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A novel method reveals how channel retentiveness and stocks of detritus (CPOM) vary among streams differing in sediment sizes and channel morphology.

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Running head: A novel method to quantify channel retentiveness in streams

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Summary

1. Coarse detritus (CPOM) is a fundamental resource in freshwater streams, providing food, shelter and habitat for diverse invertebrate taxa and playing a key role in metabolism in low order streams. Benthic CPOM stocks are determined by rates of supply and breakdown of detritus and by channel retentiveness (i.e. the capacity for the channel to trap and retain CPOM). We focussed on factors affecting the retentiveness of channels, which theoretically differs among streams with different channel morphologies and sediment sizes. Such hypotheses have been difficult to test empirically because existing release/recapture methods require time and labour to source, prepare, release and recapture particles, and the data infer retentiveness rather than measuring it directly.
2. We developed a new, rapid method to measure retentiveness using line-intercept surveys along transects. With this rapid approach we surveyed a large number of sites across multiple stream types and tested the simple hypotheses that: (1) retentiveness increases in channels with increasing channel roughness (i.e. sandy vs gravel vs cobble-bed streams); (2) different types of channel features (e.g. log jams, cobbles, depositional areas) differ in the efficiency with which they retain CPOM. The line-intercept survey method, common in studies of terrestrial plants, was readily adapted to measure retentiveness as m of retentive structure per m of transect (i.e. the Linear Coverage Index) and trapping efficiency as m of CPOM per m of retentive element, for 10 different types of retentive elements.
3. Surveys were conducted in Victoria, southeast Australia, at 32 sites with sand (smooth channels, n = 10), gravel (intermediate roughness, n = 12) and cobble (rough channels, n = 10) substrata. Unexpectedly the retentiveness of channels did not increase with channel roughness and comparing the trapping efficiencies of different retentive elements revealed why this was the case. Retentive structure in cobble sites was dominated by cobbles themselves, which were highly retentive in other studies but poorly retentive in our system. Gravel and sand sites had more log jams and depositional areas, such as pools and backwaters, and these features were more effective at trapping CPOM. Thus, retention of CPOM was highest in gravel and sand sites.

66 4. Our method provides a new tool for investigators testing hypotheses about CPOM
67 retention in streams. The method is rapid, requires a minimum of equipment and
68 personnel, and may be applied in any wade-able stream. Retentiveness is calculated in
69 intuitive units that are directly comparable among sites and may have utility as
70 variables in models of CPOM dynamics. We hope this method will open up new
71 avenues for research that may shed light on how CPOM stocks vary among streams,
72 with implications for diversity of aquatic fauna and ecosystem functions like
73 decomposition.

74

75 **Key words:** channel roughness, leaf transport, log jams, organic matter, retentiveness

76

77

78 **Introduction**

79 Terrestrially sourced plant detritus (CPOM: e.g. wood, leaves) is a key resource for
80 invertebrates in many streams, particularly those where in-stream algal growth is low
81 (Webster *et al.*, 1999; Graça, 2001). Some species directly consume wood (McKie &
82 Cranston, 1998) or leaves or scrape biofilms that develop on detrital surfaces (Graça, 2001).
83 Alternatively, CPOM can provide living space, such as hard surfaces for filter-feeders (Craig
84 & Chance, 1982) to attach to and shelter from predation and extreme events (floods and
85 droughts, e.g. Gurtz *et al.*, 1988). Furthermore, the breakdown and assimilation of CPOM is
86 crucial to the metabolic integrity of low-order streams (Cummins, 1974; Cummins *et al.*,
87 1983; Vannote *et al.*, 1980). Thus the retention of stocks of organic matter in streams is an
88 important property to assess.

89

90 Unfortunately, the study of organic matter retention in streams is a rather confused area
91 because various terminologies are used to describe the same or subtly different processes. For
92 example, “CPOM loading” and “retention” have been used interchangeably in the literature
93 with both of these terms sometimes used to mean “CPOM stocks”. It is necessary, therefore,
94 to begin by briefly defining the key processes governing retention and CPOM dynamics in
95 streams, and the terms that we use to describe them (further clarification of these processes is
96 provided in the Supporting Information, Appendix 1). Detritus enters the drift from
97 autochthonous or allochthonous sources (‘supply’) and is carried along until it is trapped and
98 retained by retentive elements within the channel (‘retention’). Retentive elements may be
99 debris dams (Bilby & Likens, 1980), macrophytes and submerged riparian vegetation

100 (Smock, Metzler & Gladden, 1989), bottom substrata such as large boulders and cobbles
101 (Webster *et al.*, 1999) and low flow habitats such as pools (Jones & Smock, 1991) (Table 1).
102 Collectively, we refer to these different types of retentive elements as ‘retentive structure’.
103 The amount and type of retentive structure within a channel determines the ‘retentiveness’ of
104 the channel.

105

106 Highly retentive channels have the potential to trap and retain large stocks of CPOM,
107 however, predicting which streams will have the most CPOM can be difficult because
108 multiple factors determine stocks. For example, allochthonous supplies of CPOM from the
109 surrounding terrestrial vegetation may depend upon vegetation density and types of species
110 present, and whether land clearance has created sparse riparian cover (Wipfli, Richardson &
111 Naiman, 2007; Reid *et al.*, 2008). Stocks may also vary in time, increasing with pulses of
112 supply or decreasing due to invertebrate consumption and microbial breakdown, physical
113 abrasion and fragmentation, burial within the stream bed or export out of channels during
114 floods (Webster, Wallace & Benfield, 1995; Pozo *et al.*, 2011; Jones, 1997). The rates of
115 each of these losses may vary between streams. Retentiveness is best conceived of, therefore,
116 as setting an upper limit on the potential stock of CPOM at a site (Supplementary Appendix
117 1). CPOM stocks may not reach this limit if supply is low or losses are high.

118

119 In this study, we focus on relationships between channel retentiveness and stocks of CPOM
120 to determine how much variation in CPOM stocks among streams may be explained by
121 channel retentiveness and whether this varies among streams with different sediment sizes.
122 For example, streams that have cobble substrata can develop a pool-riffle structure, meaning
123 they have regularly distributed depositional areas, whereas streams with finer substrata may
124 lack regularly spaced channel units but have other depositional bedforms and also some
125 capacity to bury CPOM (Gordon *et al.*, 2004). It is thus difficult to contrast streams of
126 different particle sizes without considering whether concomitant differences in channel
127 morphology also affect CPOM retention.

128

129 A complicating factor is that the current, standard method for quantifying retentiveness
130 measures the transport distances of materials rather than how material is retained and
131 therefore measures retentiveness only indirectly (Watson & Barmuta, 2010). This method
132 involves releasing marked particles (leaves, strips of plastic or paper, dowels or lumber of
133 standard dimensions) upstream of sites and recording their fates (Ehrman & Lamberti, 1992;

134 Jones & Smock, 1991; Speaker, Moore & Gregory, 1984; Webster *et al.*, 1994; Quinn,
135 Phillips & Parkyn, 2007). Retentiveness is inferred from the distance travelled by particles,
136 the proportion of particles retained within sites, or time taken for particles to pass through a
137 site (Speaker, Moore & Gregory, 1984). Properly conducted, these experiments can yield
138 informative comparisons between similar-sized channels that differ in key ways. For
139 example, restored vs channelised streams (Muotka & Laasonen, 2002; Lepori, Palm &
140 Malmqvist, 2005); or streams flowing through catchments vegetated by forest, logged forest,
141 pasture or plantation (Quinn, Phillips & Parkyn, 2007; Webster *et al.*, 1994). However, it is
142 difficult to use the particle release method to draw general conclusions about the processes
143 that govern the accumulation of detritus in streams for several reasons. Transport data reflect
144 short- rather than long-term effects of retentiveness (Speaker, Moore & Gregory, 1984) and
145 thus results are highly dependent upon conditions such as water depths or discharge
146 variability during tests, which can have strong effects on outcomes (Larrañaga *et al.*, 2003;
147 Quinn, Phillips & Parkyn, 2007). Results can also vary between different studies because the
148 travel distances of particles depend on the type of particle used (e.g. Pretty & Dobson, 2004;
149 Hoover *et al.*, 2010) and other confounding variables (Larrañaga *et al.*, 2003; Mathooko,
150 Morara & Leichtfried, 2001). It is also difficult for individual studies to compare large
151 numbers of sites (but see Larrañaga *et al.*, 2003; Quinn, Phillips & Parkyn, 2007), because
152 the method can be laborious and time-consuming.

153

154 The first aim of this study was to develop a new, rapid method to directly measure the
155 retentiveness of stream channels based on the line-intercept method, a standard transect
156 survey procedure (Brower & Zar, 1977). The second aim was to use the rapid method to
157 contrast large numbers of sites on different types of streams to answer two questions: (1) do
158 different densities or types of retentive elements retain different amounts of CPOM on stream
159 beds? (2) do streams that have rough beds (cobble-bed streams) retain more CPOM overall
160 than streams with comparatively smooth beds (gravel- and sand-bed streams)? Large
161 individual particles (e.g. cobbles and boulders) have higher retentiveness than small particles
162 (e.g. gravel or sand) (e.g. Hoover, Richardson & Yonemitsu, 2006; Webster *et al.*, 1994;
163 Larrañaga *et al.*, 2003; Miller, 2013), and consequently bed roughness is assumed to play a
164 predominant role in retention (e.g. Richardson *et al.* 2009). However direct comparisons
165 between streams with wholly different particle sizes and consequent channel morphology are
166 rare.

167

168 **Methods**

169 *Site selection*

170 Surveys were conducted in four catchments (Goulburn Broken, North Central, Port Phillip,
171 and West Gippsland catchments) in central Victoria, Australia (Supporting Information,
172 Appendix 2). We used data from a state-wide assessment of river condition (DELWP, 2010)
173 to identify 100 m long sections of river meeting three criteria: perennial flow; low gradient
174 channels (slope $\leq 2\%$); mean wet width ≥ 3 m. This confined all potential sites to a similar
175 hydrological context. These river sections were mapped (Google Earth) and a shortlist of
176 more than 100 river sections visited and assessed. We selected 32 suitable sites from 22 rivers
177 (Fig. S2). Where multiple sites occurred on the same stream, these were separated by at least
178 5 km of channel length to minimise the likelihood of CPOM transport between sites. We only
179 selected sites from the same stream if they differed substantially in the type of substrata,
180 density of riparian vegetation, or amount of retentive structure present (Supporting
181 Information, Appendix 2, Table S2). Sites found on the same stream were no more similar to
182 each other than sites on different streams so we treated the 32 sites as independent estimates.

183

184 Sites were 100 m long and encompassed multiple channel units (e.g. pools, runs, riffles) in
185 rivers of this size (3.7 m – 17.1 m mean wet channel width, Supporting Information,
186 Appendix 2). By visual assessments of the predominant substrata (sand vs gravel vs cobble,
187 see Table 1 for definitions), we classified sites into three categories: sand sites ($n = 10$);
188 gravel sites ($n = 12$); and cobble sites ($n = 10$). Within each category, sites with a range of
189 riparian vegetation characteristics were represented (Supporting Information, Appendix 2).
190 The riparian environment surrounding sites may influence the supply of wood and detritus to
191 channels, but we wished to conduct general tests of hypotheses by using rivers that span a
192 variety of conditions. Australian streams are surrounded by predominantly evergreen
193 vegetation (Lake, 1995) and so lack an autumn pulse of deciduous leaves. Most leaf fall
194 occurs in summer and some eucalypt species (red gum *E. camaldulensis*, manna gum *E.*
195 *viminalis*) also shed long ribbons of thin flexible bark that can form a large component of
196 benthic CPOM. Peak discharges in the study catchments typically occurs during winter, with
197 lowest discharges in late summer (Kennard *et al.*, 2010). Surveys were conducted in late
198 autumn / early winter (May 05 – June 15) 2017, after summer inputs of CPOM had occurred
199 but prior to high, flushing discharges. Our data thus integrate the effects on benthic CPOM
200 stocks of variation in supply and discharge over summer and most of autumn.

201

202 *Transect sampling: the Line-Intercept method*

203 To rapidly assess the roughness (sediment particle sizes) and retentiveness of river channels
204 we adapted the line-intercept method, which is a standard transect procedure used to measure
205 the density and diversity of terrestrial plants (Brower & Zar, 1977; Kent & Coker, 1994). A
206 randomly placed transect is established that cuts a straight line through the plant community,
207 and the identity and amount (m) of each plant intersecting the transect is recorded.

208 Conveniently, multiple strata (e.g. understorey, overstorey) may be sampled simultaneously
209 along the same transect, allowing the method to be easily adapted to quantify the extent to
210 which stream beds are covered by units of different kinds (e.g. substrata, retentive elements,
211 CPOM). Transects do not sample area to estimate densities of these units, but simple indices
212 may be calculated to provide relative estimates of “linear cover” (Brower & Zar, 1977, and
213 see *Data analysis* below) that can be strongly correlated with areal densities (Kent and Coker
214 1994). Line-intercept methods are used to measure loadings of large wood in streams
215 (Wallace & Benke, 1984; Gippel, Finlayson & Oneill, 1996) but have not, to our knowledge,
216 been applied at finer scales to measure channel retentiveness and retention of CPOM.

217

218 *Surveying substrata, channel retentiveness and CPOM stock*

219 Substrata, channel retentiveness and CPOM stock were all measured along the same transects
220 using the line-intercept method (Fig. 1a-c). At each site we established 15 cross-sectional
221 transects at random locations and recorded the linear cover (m/m of transect) of: (a) three size
222 classes of substrata (sand, gravel, cobble); (b) 10 types of retentive elements; (c)
223 accumulations of CPOM on retentive elements (see Table 1 for a detailed description of each
224 of these variables). Particle size data were used to class sites as either sand sites, gravel sites
225 or cobble sites based on the dominant particle sizes. The linear density (m/m) of retentive
226 elements was used to estimate the retentiveness of the channel at each site (details below).
227 The linear density (m/m) of CPOM was used to estimate the stock of CPOM in the channel at
228 each site. We also noted the type of retentive element upon which each patch of CPOM was
229 retained, to compare whether some types of retentive elements consistently retained more
230 CPOM than others.

231

232 We emphasise that our measure of channel retentiveness is based upon the amount of
233 retentive structure (physical structures and depositional areas, Table 1) within the channel.
234 We surveyed all retentive elements with the potential to accumulate CPOM, whether they

235 contained accumulations of CPOM or not, so measures of retentiveness were independent of
236 our measures of CPOM stocks.

237

238 *Particle sizes*

239 It was not feasible to measure particle sizes in a rapid methodology. Therefore, we used three
240 distinct size classes of particles that may be separated visually in the field (Table 1). The
241 ‘cobbles’ size class includes all particles greater than 128 mm b-axis and therefore includes
242 boulders etc. Particles in this size class were surveyed both as substrata and as potential
243 retentive elements (Table 1, Fig. 1a,b). We did not expect small particles to trap and retain
244 CPOM with regularity but were uncertain where the size threshold between retentive vs
245 unretentive particles might occur. As a starting point, we based our size distinction on data
246 presented by Hoover, Richardson and Yonemitsu (2006), which suggest that leaves drifting
247 through riffles are more likely to be trapped by particles that project ≥ 70 mm into the water
248 column. Small cobbles (b-axis 64 mm – 128 mm, Wentworth (1922)) include particle sizes
249 smaller than 70 mm, so we deemed this size class unretentive and chose large cobbles (b-axis
250 128 mm – 256 mm, Wentworth, 1922) as the minimum size class expected to routinely
251 project 70 mm from the river bed and trap CPOM. Small cobbles were grouped into the
252 unretentive “gravel” size class. We acknowledge that our assumption that cobble beds are
253 more hydraulically rough than sand and gravel sites need not universally be true. Cobble-beds
254 may be hydraulically smooth if the cobbles are rounded, well sorted and embedded in the
255 stream (Gordon *et al.*, 2004), but collecting detailed measures of these variables was beyond
256 the scope of our rapid methodology.

257

258 *Estimating CPOM stocks*

259 Patches of CPOM are three-dimensional, and our linear cover estimates of CPOM may not be
260 related to CPOM densities (g/m^2) if the depth of accumulated CPOM varies in space. We
261 therefore collected additional data using standard methods. CPOM was collected in 35
262 random benthic samples per site (Surber sampler, 30×30 cm frame) and oven dried (105°C
263 for 24 hrs) to estimate CPOM densities in g/m^2 .

264

265 *Data analysis*

266 Linear Coverage Index: Calculating retentiveness and CPOM stocks

267 To estimate retentiveness at each site we calculated the Linear Coverage Index (IC_i) (Brower
268 & Zar, 1977) for all retentive elements:

$$IC_i = l_i/L$$

270 Where L is the summed length of all transects sampled per site and l_i is the summed intercept
271 lengths of all retentive elements per site. Units are in m/m and describe retentiveness as the
272 proportion of the channel cross-section that is occupied by retentive structure. Values of
273 retentiveness greater than 1 m/m are possible in channels where different types of retentive
274 elements overlay one another (see Fig. 1). We used appropriate values of l_i and L to calculate
275 the linear cover of substrata (sand vs gravel vs cobble) and CPOM, and to calculate the
276 trapping efficiency (m of CPOM / m of retentive element – described further below) for each
277 type of retentive element. A list and description of the indices calculated is provided in Table
278 2.

279

280 Trapping efficiency

281 To answer whether different types of retentive elements retain different amounts of CPOM
282 (question 1), we calculated trapping efficiency for each type of retentive element at each site.
283 Trapping efficiency describes how many metres of CPOM were trapped for every metre of a
284 particular retentive element (Table 2) and is computationally equivalent to the mean amount
285 of CPOM trapped on any individual element of that type. Trapping efficiency is higher for
286 elements that trap relatively more CPOM and may vary among sites for a particular retentive
287 element, especially where there are differences in the supply of CPOM.

288 We used one-way ANOVA to test whether mean trapping efficiency differed among the 10
289 different types of retentive elements across the 32 sites. Sites differed in the types and
290 relative abundances of retentive elements present. Sites contained as few as six types of
291 retentive elements (mean 7.8 ± 1.3) and only two types of retentive elements (backwaters,
292 Fine Woody Debris) were present at all sites. Therefore, a broad array of site types and
293 combinations of retentive elements allowed us to assess trapping efficiencies under a wide
294 variety of conditions. Planned contrasts tested two *a priori* hypotheses that: (1) log jams have
295 significantly higher trapping efficiencies than other elements because they are persistent,
296 often span the entire channel width, and are commonly found to trap and retain large amounts
297 of CPOM (e.g. Webster *et al.*, 1994; Jones, 1997); (2) submerged cobbles and macrophytes
298 have lower trapping efficiencies than emergent cobbles and macrophytes, due to larger
299 roughness heights of emergent elements. Additionally, we tested a null hypothesis that wood,
300 deposition and emergent retentive elements have the same trapping efficiency.

301

302 Effective retentiveness

303 Estimates of total retentiveness (m of retentive structure /m of transect) are not informative if
304 different retentive elements have very different trapping efficiencies (which proved to be the
305 case, as reported below). For example, sites with few, but effective, retentive elements might
306 trap more CPOM than sites with large amounts of ineffective retentive elements. It was
307 necessary to weight our estimates of retentiveness to make meaningful comparisons among
308 sites. To achieve this, we calculated the mean trapping efficiency of each type of retentive
309 element across all sites (we call these grand means). Grand means thus estimate overall
310 trapping efficiency over a wide range of conditions (variable supplies of CPOM, densities of
311 retentive elements, stream types) and are consequently independent of conditions at
312 individual sites. To weight our estimates of retentiveness we multiplied the linear cover
313 (m/m) of each retentive element by the grand mean trapping efficiency of that element. For
314 example, suppose that the density of log jams at site x is 0.7 m/m and the relevant grand mean
315 trapping efficiency (i.e. averaged across all sites) is 0.5 m of CPOM per m of log jam. The
316 weighted (effective) density of log jams at the site becomes $0.5 \times 0.7 = 0.35$ m/m. We
317 predicted that such values of effective retentiveness provide a more informative estimate of
318 retentiveness than unweighted values. Both measures of retentiveness are compared in the
319 Results with the expectation that effective retentiveness provides a better prediction of
320 CPOM stocks.

321

322 Comparisons among stream types

323 A key prediction was that retentiveness should be higher in increasingly rough channels.
324 Using one-way ANOVA (followed by Tukey HSD tests), we compared total and effective
325 retentiveness and linear cover of CPOM (m/m) among sand, gravel and cobble sites to test
326 this hypothesis. Additionally, we used linear regression to test for relationships between
327 channel retentiveness (effective retentive structure, m/m) and CPOM stocks (m/m) in each
328 stream type (sand, gravel, cobble). Such relationships may be affected by variability in the
329 supply of CPOM (e.g. Fig S2, Supporting Information, Appendix 1), which was not
330 measured, however linear regression should be adequate to detect any overall trends.
331 Linear regression was also used to test for relationships between linear cover of CPOM in
332 m/m and densities of CPOM in g/m^2 in each stream type. Relationships between the linear
333 cover and density of CPOM at sites should be strongest if CPOM accumulates to a relatively
334 constant depth at each site. Alternatively, large differences among sites in the depth of
335 accumulated CPOM will result in no strong relationship between these variables.

336

337 **Results**

338 *Comparing substrata and retentive structure among stream types*

339 Our visual classifications of sand vs gravel vs cobble sites during site selection were largely
340 borne out by transect estimates of the relative abundances of sand, gravel and cobble
341 substrata, although cobble sites had more gravel than anticipated (Fig. 2). Notably, each
342 stream type was characterised by different types of retentive elements beyond those generated
343 by particle sizes (Fig. 2). Sand sites had more wood than gravel and cobble sites but lacked
344 pools and cobbles entirely. Gravel sites had abundant depositional structure, particularly
345 pools. Cobble sites were dominated by submerged cobble but, other than this element, they
346 contained similar amounts of retentive structure to sand sites and less retentive structure than
347 gravel sites.

348

349 *Trapping efficiency*

350 Averaged across all sites, there were large differences in the mean amounts of CPOM
351 retained by the 10 retentive elements (Fig. 3). Tests of differences in trapping efficiency
352 grouped retentive elements into three distinct sets (Table 3, Fig. 3_{i-iii}) that did not align with
353 the three broad types of retentive elements (wood, deposition, roughness elements). Log jams
354 were highly efficient, trapping more than 2X the amount of CPOM per m than any other
355 retentive element (Fig. 3_i). Submerged cobbles and macrophytes were the least effective
356 retentive elements and were significantly less efficient at trapping CPOM than emergent
357 cobbles and macrophytes (Fig. 3_{ii,iii}). The remaining retentive elements had similar trapping
358 efficiencies (Fig. 3_{ii}).

359

360 *Retentiveness of sites with different channel roughness*

361 Mean densities of total retentive structure were similar in cobble and gravel sites but, as
362 expected, were lowest in sand sites ($F_{2,31} = 7.930$, $P = 0.002$, Fig. 4a, open bars). After
363 weighting these totals by trapping efficiency, the mean densities of effective retentive
364 structure were still highest in gravel and cobble sites and lowest in sand sites, but in this case
365 the latter did not differ from cobble sites ($F_{2,31} = 4.588$, $P = 0.019$, Fig. 4a, solid bars).
366 However, CPOM stocks were lowest in cobble sites, with the highest stocks in gravel sites
367 and sand sites intermediate between these two and not different from either of them ($F_{2,31} =$
368 8.502 , $P = 0.001$, Fig. 4a, grey bars). These results were clarified by comparing the relative
369 abundances of retentive elements with high, medium, and low trapping efficiencies, as
370 determined by ANOVA (i.e. Fig. 3, groups i, ii, iii, respectfully). Sand and gravel sites had

371 mostly retentive elements with medium or high trapping efficiency, and both stream types
372 had relatively small amounts of poorly retentive elements (Fig. 4b, c). In contrast, cobble
373 sites showed large differences in total vs effective retentive structure because they were
374 dominated by retentive elements with low trapping efficiencies (Fig. 4d), comprised chiefly
375 of their submerged cobble substrata (Fig. 2).

376

377 *Retentiveness vs CPOM stocks*

378 Sand bed sites showed a strong relationship between linear cover (m/m) of effective retentive
379 structure and CPOM, whereas cobble and gravel sites did not (Fig. 5a). Across all sites there
380 was a wide range of values for CPOM, particularly at higher values of effective retentiveness,
381 and this resulted in a wedge-shaped distribution of points overall.

382

383 Relationships between linear cover and densities (g/m^2) of CPOM differed by stream type
384 (Fig. 5b). A significant relationship was detected for sand streams, but not cobble sites. A
385 linear relationship for gravel sites was strongly leveraged by two sites with very high
386 densities of CPOM. The regression was not significant with these values removed.

387

388 **Discussion**

389 By applying the line intercept method to survey channel retentiveness, we rapidly collected
390 data from a larger sample of sites and stream types than is typically feasible with existing
391 methods (e.g. particle release methods). For reference, the data presented here were collected
392 by two personnel within the space of three working weeks (about 15 days). This new
393 approach allowed us to compare, empirically, the relative performance of different types of
394 retentive elements in a variety of streams and to test the simple hypothesis that retentive
395 capacity increases with channel roughness.

396

397 *Trapping efficiency of retentive elements*

398 As predicted, the trapping efficiency of log jams was much greater than for all other types of
399 retentive elements. Log jams are relatively large and persistent features and are usually highly
400 retentive (Jones, 1997; Speaker, Moore & Gregory, 1984; Webster *et al.*, 1994) and in this
401 study contained large branches and dense packs of accumulated CPOM. In contrast, trapping
402 efficiency was lowest for submerged roughness elements (cobbles and macrophytes), which
403 contributed surprisingly little to overall retentiveness at most sites. Emergent cobbles and
404 macrophytes were nonetheless effective CPOM traps because CPOM was unable to drift over

405 the top of these structures. Depositional areas (pools, backwaters, banks) were equally
406 effective at retaining detritus as LWD and emergent cobbles and macrophytes, but had more
407 linear cover than the latter elements so contributed a large amount of the effective retentive
408 structure in all stream types.

409

410 It is important to acknowledge that the estimates of trapping efficiency we report for our 10
411 retentive elements may not be the same or even in the same rank order in other studies or
412 systems. Many studies report much better performance of submerged cobbles as retentive
413 structures, but many of these studies are conducted in very small streams where cobbles may
414 constitute relatively large channel features with large roughness heights (e.g. Hoover,
415 Richardson & Yonemitsu, 2006; Miller, 2013; Larrañaga *et al.*, 2003). For example, in
416 small reaches (mean width 1-3 m; mean depth \leq 210 mm) cobble-sized particles projected
417 from surrounding substrata to intercept up to 37 % of the water column in pools and up to 92
418 % of the water column in riffles (Hoover, Richardson & Yonemitsu, 2006). It is not
419 surprising that cobbles were more effective at trapping CPOM in these small systems than in
420 the larger channels that we surveyed.

421

422 Furthermore, the composition of CPOM itself may influence the trapping efficiency of
423 different retentive elements. The eucalyptus leaves which predominate in our study system
424 are relatively stiff and do not fold around objects or plaster onto rocks as readily as do soft
425 deciduous leaves, and this may contribute to the poor trapping efficiency of cobble substrata
426 in this study compared to systems dominated by CPOM with different properties. Larrañaga
427 *et al.* (2003) studied the retention of different types of drifting particles and showed that
428 eucalyptus leaves are less readily retained and travel three times further than the alder leaves
429 and plastic strips that are commonly used in particle release studies. Finally, temporal
430 changes in hydrology may potentially affect the trapping efficiencies of different retentive
431 elements in different ways (Small *et al.*, 2008). For example, in streams of the Agüera basin
432 (Spain) retention of leaves on cobbles and bedrock declined at high discharges, but retention
433 on sand, gravel, boulders and wood increased (Larrañaga *et al.*, 2003). We carried out our
434 research during periods of relatively low flow, and selected sites with gradients of $< 2\%$, but
435 choices of streams across a greater range of gradients and incorporating temporal variability
436 in hydrology may produce different findings.

437

438 These considerations show that trapping efficiencies need to be calibrated for the types of
439 detritus, retentive elements and streams being studied. The line-intercept method enables
440 such research and it will be interesting to see if studies employing this standardised method
441 find consistent patterns in performances of different types of retentive structures in different
442 parts of the world.

443

444 *Retentiveness of channels with different roughness and morphology*

445 In terms of the total amount of retentive structure present within the channel, cobble and
446 gravel sites had more retentive structure than sand bed sites, and this is consistent with our
447 hypothesis that streams with rough beds have greater retentiveness than streams with
448 relatively smooth beds. However, the amount of “effective” retentive structure, weighted by
449 the trapping efficiencies of different retentive elements, was highest for gravel sites and
450 cobble sites were no more retentive than sand bed sites. This contradicts our hypothesis and
451 suggests that effective channel retentiveness does not increase with channel roughness.
452 Stocks of CPOM more closely matched estimates of effective retentiveness than total
453 retentiveness, and were highest in gravel sites but lowest in cobble sites, with sand bed
454 streams intermediate between these two. The reason for the discrepancy between total vs
455 effective retentiveness of cobble sites is that most of the retentive elements in cobble sites
456 were submerged cobbles, which were relatively inefficient at trapping CPOM. Furthermore,
457 cobble sites had low densities of the retentive elements with high trapping efficiencies, such
458 as the pools and log jams that trapped most of the CPOM in sand and gravel sites. It is
459 unclear why cobble sites had fewer log jams but this may reflect the nature or density of
460 riparian vegetation, which supplies both logs and CPOM to streams but which we have not
461 considered in this study. Additionally, rivers were systematically de-snagged across Victoria
462 during the 1900s (Strom, 1962), and perhaps cobble streams were affected more than other
463 types of streams.

464

465 Channel morphology and its interaction with discharge variation affects retentiveness of
466 channel units like pools (Small *et al.*, 2008; Nakajima *et al.*, 2006) and other types of
467 depositional areas. For example, James and Henderson (2005) showed that backwaters
468 (“eddies”) retained different amounts of CPOM in meandering vs straight channel sections.
469 Streams with different particle sizes develop different morphologies (Gordon *et al.*, 2004).
470 Thus riffle-pool sequences are commonest in meandering streams with pea- to boulder-sized
471 bed material. When streams are uninterrupted by bedrock or logs, pools are theoretically

472 spaced regularly along the channel at a frequency of ~ 5-7 channel widths (Gordon et al.
473 2004), which delivers substantial depositional area. In contrast, sand bed streams develop
474 dunes and ripples in complex ways that depend on stream power; these bedforms produce
475 depositional areas between ripples and dunes that are distributed across the stream bed and
476 are not organised into whole channel units like pools (Gordon *et al.*, 2004). Thus the
477 frequencies and areas of depositional places are expected to vary among cobble, gravel and
478 sand bed streams. Our data suggest that, over 100 m lengths, gravel bed streams had more
479 pools (as we defined them) than cobble bed streams, and sand bed streams had more bank
480 depositional areas than either of these two types. Depositional elements were the dominant
481 form of retentive structure in sand and gravel sites, and the most abundant form of effective
482 retentive structure in all stream types. This outcome would not have been revealed by
483 focusing only on the retentive properties of particle sizes and thus emphasizes the necessity to
484 consider retentiveness created by channel morphology alongside roughness elements.

485

486 *Effective retentiveness vs CPOM stock*

487 Only sand-bed sites delivered a convincing relationship between CPOM linear cover and
488 effective retentiveness. A scatterplot of m/m of CPOM vs effective retentiveness across all
489 streams resulted in a wedge-shaped distribution of points. Such distributions can occur when
490 the independent variable (here, retentiveness) limits the maximum value in the dependent
491 variable (CPOM linear cover), but where other variables cause a wide range of outcomes
492 below the maximum. Variability in the supply of CPOM is an obvious source of such scatter
493 among sites that have the same retentiveness. It is possible to test for the existence of limiting
494 relationships using quantile regression (Cade & Noon, 2003) but we refrained from this
495 approach because stream types showed different patterns and grouping these data into a
496 single analysis would be misleading. However, it makes sense to postulate that retentiveness
497 acts by setting maximum limits to benthic CPOM (a matter we will examine in a forthcoming
498 manuscript).

499

500 *Linear cover vs density of CPOM*

501 A strong relationship between the linear cover and density (g/m^2) of CPOM in sand sites
502 suggests that, on average, CPOM accumulates to a relatively constant depth. In contrast,
503 densities of CPOM were unrelated to linear cover estimates in cobble and gravel sites. These
504 patterns reflect probable differences in both the supply and fate of deposited CPOM. For
505 example, in sand sites, CPOM can be fragmented and buried and the metabolism of POM

506 within sand can be rapid (Atkinson *et al.*, 2008), whereas CPOM buried under gravel may
507 break down at a similar rate to CPOM on the riverbed (Smith & Lake, 1993). Relations
508 between areas and volumes of detrital packs are affected also by the intrinsic rate at which
509 materials decompose and/or are eaten by macroinvertebrates, which may vary also among
510 streams or retentive elements. Our streams were surrounded mostly by *Eucalyptus*, but
511 different species decompose at different rates. Thus, *E. viminalis* leaves break down
512 moderately fast while those of *E. camaldulensis* are more slowly broken down (Lake, 1995).
513 Additionally, large, voluminous packs of detritus within pools can house different
514 macroinvertebrates to smaller packs retained in flowing water (Lancaster & Downes, 2014).
515 If the functional composition of invertebrates differs between accumulations of CPOM (e.g.
516 proportions of shredders, scrapers, detritivores) this may also contribute to different
517 breakdown rates. The distribution of CPOM is affected also by the season when it is supplied
518 to streams and whether it is lost from the channel due to raised discharge, which in turn
519 depends on type of retentive element. Thus, in temperate deciduous forest streams in the
520 northern hemisphere, large amounts of CPOM are delivered in a sharp seasonal burst and
521 then metabolized, whereas in Australian streams CPOM inputs are higher in summer but can
522 be almost aseasonal (Lake, 1995). Thus, various factors affect the relation between linear
523 cover and density of CPOM, but whether this matters depends on the question being asked.

524

525 In conclusion, the line-intercept method provides a new approach for testing hypotheses
526 about CPOM retention that is rapid (sites can be completed in hours rather than days) and
527 requires no preparation ahead of time (e.g. particles to release) or special equipment. A wide
528 range of streams can be measured, provided they are wade-able, and the method delivers
529 meaningful units of retentiveness (m of retentive structure / m of channel cross section) that
530 are directly comparable among sites. Models of CPOM dynamics have lacked suitable terms
531 to describe elements of channel complexity affecting retentiveness (Richardson, Hoover &
532 Lecerf, 2009) and our values of channel retentiveness in m/m may be suitable to fulfil this
533 need. We acknowledge that channel retentiveness is just one factor affecting complex CPOM
534 dynamics in streams. Retentiveness may set upper limits to the potential stocks of CPOM in
535 sites, but variations in the supply of CPOM and outputs via export and decomposition will
536 determine the timing and frequency with which these potential stocks are realised.
537 Nevertheless, the value of attaining rapid, meaningful estimates of the potential for stream
538 channels to retain detritus should not be understated and we hope this method will open up
539 new avenues for investigation of the many hypotheses about why some streams retain more

540 detritus than others. Additionally, many stream channels have been straightened and
541 simplified in urban and agricultural environments. Lack of retentiveness has been posited as a
542 major reason for losses of species diversity of invertebrates (e.g. Miller, 2013) or plants that
543 establish via hydrochory (Engstrom, Nilsson & Jansson, 2009). This new method should
544 enable management agencies to rapidly assess whether the retentiveness of degraded streams
545 is poor and therefore consider whether improving retentiveness may improve species
546 diversity.

547

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558 assistance in the field.

559

560 **Data availability**

561 The data that support the findings of this study may be made available by the corresponding
562 author upon reasonable request.

563

564 **Conflict of interest**

565 The authors declare no conflict of interest.

566

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714 **Tables**

715 **Table 1.** Definitions for (a) three classes of substrata particle sizes, (b) 10 types of retentive
 716 elements, and (c) CPOM patches that were recorded along transects. Size classes for mineral
 717 particles are based on classifications by Wentworth (1922). The threshold for wood sizes
 718 were appropriate for wood that arises in streams in south-eastern Australia (e.g. Downes *et*
 719 *al.*, 2006).

Channel feature	Definition
(a) Substrata size classes	
Sand	Particles ≤ 2 mm b-axis (sand, silt, clay)
Gravel	Particles 2-128mm b-axis (this category includes small cobbles 64-128 mm b-axis).
Cobble	Particles ≥ 128 mm b-axis (large cobbles & boulders)
(b) Retentive elements – collectively referred to as ‘retentive structure’	
<i>Wood</i>	
Fine Woody Debris (FWD)	Pieces of wood between 20 mm and 50 mm diameter
Large Woody Debris (LWD)	Pieces of wood greater than 50 mm diameter
Log jams	Accumulations of primarily LWD and FWD spanning part or all of the channel, often damming the channel with associated pools above and/or below (scour pools) the log jam.
<i>Deposition</i>	
Pool	Channel sections with slow, depositional flow as evidenced by obvious presence of fine silt on the bed
Backwater	Depositional areas where flows are slowed or reversed by physical structures immediately upstream
Depositional bank	Depositional areas, as evidenced by obvious presence of fine silt, near the bank where flows are slowed by friction with the streambank.
<i>Roughness elements</i>	
<i>Sensu</i> Gordon <i>et al.</i> (2004, p138)	
Cobbles (submerged)	Particles ≥ 128 mm b-axis, which was the minimum particle size expected to retain CPOM in interstices or by direct plastering on to the upstream surface.
Cobbles (emergent)	Particles ≥ 128 mm b-axis, that protrude from the water surface. Emergent elements are expected to catch a higher

	proportion of CPOM, which cannot drift over the top of such elements.
Macrophytes (submerged)	Vascular plants growing entirely beneath the water surface
Macrophytes (emergent)	Vascular plants that protrude from the water surface.
(c) CPOM	Organic particles (leaves, twigs, bark etc.) ≤ 20 mm diameter. Patches of CPOM < 50 mm in diameter were not sampled.

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747 **Table 2.** Various values of l_i and L were used to calculate the Linear Coverage Index ($IC_i =$
 748 l_i/L) for multiple features along the three transect strata (Fig. 1 a-c). Trapping efficiency was
 749 calculated using the same formula, but with l_i and L summed across all sites to estimate the
 750 grand means. Values of linear cover for retentive elements were then weighted by trapping
 751 efficiency to calculate the m of “effective” retentive structure per m of transect, which we
 752 propose is an informative measure of channel retentiveness.

Summed (per site) intercept lengths of...		
Statistic	l_i	L
Linear cover		
(a) Substrata	Sand, gravel or cobble	All transects
(b) Retentiveness (total)	All retentive elements	All transects
(c) CPOM stock	Patches (> 50 mm diameter) of CPOM	All transects
Trapping efficiency*	CPOM on a particular retentive element (summed across sites)	That retentive element (summed across sites)
Retentiveness (effective)	All retentive elements weighted by their grand mean trapping efficiencies	All transects

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769 **Table 3** Results of one-way ANOVA comparing the trapping efficiency (m of CPOM / m of
 770 retentive structure) of the 10 retentive elements including planned contrasts (numbered) that
 771 test *a priori* hypotheses that: (1) Log Jams are more retentive than other elements (excluding
 772 submerged elements with expected low trapping efficiencies); (2) submerged cobbles and
 773 macrophytes are less retentive than emergent cobbles and macrophytes; (3-5) A null
 774 hypothesis that wood, deposition and emergent retentive elements have the same trapping
 775 efficiency.

	SS	df	MS	F	p
Between Retentive elements	9.400	9	1.044	14.981	< 0.001
1. Log Jams vs All (except submerged)	17642.830	1	17642.830	73.512	< 0.001
2. Submerged vs Emergent elements	5309.657	1	5309.657	22.124	< 0.001
3. Wood vs Deposition elements	523.004	1	523.004	2.179	0.141
4. Wood vs Emergent elements	71.827	1	71.827	0.299	0.585
5. Deposition vs Emergent elements	138.054	1	138.054	0.575	0.449
Error	16.733	240	0.070		
Total	26.133	249			

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789 **Figure captions**

790 **Fig. 1** Cross section of a hypothetical river channel (wetted channel only). Along cross-
 791 sectional transects (0 m – d m, where d is the distance covered by the transect) we surveyed
 792 the intercept lengths (m) of: (a) each type of substrata; (b) different types of retentive
 793 elements (dark grey); (c) accumulations of CPOM (light grey). Note that cobble substrata (\geq
 794 128 mm) were recorded both as substrata and as potential retentive elements (see Table 1).
 795 Intercept lengths for each item (i.e. m of transect crossing each item) in the hypothetical
 796 channel are depicted below the figure. Summing the intercepts for a particular item across all
 797 transects in a site (l_i), and dividing by the summed length of transects (L), provides an
 798 estimate of linear cover (m of item / m of transect) that may be used to calculate the
 799 retentiveness of streams, CPOM stock, and trapping efficiency of different types of retentive
 800 elements (Table 2). Linear cover is always 1 m/m for substrata but may exceed 1 m/m for
 801 retentiveness if retentive elements may stack on top of one another (e.g. LWD overlaying
 802 cobble).

803 **Fig 2.** For sand, gravel and cobble sites: (LH panels) the relative amounts of sand, gravel and
 804 cobble substrata; (RH panels) relative amounts of 10 retentive elements grouped into three
 805 broad categories (wood, deposition, roughness). Data presented separately for submerged
 806 (sub) vs emergent (em) cobbles and macrophytes. Data are estimates of linear cover (m/m of
 807 transect; error bars ± 1 SE) and sum to 1 for substrata (but not retentive structure), because
 808 substrata are continuous across the channel width.

809 **Fig. 3** Grand mean trapping efficiency (average m of CPOM / m of a particular retentive
 810 element) for each of the 10 retentive elements calculated as the m of CPOM per m of
 811 retentive element, averaged across sites (error bars 95% CI). Trapping efficiency differed
 812 between three groups of retentive elements (i, ii, iii) identified with planned contrasts (Table
 813 3).

814 **Fig. 4** (a) Average linear densities of total retentive structure, ‘effective’ retentive structure,
 815 and CPOM in sand vs gravel vs cobble sites. Different ($P < 0.05$) mean values are denoted
 816 by a & b (post-hoc Tukey HSD) for each factor. (b-d) For sand, gravel and cobble sites, the
 817 average linear densities of total retentive structure; ‘effective’ retentive structure and CPOM
 818 contributed by retentive elements with high, medium and low trapping efficiency (TE) (i.e.
 819 groups i-iii identified by ANOVA in Fig. 3). Error bars 95 % CI.

820 **Fig. 5** (a) Linear cover (m/m) of CPOM per site as a function of retentiveness (linear density
 821 of effective retentive structure) in sand, gravel and cobble sites. Linear regression was
 822 significant for sand streams only ($F = 15.344$, $P = 0.004$, $R^2 = 0.657$). (b) Relationship

823 between densities (gm^{-2}) and linear densities (m/m) of CPOM per site in sand, gravel and
824 cobble sites. Linear regression revealed significant relationships for sand streams ($F =$
825 11.966 , $P = 0.009$, $R^2 = 0.599$) and gravel sites ($F = 9.929$, $P = 0.010$, $R^2 = 0.498$).

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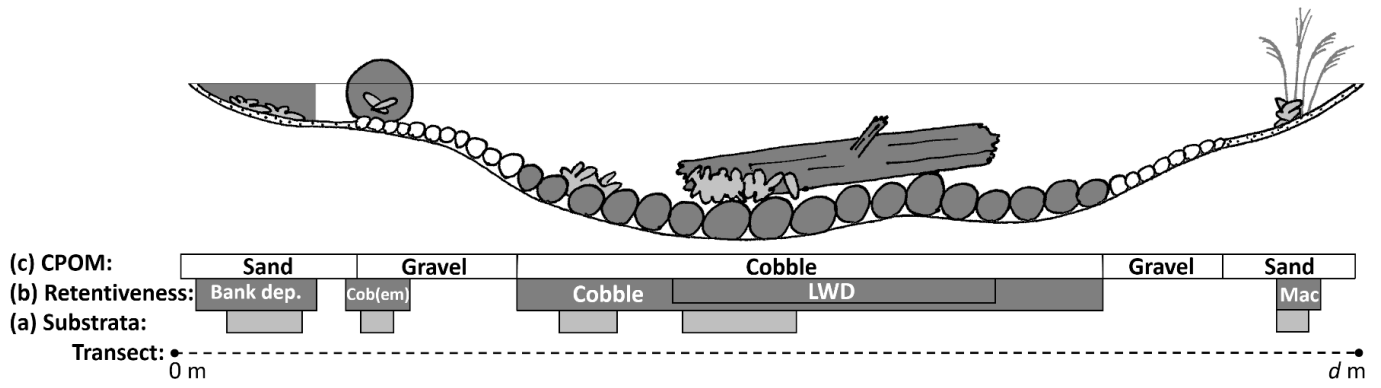


Fig.1

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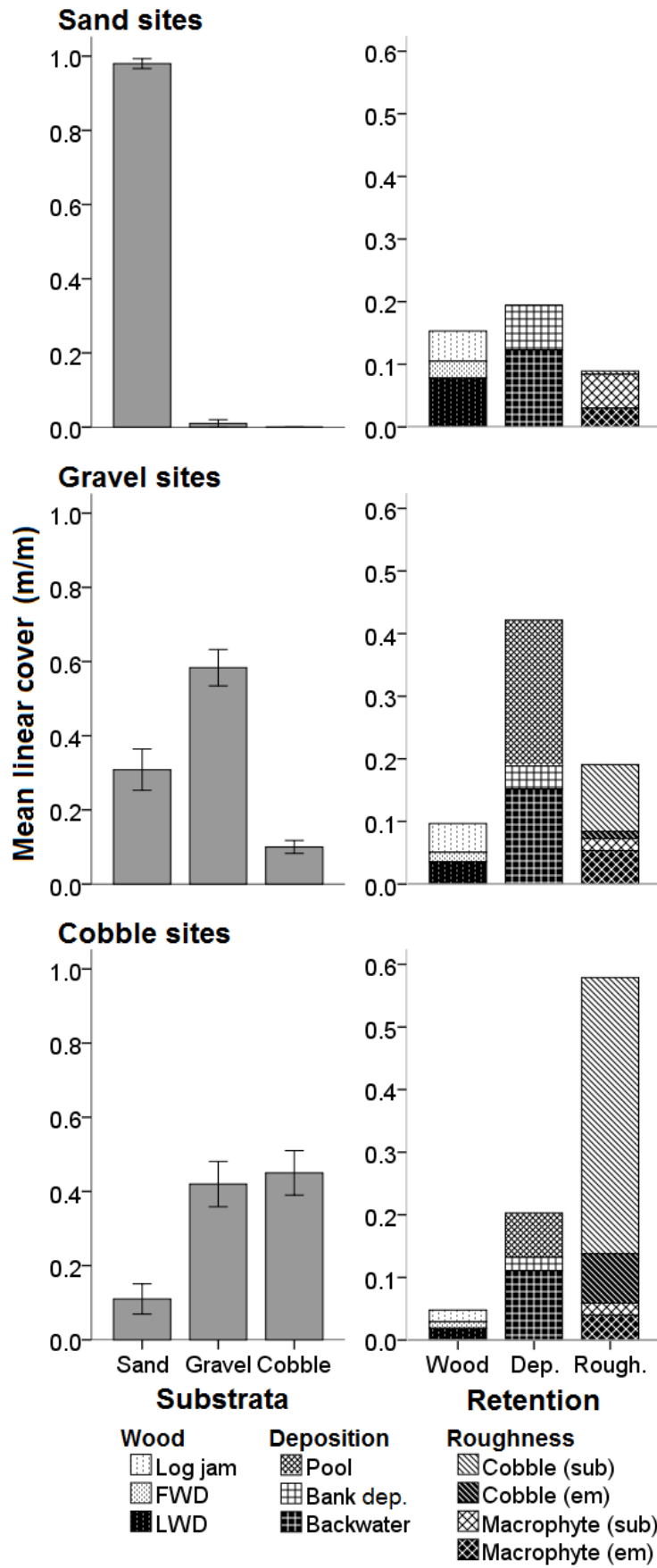


Fig. 2

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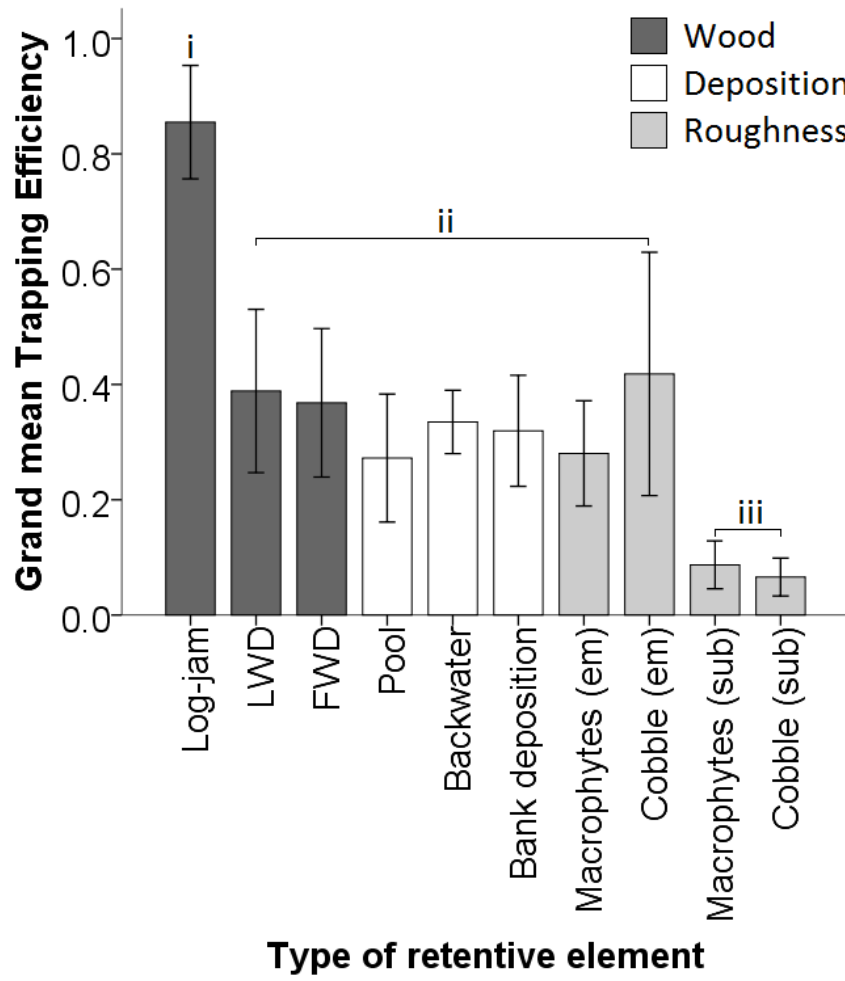


Fig. 3

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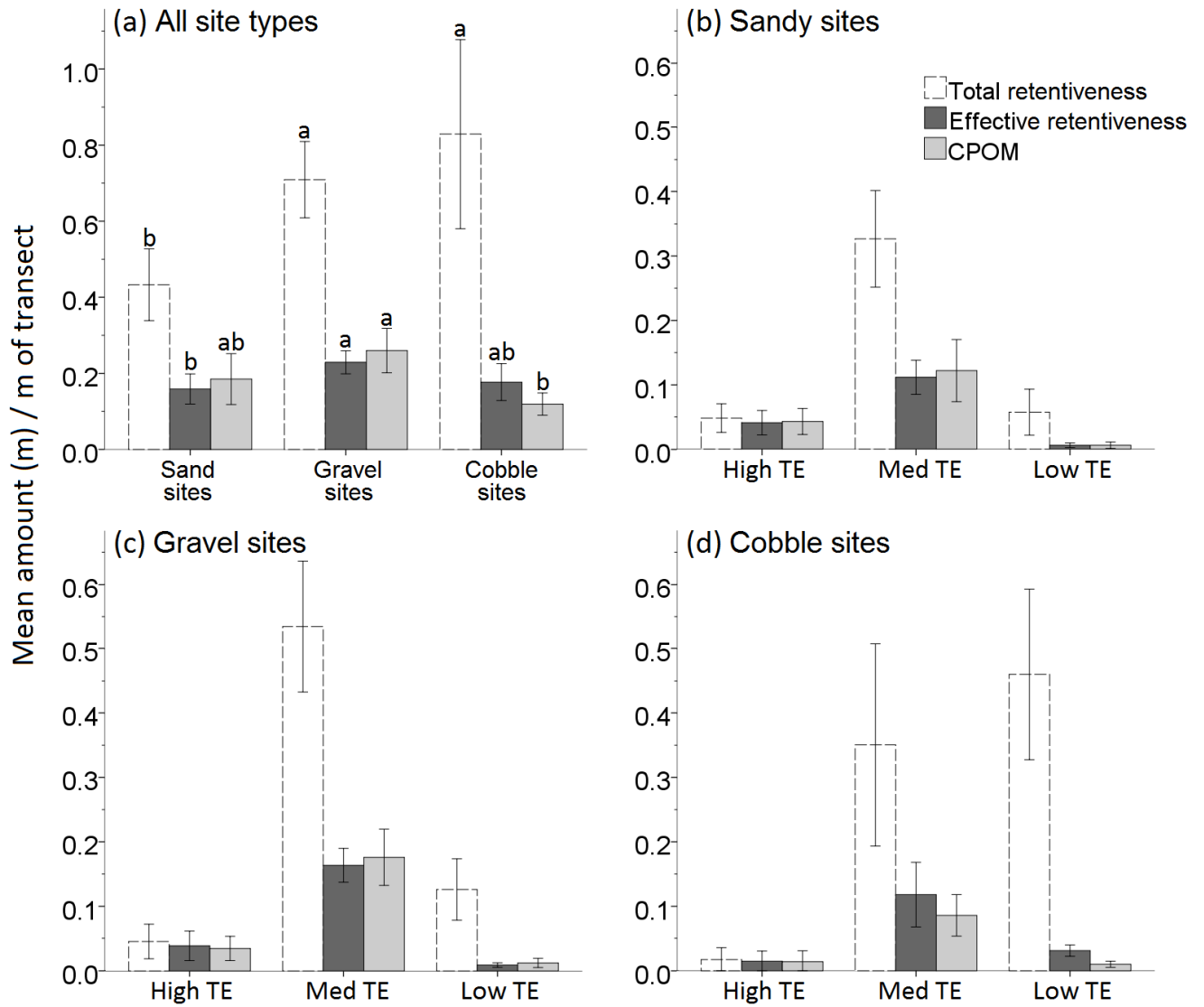


Fig. 4

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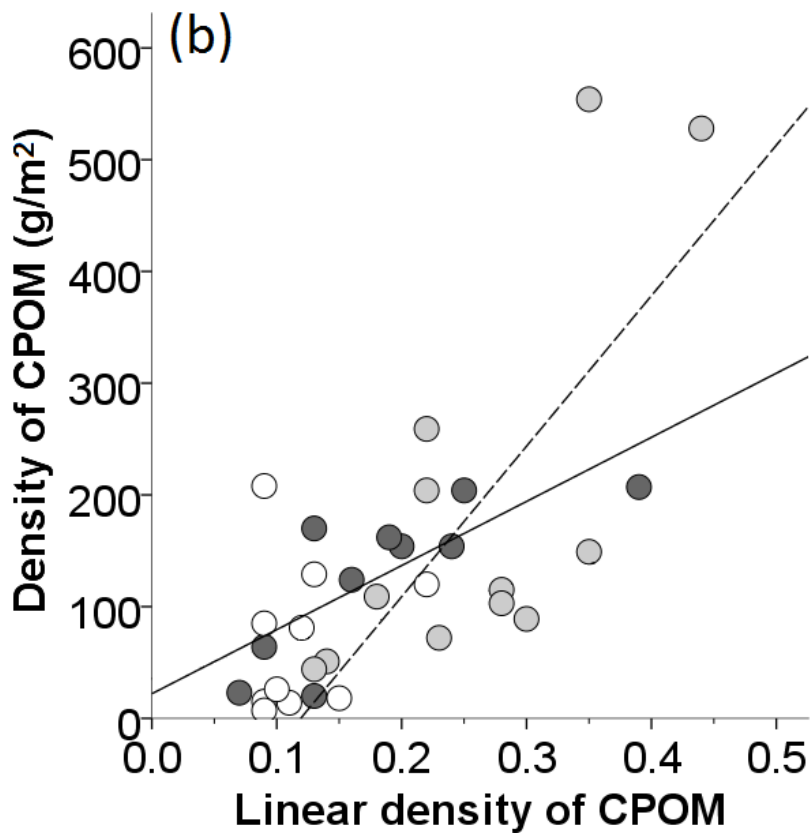
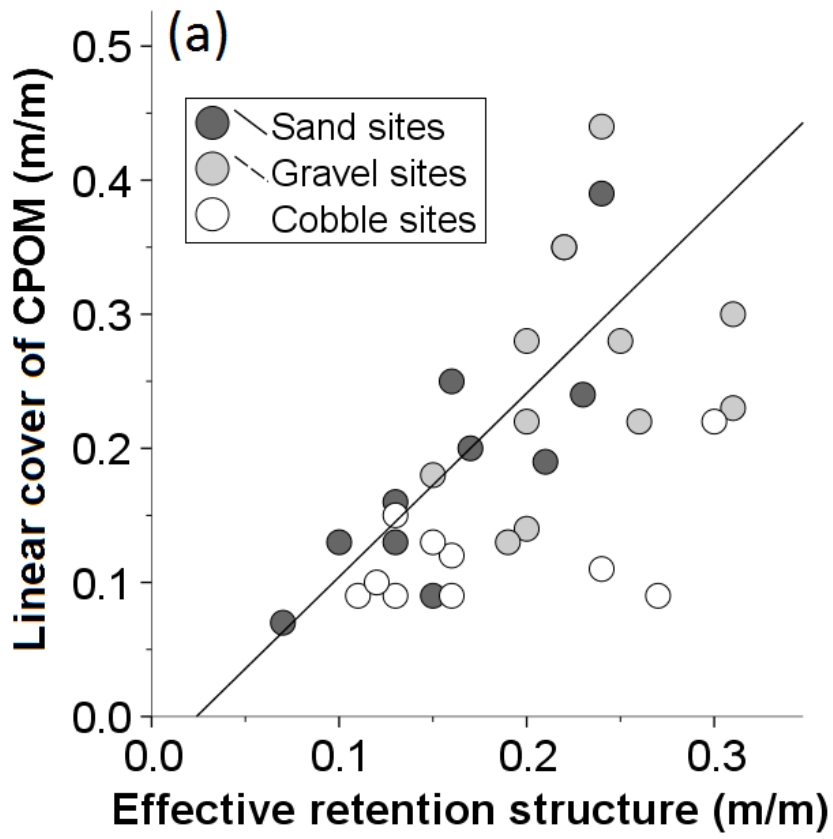


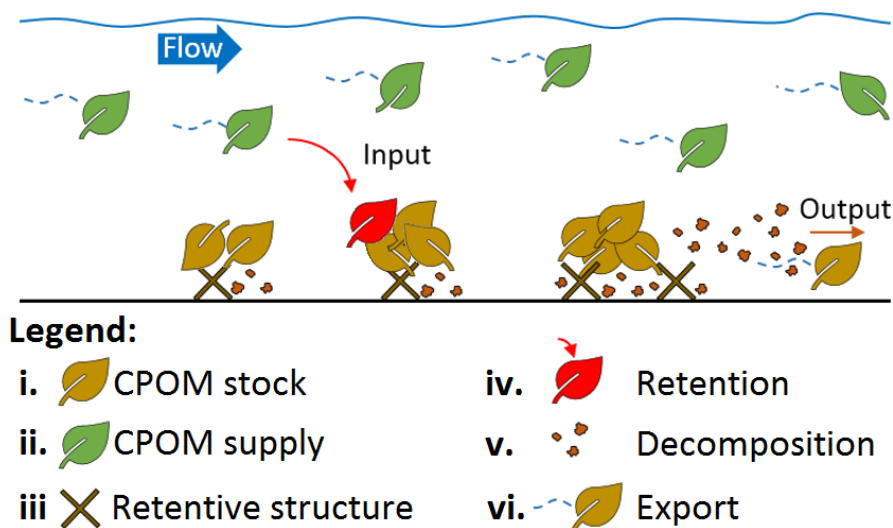
Fig. 5

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914 **Supporting Information**915 **Appendix 1. Definitions of terms**

916 The stock of CPOM at any moment in time is determined by the balance of CPOM inputs
 917 (supply and retention) versus CPOM outputs (decomposition and export/remobilisation
 918 during spates) (Fig. S1). Retention of CPOM is related to the retentiveness of the channel, i.e.
 919 the capacity for the channel to trap drifting CPOM from the water column and retain it in the
 920 benthos. Retentiveness, as defined here, increases with the amount of retentive structure in
 921 the channel (Fig. S1 iv). Although we recognise the effects of other factors (supply,
 922 decomposition, export) on stocks of CPOM (Fig. S1), this study is focused on relationships
 923 between channel retentiveness and stocks of CPOM. We investigate the extent to which
 924 differences in retentiveness may explain differences in stocks of CPOM from site to site (Fig.
 925 S2), and whether this differs between sites with different compositions of substrata.

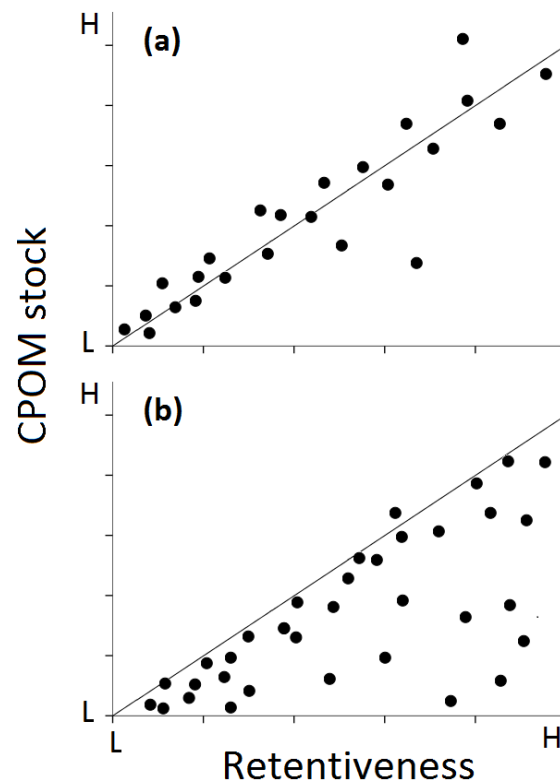
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928 **Fig. S1** Factors affecting the stock of detritus (CPOM) in streams (i). Detritus is supplied to
 929 the water column (ii) and drifts until it encounters retentive structure (iii), such as physical
 930 structures and areas of slow flow. Some portion of the detritus is trapped or retained on the
 931 retentive structure (iv), increasing the stock of CPOM. In time the CPOM is decomposed and
 932 either assimilated or buried within the site or transported downstream (v). Changes in
 933 hydrology may also cause CPOM to be re-entrained in the water column and exported
 934 downstream (vi). The stock of CPOM on a riverbed is, therefore, highly dynamic and may
 935 vary through time and space with changes in inputs (ii, iv), outputs (v, vi) and channel
 936 retentiveness (determined by the amount of retentive structure, iii).

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939 **Fig. S2** Channels with high retentiveness (large amounts of retentive structure) have potential
 940 to store larger stocks of CPOM than channels with low retentiveness. If inputs (supply,
 941 retention) and outputs (export, decomposition) are relatively constant, stocks of CPOM are
 942 expected to be higher in channels with higher retentiveness (a). In practice, however, sites
 943 with high retentiveness may nevertheless have poor CPOM stocks if supply is low and/or
 944 decomposition and export rates are high. The relationship between channel retentiveness and
 945 stocks of CPOM is, therefore, best conceived as a limiting one as depicted in (b), with a line
 946 describing the potential stock of CPOM for increasing values of retentiveness fit to the top of
 947 wedged shaped distribution of points. Such relationships may be modelled using quantile
 948 regression (Cade & Noon, 2003).

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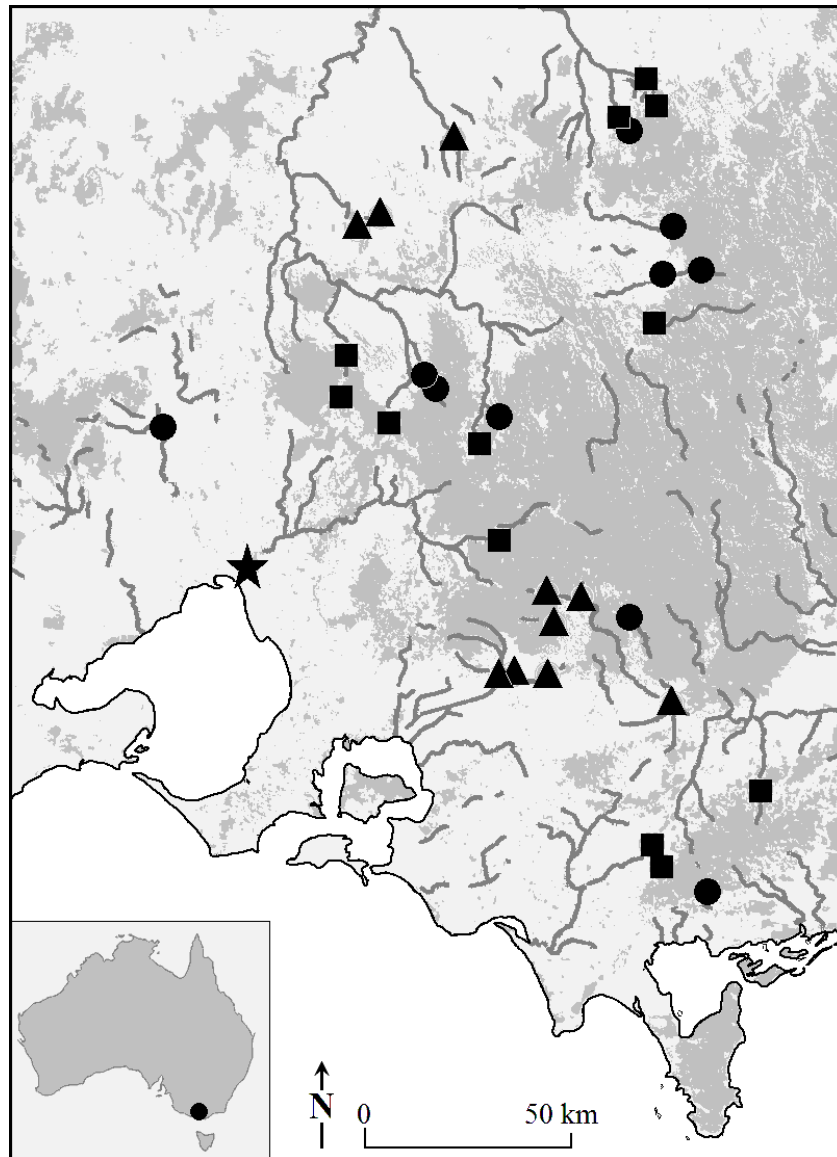
957 **Table S1** Glossary of key terms used in this article, with some synonymous terms that are
 958 used in other studies.

Term (<i>synonyms</i>)	Description	Measurement
CPOM supply	The amount of CPOM entering the water column from allochthonous or autochthonous sources.	
CPOM stock (<i>CPOM loading, retention</i>)	The amount of CPOM held within in the channel.	<i>Linear cover:</i> m of CPOM / m of transect <i>Density:</i> g of CPOM / m ²
Retention (<i>entrapment/trapping of CPOM</i>)	The act of a piece of CPOM becoming trapped by a retentive element (below) and retained within the site.	
Retentive elements	Different types of channel features and structures within the channel that have capacity to retain CPOM (e.g. logs, cobbles, backwaters, macrophytes).	
Retentive structure	A collective term for retentive elements of different types.	
Trapping efficiency	An estimate of how efficient each type of retentive element is at trapping and retaining CPOM.	m of CPOM retained / m of retentive element, averaged across all sites. Returns values from 0 – 1.
Effective retentive structure	The amount of retentive structure at a site, weighted by trapping efficiency, to describe the amount of retentive structure that is expected to trap CPOM.	At each site: Sum of the linear covers (m/m) of each type of retentive element, multiplied by the respective mean trapping efficiencies of each type of retentive element.
Retentiveness	A measure of how effective a channel is at trapping and retaining drifting	We estimate retentiveness as ‘the amount of effective

(*retentivity, retention capacity*) CPOM. Sometimes called ‘retention capacity’ because retentiveness sets an upper limit on the amount of CPOM that may be retained within a site (see Fig S2). retentive structure within a channel’.

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Fig. S2 Map of survey sites located east of the city of Melbourne (star) in Victoria, southeast Australia (inset). Shown are the population of stream sections meeting prerequisite conditions of slope, width and perennial flow (see methods). Forested areas are shaded dark grey. We surveyed sand sites (triangles), gravel sites (squares) and cobble sites (circles). Within each category, sites varied in the quantity, quality and composition of riparian vegetation (Appendix 1).