoid copepod *Acanthocyclops vernalis* significantly increased in  
251 Wolf Point Creek (Fig. 4b).

252 The total abundance of macroinvertebrates declined following the flood in all streams  
253 except Ice Valley, but effects were statistically significant only in Stonefly Creek ( $F_{1,8}$   
254 = 33.25,  $P < 0.001$ ). Macroinvertebrate taxon richness was only significantly reduced  
255 by flooding at Wolf Point Creek ( $F_{1,8} = 11.94$ ,  $P < 0.01$ ). In this stream,  
256 macroinvertebrate taxa absent in post-flood samples were Coleoptera, *Ephemera*,  
257 EphemereLLidae, Hydracarina, *Suwallia forcipata*, and Trichoptera. For  
258 macroinvertebrates, SIMPER revealed that shifts in the abundance of Chironomidae  
259 and Simuliidae were observed in all streams pre- versus post-flood (Fig. 4a, Table  
260 4), and that responses of some Plecoptera (*Suwallia forcipeta*) accounted for  
261 community change in Stonefly Creek, Wolf Point Creek and Berg Bay South Stream  
262 (Table 4). Abundances of these key taxa generally declined following the flood, but  
263 Chironomidae and *Ephemera* in Ice Valley Stream and Simuliidae and *Suwallia*  
264 *forcipata* in Berg Bay South Stream increased post-flood (Fig. 4a).

265 Macroinvertebrate community composition was significantly altered by the flood in  
266 the two younger streams Wolf Point Creek (ANOSIM  $r^2 = 0.868$ ,  $P < 0.01$ ) and  
267 Stonefly Creek (ANOSIM  $r^2 = 0.868$ ,  $P < 0.01$ ) but not in the older Ice Valley and  
268 Berg Bay South streams (Fig. 1). NMDS sample scores were more tightly clustered  
269 post-flood reflecting increased similarity among macroinvertebrate assemblages  
270 simplified by disturbance (Fig. 5a).

271 The highest abundance of spawning adult pink salmon and CPUE for juvenile coho  
272 were recorded in Wolf Point Creek, prior to the flood and densities in this stream also  
273 declined most strongly post-flood, with an eight-fold decline in returning spawning  
274 adult pink salmon and a fifteen-fold fall in coho juvenile CPUE (Table 2). In contrast,  
275 returns of adult pink salmon declined three-fold in Berg Bay South Stream after the  
276 flood and there was a slight increase in juvenile coho CPUE. In Ice Valley Stream,  
277 low numbers of returning pink salmon were recorded in both the pre- and post-flood  
278 years and juvenile coho CPUE declined three-fold following the flood (Table 2).

279

## 280 **Discussion**

281 Predicting how extreme rainfall and flooding will affect river ecosystems as the  
282 climate changes requires an understanding of how flood impacts vary across  
283 multiple catchments in response to factors such as rainfall severity, channel  
284 morphology and channel complexity, and, how different organismal groups respond  
285 to high flows. This study revealed that the effects of flooding caused by a single  
286 rainstorm varied markedly across our study streams in southeast Alaska. Several  
287 factors may account for the contrasting responses to this extreme climatic event

288 observed among stream catchments, including stream geomorphology and  
289 catchment vegetation cover.

290 Geomorphic responses to the extreme rainfall and flooding event varied between the  
291 study streams [H1]. In the two younger streams, Stonefly Creek and Wolf Point  
292 Creek, where the highest rainfall occurred (>400mm in 4 days), there was a similar  
293 response of channel incision and increasing entrenchment due to channel bed and  
294 bank scouring. However, in the two older streams, Ice Valley and Berg Bay South,  
295 where rainfall was less intense (<300mm over 4 days), channel entrenchment  
296 decreased and the stream channels generally widened and decreased in depth.  
297 These variable responses may result in part from differences in channel bed  
298 sediment structure associated with stream age, which varied from 38 – 180 years  
299 (Stover & Montgomery, 2001; Sipos *et al.*, 2008). Younger streams (i.e. 38 - 65  
300 years) are often dominated by unconsolidated glacial material which is more likely to  
301 be scoured from channel banks and bed during high flows (Carrivick *et al.*, 2013;  
302 Milner *et al.*, 2013), resulting in a more defined, incised channel. However, older  
303 streams (140 - 180 years) tend to have larger (Klaar *et al.*, 2011), and more stable  
304 bed substrates, as unconsolidated material has generally already been transported  
305 from the channel. In these older stable streams, flood water is more likely to spill out  
306 onto the floodplain, increasing channel width and decreasing channel depth as  
307 material transported from terrestrial and upstream locations is deposited further  
308 downstream.

309 The variable responses of the study streams to the extreme rainfall and flooding  
310 event may also result from differences in vegetation cover in the catchments. Older  
311 stream catchments are covered by more mature forest which may attenuate the  
312 effects of extreme rainfall, whereas younger catchments are more sparsely

313 populated by less complex vegetation (e.g. Chapin *et al.*, 1994; Fastie, 1995; Milner  
314 *et al.*, 2007). Engstrom *et al.* (2000) suggested that catchment development over  
315 time can change soil structure, leading to greater surface runoff, which can in turn  
316 modify stream hydrology. Sediment structure, catchment vegetation (both of which  
317 vary with stream age) and rainfall intensity may interact to impact stream channel  
318 morphology following an extreme event, but more detailed geomorphological data  
319 collection would be required to untangle this further.

320 Changes in the meiofauna partially supported our second hypothesis, that  
321 community composition would change markedly in the months following the flood.  
322 Meiofaunal total abundance, taxon richness and community composition differed  
323 significantly in three of the four streams and became more similar post-flood,  
324 probably because the communities were reset to earlier stages of development  
325 (sensu Milner *et al.*, 2013) as a result of channel morphology change. Meiofauna are  
326 small and their resultant vulnerability to high flows is well documented (e.g.  
327 Robertson *et al.*, 1995); however, they can be persistent in streams (Robertson,  
328 2000) as demonstrated by our finding that post-flood taxon richness either fell within  
329 the envelope of pre-flood (2000-2004) taxon richness, or that pre-flood taxa were  
330 recorded in at least one post-flood sample. The abundance of most taxa declined  
331 following the flood, but in Wolf Point Creek, that of the predatory cyclopoid copepod  
332 *Acanthocyclops vernalis* increased markedly, possibly as a result of predatory/  
333 competitive release (Gendron & Laville, 2000; Anderson & Ferrington, 2013) or the  
334 removal of fine sediments (Robertson & Milner, 2006).

335 Our results indicate that, for meiofauna, lower rainfall intensity did not necessarily  
336 cause a lesser community response because meiofaunal community composition  
337 differed significantly in Berg Bay South (experiencing lower rainfall intensity) as well

338 as Stonefly and Wolf Point Creek (higher intensities) and the percent decline in  
339 abundance was similar in all three streams. Thus, for the meiofauna, our third  
340 hypothesis, that higher rainfall will lead to larger community response, was  
341 unsupported. Meiofauna have a low threshold of entrainment into the water column  
342 (Palmer *et al.*, 1992) and thus washout may occur at relatively low flows.

343 Macroinvertebrate community composition changed significantly in some streams  
344 but not others and NMDS suggested that communities in three streams became  
345 more similar after the flood than before, providing further partial support for our  
346 second hypothesis. As has been found in many other studies, invertebrate total  
347 abundance and taxon richness generally declined following the floods (e.g. McCabe  
348 & Gotelli, 2000; Fritz & Dodds, 2004; Stanley *et al.*, 2010), although this was  
349 statistically significant only for some groups and some streams. Macroinvertebrate  
350 taxa absent from Wolf Point Creek and Stonefly Creek tended to be those favouring  
351 slow flowing/ depositional areas of streams thereby reflecting the reduction of these  
352 habitats post-flood (Milner *et al.* 2012). Significant changes in macroinvertebrate  
353 community composition following the floods were found only in the least stable,  
354 younger channels of Wolf Point and Stonefly Creeks where the most intense rainfall  
355 occurred. These streams were the only ones showing significant changes in total  
356 abundance (Stonefly Creek) and taxon richness (Wolf Point Creek), providing some  
357 support for our third hypothesis that streams experiencing the greatest rainfall would  
358 show the greatest changes in invertebrate communities. The response of juvenile  
359 coho salmon to flooding was also distinctive; CPUE declined post-flood in Wolf Point  
360 Creek but increased in Berg Bay South Stream, perhaps in response to the greater  
361 percentage of pools in the post-flood stream (Rosenfeld *et al.*, 2000; Roni, 2002).  
362 The number of adult pink salmon spawners decreased markedly in Wolf Point Creek

363 and Berg Bay South Stream but recovered rapidly in the former in 2009 and 2011  
364 (Milner *et al.*, 2013).

365

366 We found differences in the response of the three organismal groups to extreme  
367 flooding, for example, the meiofauna showed a greater response to the flood than  
368 macroinvertebrates, providing partial support for our fourth hypothesis. Our finding  
369 highlights the importance of considering the responses of multiple organismal groups  
370 to fully capture the effects of extreme events on stream communities.

371 Invertebrates in Ice Valley stream were apparently not affected by the flood, despite  
372 this stream experiencing the greatest degree of channel change. Here, abundance  
373 and taxon richness were both low prior to the flood, perhaps reflecting low channel  
374 stability and the higher proportion of bedrock in the channel (Barnes *et al.*, 2013),  
375 and the invertebrate community was dominated by Chironomidae, a group thought to  
376 be resilient to flooding events (Death, 2007; Collier & Quinn, 2003).

377 We examined stream community response to a synoptic-scale extreme rainfall event  
378 across several independent catchments. Multiple interacting factors determined  
379 community response to these events. Rainfall intensity varied across catchments  
380 and stream community response also differed among streams, perhaps in response  
381 to this variation. The stream catchments also differed in developmental stage leading  
382 to variation in channel morphologies, sediment composition and catchment  
383 vegetation cover and type. These differences undoubtedly modulated the effect of  
384 the rainfall on the stream communities. Our findings are consistent with those of  
385 Collier & Quinn (2003), who found that streams draining catchments with less  
386 complex vegetation (pasture) were more affected by flooding than those draining

387 forested catchments, and Death & Zimmermann (2005) reported that the effects of  
388 flood on invertebrate diversity were less in forested reaches than in downstream  
389 pasture reaches because communities in forests were not reliant on recovery of the  
390 periphyton food base. There were also significant hydrological contrasts among  
391 catchments under different vegetation cover (e.g. Schoonover *et al.*, 2006; Germer  
392 *et al.*, 2010; Brown *et al.*, 2010) which can undoubtedly affect the composition and  
393 dynamics of constituent biological groups of streams in these environments.  
394 Predicting the ecological effects of extreme events across different catchments will  
395 undoubtedly require a more detailed understanding of how these systems function  
396 hydrologically.

397 Our study highlights the difficulties that arise when examining cross-catchment  
398 responses to disturbance. Potentially, ecosystem responses to extreme rainfall and  
399 subsequent flooding were 'confounded' by differences in rainfall and age across the  
400 catchments. Disentangling these interactions requires investment in spatially  
401 distributed, long-term monitoring networks to capture multiple events across a variety  
402 of river systems, and/or to continue with opportunistic sampling of extreme events so  
403 that future meta-analyses can extract information on common responses (Olden *et al.*  
404 *et al.*, 2014). Regrettably, both of these options are limited by both time and resources.  
405 There is an emerging consensus that extreme events will increase in frequency and  
406 magnitude over coming decades as the climate changes and thus identifying and  
407 implementing strategies to manage this change is of primary importance, tasks that  
408 are currently hampered by our lack of knowledge and understanding regarding  
409 ecosystem responses to extreme flooding across multiple catchments.

410

411 **Acknowledgments**

412 We thank Mike McDermott and Sarah Hainie for assistance in the field. Justin Smith  
413 of the *mv* Capelin provided access to the streams. Numerous others in the National  
414 Park Service provided logistic support. Research has been supported by various  
415 bodies including NERC (GR9/2913, NE/E003729/1, NE/E004539/1 and  
416 NE/E004148/1), the Royal Society and the Universities of Roehampton, Birmingham,  
417 Worcester and Leeds. We thank Erik Knudsen for providing pre-flood data. The  
418 comments of two anonymous reviewers improved an earlier version of the  
419 manuscript.

420

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574 FIGURES.

575 Fig. 1 Map of Glacier Bay showing location of the four streams (1. Stonefly Creek, 2.  
576 Wolf Point Creek, 3. Ice Valley Stream, 4. Berg Bay South Stream). Inset bar charts  
577 show daily rainfall (cm) recorded over 5 days in November 2005 near Wachusett  
578 Inlet and Berg Bay.

579 Fig. 2 Channel cross-sections for the four streams, showing channel morphology  
580 before and after the 2005 flood. SFC Stonefly Creek, WPC Wolf Point Creek, IVS Ice  
581 Valley Stream, BBS Berg Bay South Stream. Note both axes are scaled to data.

582 Fig. 3 Taxon richness of the post-flood meiofaunal community ( $\bar{x} + 1SE$ ) in (a)  
583 Stonefly Creek, (b) Wolf Point Creek, (c) Ice Valley Stream and (d) Berg Bay South  
584 Stream. The hatched rectangle shows the range of taxon richness in pre-flood  
585 samples (2000-2004). The y-axis is scaled to data.

586 Fig. 4 Abundance  $m^{-2}$  ( $\bar{x} + 1SE$ ) of the five taxa contributing most to dissimilarity of  
587 (a) macroinvertebrate and (b) meiofaunal communities before and after the flood in  
588 (i) Stonefly Creek, (ii) Wolf Point Creek, (iii) Ice Valley Stream and (iv) Berg Bay  
589 South Stream. The y-axis is scaled to data.

590 Fig. 5 NMDS plots of (a) macroinvertebrates in summer 2005 and 2006 and (b)  
591 meiofaunal communities in summer 2004 and 2006. SF Stonefly Creek, WPC Wolf  
592 Point Creek, IV Ice Valley Stream, BBS Berg Bay South Stream.

593

594 Table 1. Characteristics of Stonefly Creek (SFC), Wolf Point Creek (WPC), Ice Valley Stream (IVS) and  
 595 Berg Bay South Stream (BBS), Glacier Bay.

	Age	Reach gradient (%)	Stream length (km)	Drainage area (km <sup>2</sup> )	Stream order	Average discharge (m <sup>3</sup> s <sup>-1</sup> )	Dominant substrate	Dominant riparian vegetation
SFC	38	1.75	3.5	10.0	2	1.28	Cobble	Alder
WPC	65	1.14	5.6	29.8	2	2.29	Cobble	Alder
IVS	140	0.98	8.3	19.4	2	3.02	Cobble	Alder/ cottonwood
BBS	180	0.80	7.2	33.1	3	4.95	Large gravel/small cobble	Alder/ cottonwood/ Sitka spruce

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597

598 Table 2. Channel entrenchment ratios, percentage of pools in the study reaches and  
 599 coho (*Oncorhynchus kisutch*) juvenile fish CPUE in Stonefly Creek (SFC), Wolf Point  
 600 Creek (WPC), Ice Valley Stream (IVS) and Berg Bay South Stream (BBS), Glacier  
 601 Bay before (summer 2005) and after (summer 2006) extreme flooding in the winter  
 602 of 2005. Pre-flood adult pink salmon (*Oncorhynchus gorbuscha*) counts are for  
 603 summer 2005 and post flood are summer 2007. Fish data not available (-) for  
 604 Stonefly Creek.

	Entrenchment ratio		% pool		Coho CPUE		Adult Pink Salmon	
	Pre-flood	Post-flood	Pre-flood	Post-flood	Pre-flood	Post-flood	Pre-flood	Post-flood
SFC	1.3	1.4	0	0	-	-	-	-
WPC	3.4	2.4	0.2	0	9.3	0.6	13000	1500
IVS	1.9	2.2	3.8	3.7	5.3	1.6	<100	<100
BBS	1.1	3.0	2.2	5.6	5.5	8.3	7000	1500-2500

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609 Table 3: One-Way ANOVA testing the effect of the flood on the meiofaunal  
610 community in four study streams. N.S., non significant ( $P>0.05$ ).

	Total abundance		Taxon richness	
	<i>F</i> value	<i>P</i>	<i>F</i> value	<i>P</i>
Stonefly Creek	$F_{(1,8)} = 33.01$	0.001	$F_{(1,8)} = 18.75$	0.003
Wolf Point Creek	$F_{(1,8)} = 31.22$	0.001	$F_{(1,8)} = 14.5$	0.005
Ice Valley Stream	$F_{(1,8)} = 0.77$	N.S.	$F_{(1,8)} = 1.44$	N.S.
Berg Bay South Stream	$F_{(1,8)} = 22.78$	0.001	$F_{(1,8)} = 43.63$	<0.001

611

612 Table 4. SIMPER results for five taxa contributing most to pre- vs. post-flood  
 613 macroinvertebrate assemblage dissimilarity in four streams in Glacier Bay, Alaska.  
 614 Mean community dissimilarity before and after flooding: Stonefly 86.7%, Wolf Point  
 615 23.2%, Ice Valley 79%, Berg Bay South 46.2%.

616 (a)

Macroinvertebrates	Stonefly Creek	Wolf Point Creek	Ice Valley Stream	Berg Bay South Stream
Chironomidae	15.7%	5.7%	42.9%	13%
Simuliidae	53.6%	23%	9.9%	17.7%
Ceratopogonidae	-	10.1%	-	-
Tipulidae	6.8%	-	-	-
Plecoptera	5.6%	24.2%	-	12.7%
<i>Suwallia forcipeta</i>	5.6%	23.7%	-	11.8%
<i>Ephemera</i>	-	-	4.2%	-
<i>Malenka californica</i>	-	-	-	13%
Neophemeridae	-	-	4.2%	-
<i>Arthropleona</i>	-	-	12.9%	-

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618

619 Table 5. SIMPER results for five taxa contributing most to pre- vs. post-flood  
 620 meiofaunal assemblage dissimilarity in four streams in Glacier Bay, Alaska. Mean  
 621 community dissimilarity before and after flooding: Stonefly 52.2%, Wolf Point 63%,  
 622 Ice Valley 62.4%, Berg Bay South 62.8%.

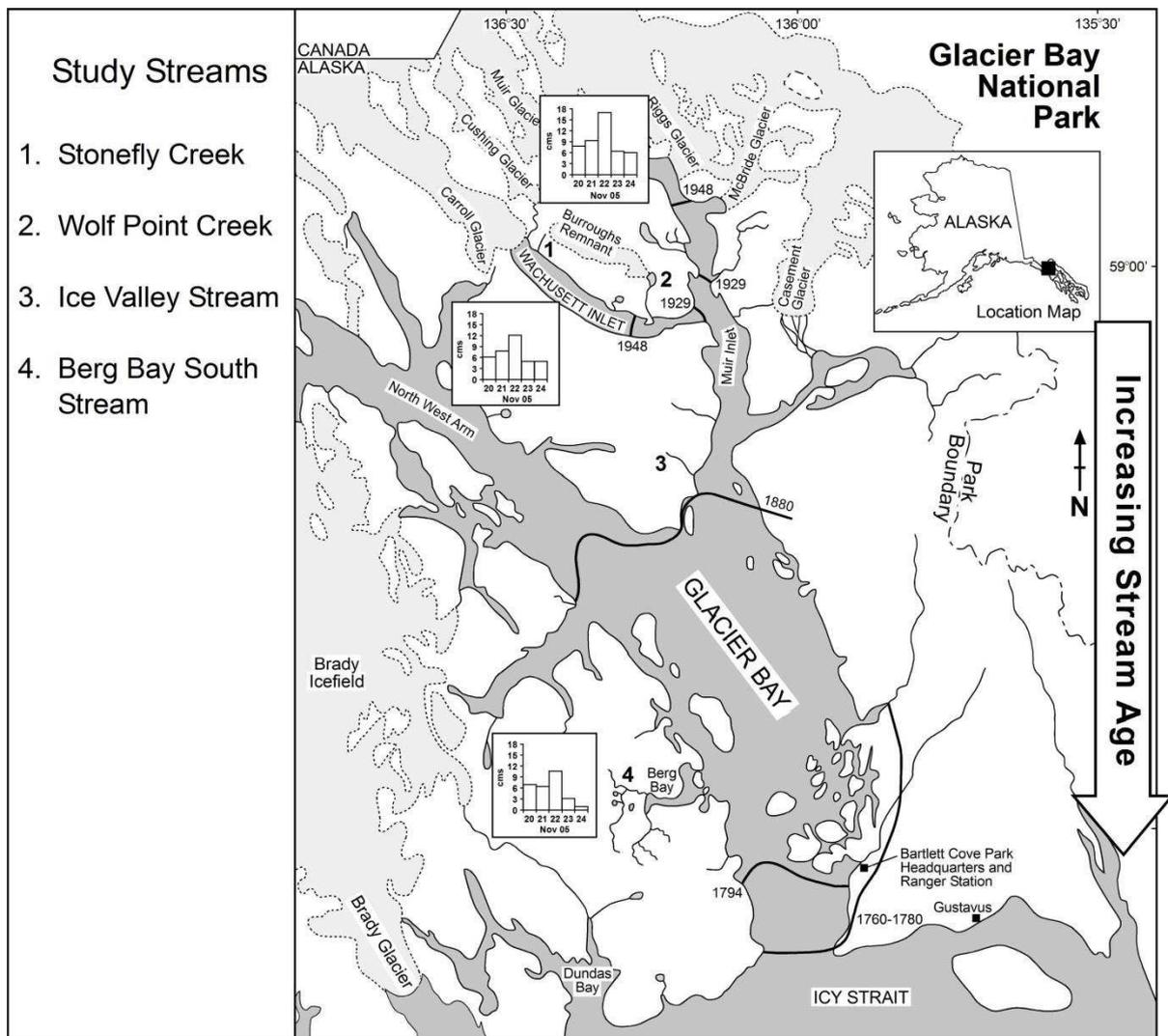
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Meiofauna	Stonefly Creek	Wolf Point Creek	Ice Valley Stream	Berg Bay South Stream
Chironomidae	-	-	61.5%	13.2%
Simuliidae	-	14.8%	-	7.9%
Plecoptera	-	-	20.1%	9.3%
Ephemeroptera	8.4%	-	-	27.3%
Oligochaeta	-	17.3%	-	-
<i>Chaetogaster</i>	17.1%	-	-	-
Nematoda	11%	-	-	-
Tardigrada	15.1%	-	8.6%	-
<i>Acanthocyclops vernalis</i>	12.6%	17.4%	-	-
<i>Cyclops scutifer</i>	-	15.8%	-	-
<i>Bryocamptus zschokkei</i>	-	-	-	7%
Hydracarina	-	15.4%	-	-

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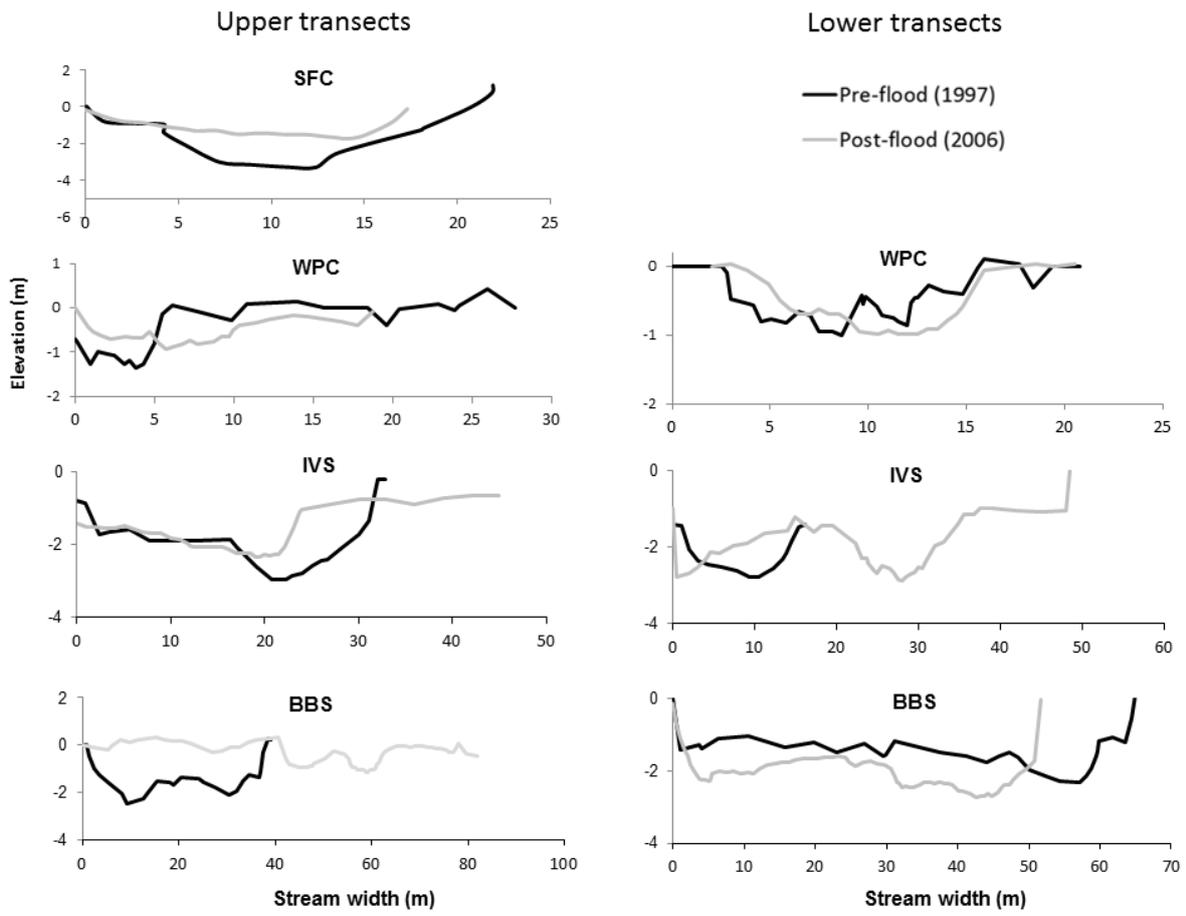
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626 Fig. 1



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629 Fig. 2



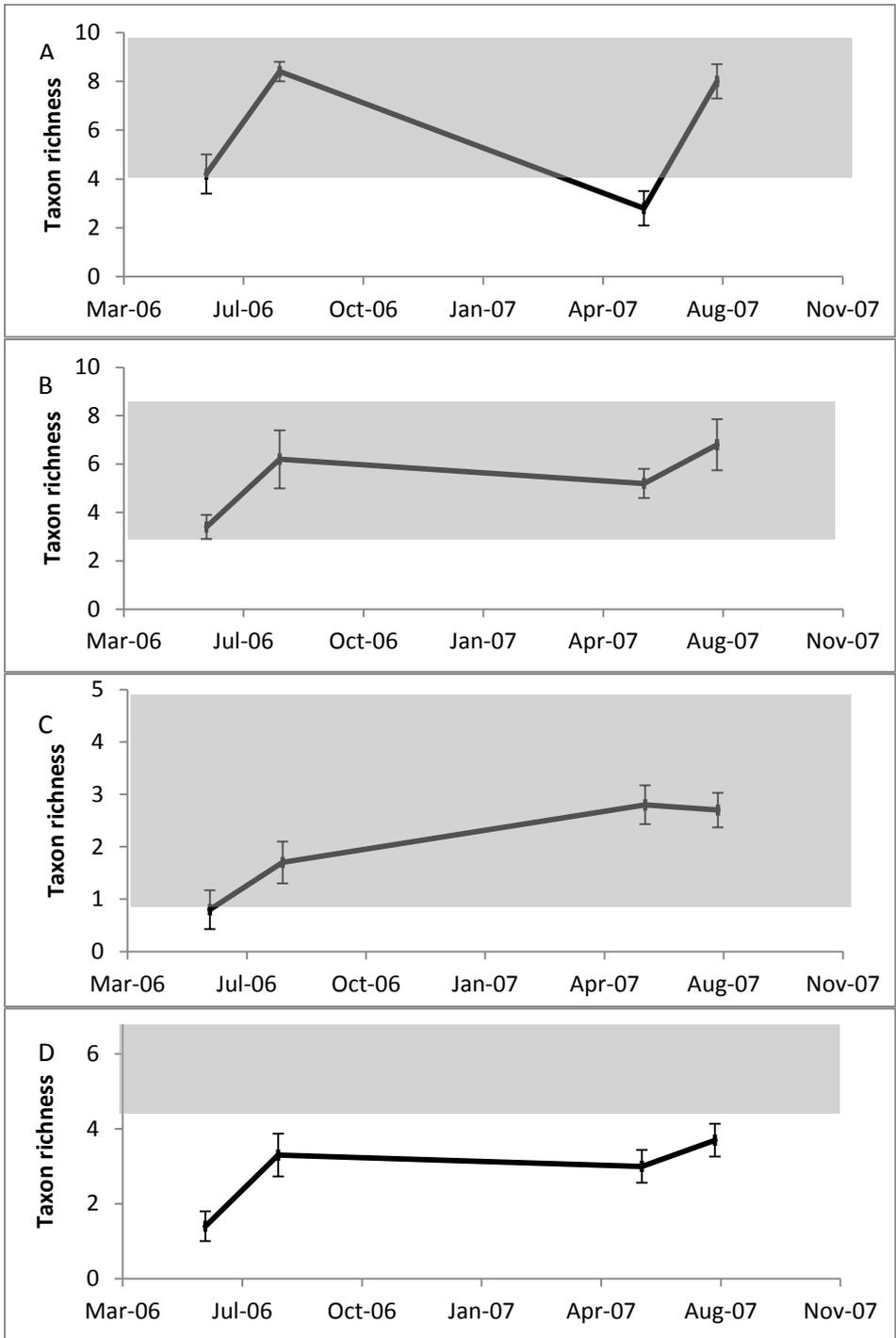
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633 Fig. 3

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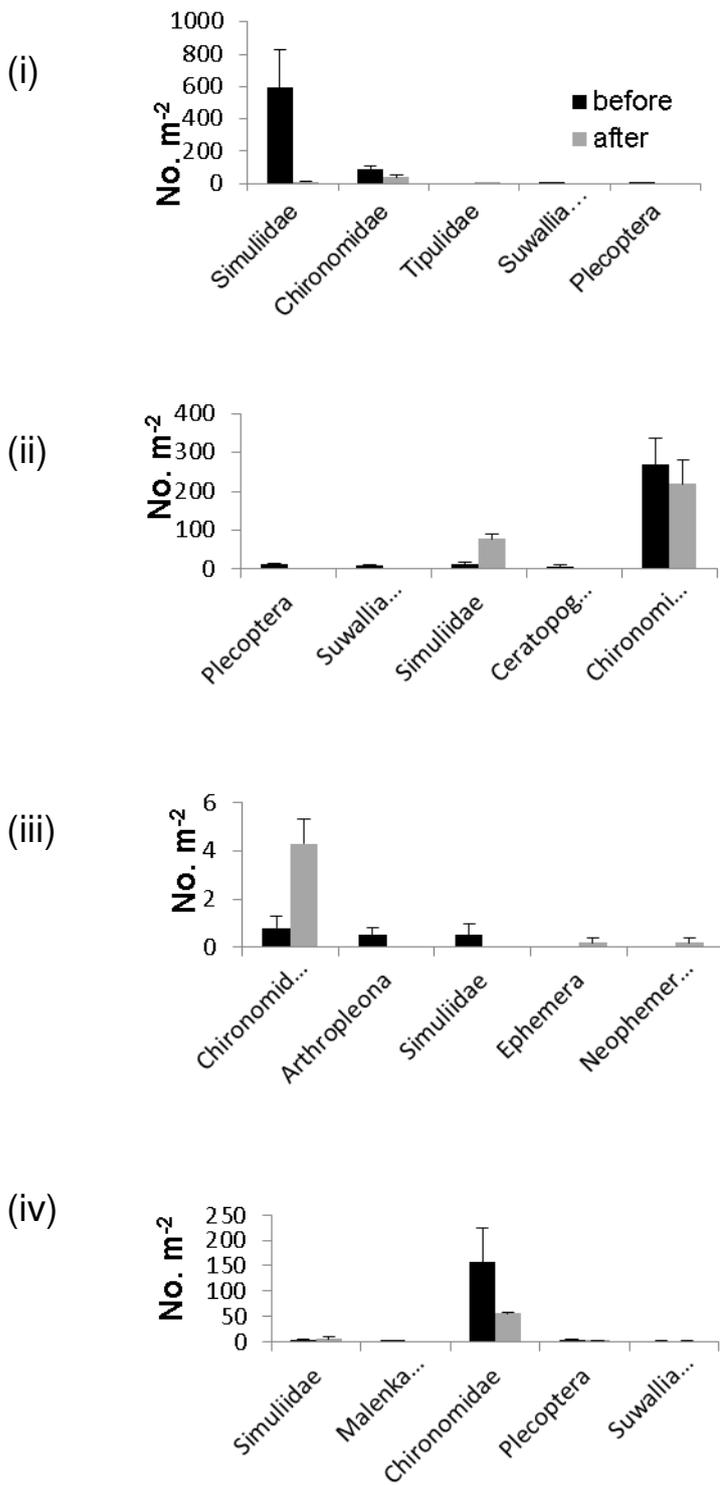
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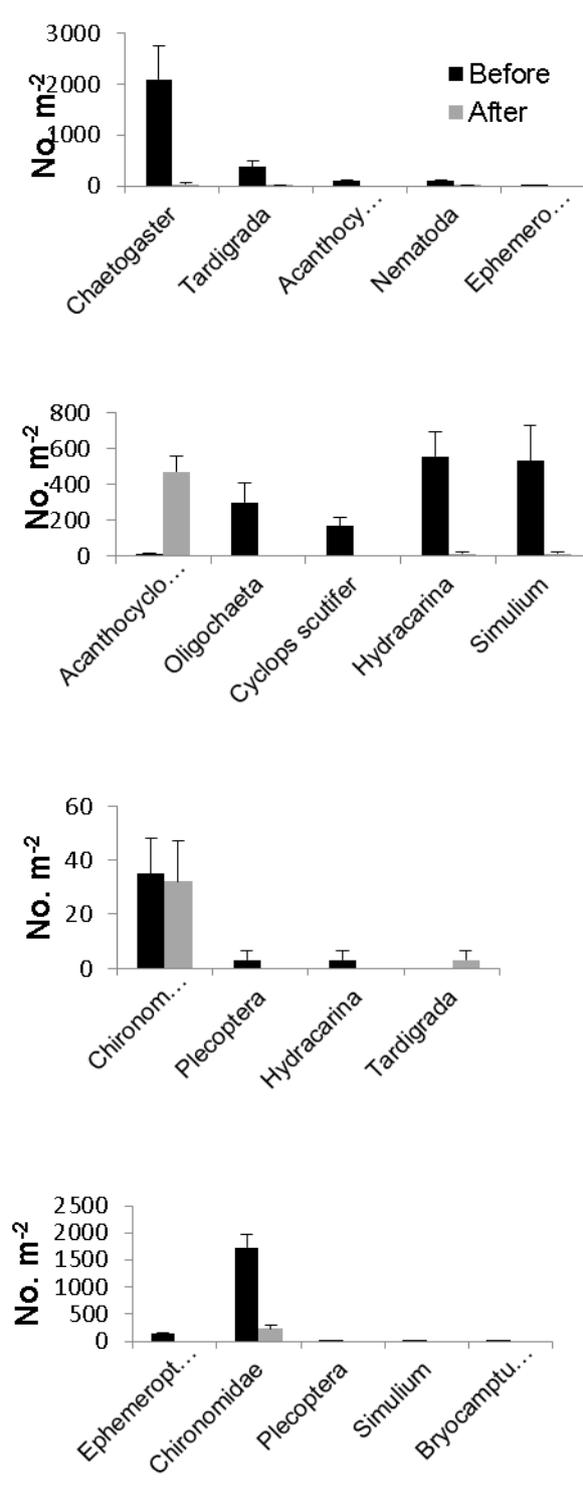
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642 Fig. 4.. A Macroinvertebrates



B Meiofauna

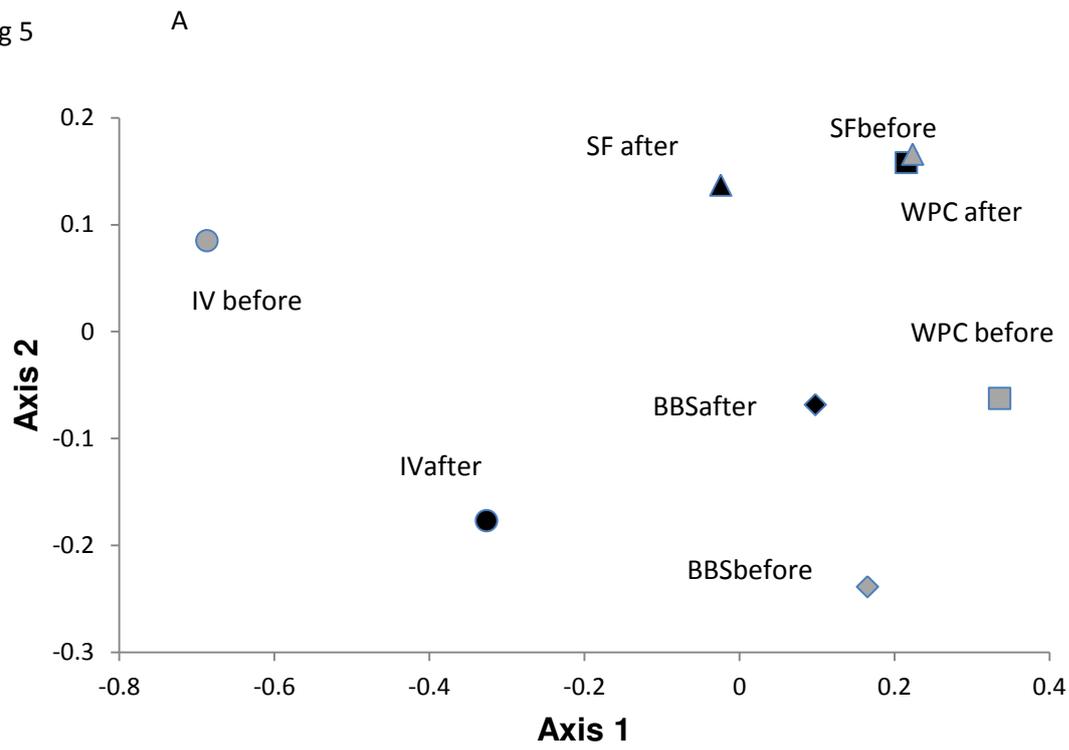


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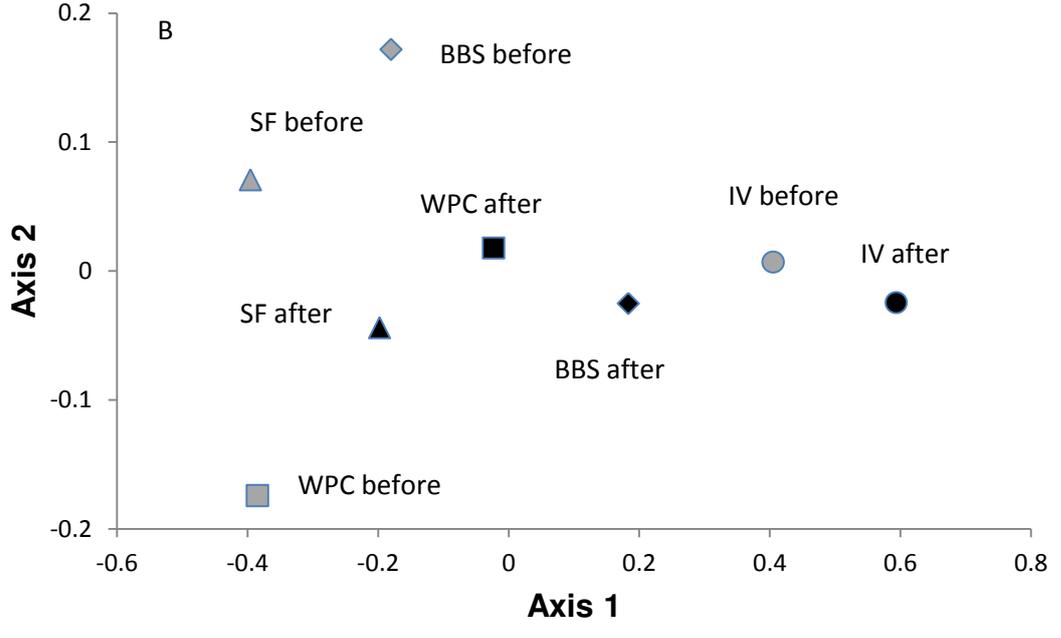
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646 Fig 5



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