River Research and Applications

Assessing the mechanistic basis for fine sediment biomonitoring: Inconsistencies among the literature, traits and indices

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1   **Assessing the mechanistic basis for fine sediment**

2   **biomonitoring: Inconsistencies among the literature,**

3   **traits and indices**

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1

17   **Abstract**

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19   Classification of species sensitivity for biomonitoring has been approached

20   under two different frameworks, using either empirical data or expert opinion.

21   Two tools for fine sediment (i.e. clogging, colmation) biomonitoring in the United

22   Kingdom tend towards these contrasting approaches. The Proportion of

23   Sediment-sensitive Invertebrates (PSI) index was developed using expert

24   judgement. Empirical weightings were subsequently added at genus or species

25   (EPSI) and mixed ($EPSI_{mixed}$) taxonomic levels but scores remain constrained by

26   the original categories. In contrast, the Combined Fine Sediment Index (CoFSI),

27   composed of separate taxon scores along organic matter (OFSI) and total fine

28   sediment (ToFSI) gradients, was developed using a purely empirical approach.

29   We tested the mechanistic bases for these indices by relating taxon scores to

30   species traits. We compared the results with those for the well-established

31   Walley Hawkes Paisley Trigg (WHPT) index of organic pollution. After

32   controlling for varying sample sizes, WHPT could be better predicted by a linear

33   combination of all available traits (mean $R^2=0.92$) than any of the fine sediment

34   indices (0.68<mean R^2<0.76). When only traits expected to respond to fine

35   sediment were offered as independent variables, the goodness-of-fit was

36   substantially reduced for all fine sediment indices (0.27<mean R^2<0.46). Our

37   findings demonstrate the lack of integration between the literature on

38   macroinvertebrate responses to fine sediment, the available trait data, and taxon

39   scores. Refinement of the trait database is recommended to build on the valuable

40   work done to date. Since the United Kingdom has taken the lead in embedding

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41   fine sediment into routine biomonitoring programmes, these findings have

42   important international implications.

43   **Introduction**

44

45   Classifications of sensitive or tolerant species have long been used to monitor the

46   aquatic environment (e.g. Kolkwitz & Marsson, 1909). Worldwide, this activity

47   has been undertaken within two very different frameworks: on the one hand

48   using an objective, data-driven approach to locate taxa along a stress gradient

49   (e.g. Whittier & Hughes, 1998; Pirhalla, 2004; Murphy et al., 2015), and on the

50   other hand through relying on expert judgement to assign scores to taxa based

51   on existing information about their sensitivity or tolerance to the stressor of

52   interest (e.g. Armitage et al., 1983; Barbour et al., 1999; Extence et al., 2011). A

53   current debate about biomonitoring for fine sediment in the United Kingdom

54   rests on the contrast between these two approaches. Resolving this debate has

55   important consequences for the practice of biomonitoring throughout Europe

56   and other regions of the world, where pressure-specific indices for fine sediment

57   have yet to be widely developed.

58

59   Fine sediment is a particularly pervasive stressor of river ecosystems, with

60   adverse impacts arising from its accumulation within substrata (*i.e.* clogging,

61   colmation) and its transportation in suspension (Wood & Armitage, 1997; Bilotta

62   & Brazier, 2008; Jones et al., 2012). Negative impacts are evident at all trophic

63   levels, from primary producers (Van Nieuwenhuyse and LaPerriere, 1986; Klco,

64   2008) to top predators relying on visual searching behaviour (Gardner, 1981;

65   Berkman and Rabeni, 1987). This is of particular concern in sport fish spawning

66   gravels which are directly affected by the reduction in suitable spawning habitat,

67   smothering of redds and reduced overwintering and fry emergence, in addition

68 to indirect impacts related to prey abundance (Sear et al., 1993; Kemp et al.,

69 2011; Relyea et al., 2012). It is now a primary research area for many freshwater

70 ecology and environmental engineering groups around the world. In Europe, this

71 is partly a result of the focus brought by the implementation of the Water

72 Framework Directive (WFD), leading to the realisation that fine sediment is an

73 important and widespread cause of ecological deterioration linked to drivers as

74 diverse as agriculture, urbanisation, flood management and flow regulation

75 (Collins & Anthony, 2008; Taylor & Owens, 2009; Acreman & Ferguson, 2010).

76

77 Authorities in the United Kingdom use a macroinvertebrate community index

78 known as Walley Hawkes Paisley Trigg (WHPT) for WFD status classification.

79 WHPT scores taxa based on their occurrence (presence-absence) or assigns a log

80 abundance-weighted score in one of four categories (1-9; 10-99; 100-999; and

81 >999 individuals). WHPT evolved from the Biological Monitoring Working Party

82 (BMWP) method, in which taxa were attributed organic pollution sensitivity

83 scores based on expert judgement (Armitage et al., 1983). The index has been

84 refined since the inception of BMWP, most recently by using data-driven

85 optimisation (Paisley et al., 2014). WHPT is among the most well developed

86 biomonitoring tools in the world. This is evidenced by its long history of

87 optimisation and the adoption of the method in many parts of the world (e.g.

88 Diaz et al., 2004; Herman & Nejadhashemi, 2015). This history demonstrates the

89 pioneering role that the United Kingdom has played in index development,

90 something which it continues to do in the context of fine sediment

91 biomonitoring.

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93   Whilst WHPT is a central pillar of WFD classification in the UK, diagnosing the

94   cause of ecological degradation and classifying ecological status more accurately

95   requires the use of a range of pressure-specific indicators. In the United Kingdom

96   there are currently two such groups of indices for fine sediment: those related to

97   the Proportion of Sediment-sensitive Invertebrates (PSI) index; and those

98   comprising the Combined Fine Sediment Index (CoFSI). In the development of

99   the PSI scoring system taxa were subjectively assigned to one of four Fine

100   Sediment Sensitivity Rating (FSSR) categories: (A) highly sensitive; (B) sensitive;

101   (C) tolerant; and (D) highly tolerant, based on a review of existing empirical

102   information primarily published in ecological monographs and identification

103   keys (Extence et al., 2011). Weightings for each taxon were later computed using

104   extensive monitoring data by Turley et al. (2015) at the genus and species levels

105   (EPSI), and by Turley et al. (2016) at mixed taxonomic levels (EPSI$_{mixed}$), to

106   enhance the empirical basis for PSI. However, the resulting scores (%) still

107   remain constrained by the original FSSR categories.

108

109   CoFSI was developed more recently using a highly statistical approach (Murphy

110   et al., 2015) whereby a number of environmental gradients, determined from

111   extensive fieldwork, were reduced to two axes using partial Canonical

112   Correspondence Analysis (pCCA). The resulting axes, describing gradients of

113   total fine sediment (Total Fine Sediment Index; ToFSI) and organic matter

114   (Organic Fine Sediment Index; OFSI), were then used to derive species scores

115   based on their projected position along each axis, followed by calculation of a

116   combined score at the community level. Thus the procedure was entirely data-

117   driven, leaving no room for the use of extensive prior knowledge from the

118   literature. As a result of differences in their development, the two tools (EPSI and

119   CoFSI) often assign different scores to the same taxa (e.g. Figure 1).

120

121   Direct comparison of the two sets of indices (PSI- and CoFSI- related) is

122   challenging due to differences in the methods used in their development. The

123   original PSI index was calibrated using visual estimates of surface fine sediment

124   cover (Turley et al., 2014). In contrast, CoFSI was calibrated using the sediment

125   resuspension technique (Duerdoth et al., 2015). We avoid the pitfalls of direct

126   comparisons by focusing on the mechanistic basis for fine sediment

127   biomonitoring using data on species traits.

128

129   Trait-based approaches to freshwater biomonitoring have been growing in

130   popularity (Menezes et al., 2010; Statzner & Běche, 2010). This is due to

131   methodological advances (Cornwell et al., 2006; Poff et al., 2006; Villéger et al.,

132   2008; Laliberte & Legendre, 2010; Schleuter et al., 2010) and the availability of

133   fuzzy coded data describing species traits (e.g. Tachet et al., 2010). However,

134   attempts to develop robust predictive tools based on trait-environment

135   relationships have been met with frustration (Verberk et al., 2013), and many

136   trait-based approaches to the development of biomonitoring tools are informed

137   by expert interpretation of primary literature rather than any published trait

138   databases (e.g. Extence et al., 2011).

139

140   We assessed the degree to which taxon scores under EPSI and CoFSI are related

141   to species traits drawn from the widely used trait database of Tachet et al.

142   (2010). We considered linear models for each index using a series of traits

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143 describing life-history, morphology, physiology and behaviour as independent

144 variables. As the most well-developed biomonitoring index, we compare the

145 results with models for WHPT. Our objectives were to (i) test the relative

146 performance of the two fine sediment biomonitoring tools with respect to trait

147 associations and against a benchmark provided by WHPT and (ii) test the

148 absolute power of currently available traits to predict taxon scores under these

149 tools. Objective (ii) also included a secondary aim to assess the predictive power

150 of a subset of traits drawn from the literature. We hypothesised that traits would

151 be a better fit to taxon scores under WHPT due to its long history of

152 development, followed by EPSI due to its origin as a trait-driven index, then

153 finally CoFSI as the most empirically-based tool.

154

155 **Methods**

156

157 *Index scores and trait values*

158

159 Taxon scores for WHPT (UKTAG, 2014), empirical weightings for EPSI (Turley et

160 al., 2015) and EPSI$_{mixed}$ (Turley et al., 2016) and taxon scores under CoFSI

161 (Murphy et al., 2015) were taken from their respective sources. We considered

162 models for OFSI and ToFSI scores as well as the combined CoFSI score for each

163 individual scoring taxon (see equation 2 in Murphy et al., 2015). For WHPT we

164 explored separate models predicting scores for presence-absence, the mean of

165 abundance-weighted scores for each scoring taxon, and the high abundance

166 score for each scoring taxon. The results of these alternative models were very

167 similar (Figure A1). We therefore focused on WHPT presence-absence scores for

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168   simplicity in the remainder of our modelling. Prior to the modelling all index

169   scores were centred and standardised in order to aid interpretation of model

170   coefficients.

171

172   Where possible, taxon scores were matched with fuzzy coded trait values from

173   Tachet et al. (2010) as alternative databases were largely incomplete (e.g.

174   Schmidt-Kloiber & Hering, 2015) for 'true' traits, *i.e.* not those reflecting

175   ecological preferences (Statzner & Běche, 2010; Verberk et al., 2013). In

176   instances where index scores were available at a coarser taxonomic level than

177   traits, fuzzy values were averaged across genera or species. This resulted in a

178   total number of taxa for which matched trait data were available of 106 (WHPT),

179   421 (EPSI), 348 (EPSI$_{mix}$) and 95 (CoFSI, OFSI, ToFSI) for the respective indices.

180   Taxonomic resolution for WHPT was family level, whereas fine sediment indices

181   were generally at species level (see supplementary material).

182

183   The complete trait dataset encompassed 63 trait modalities (hereafter referred

184   to as 'traits' for brevity) in 11 trait categories (Table A1). After compiling lists of

185   scoring taxa and their traits separately for each index, individual trait modalities

186   were centred and standardised within a trait category to give equal weights

187   across all trait categories. As some traits describing type of food and feeding

188   mode were moderately correlated ($0.6<r<0.75$) we considered removing the

189   correlated food types. However, since variance inflation factors (VIFs) were low

190   (<2), it was decided to keep the full set of food types. Finally, a subset of traits

191   that are purported to be instrumental in conferring tolerance or sensitivity to

192   fine sediment was selected based on a review of the literature (Table A1).

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Modelling approach

A multiple linear regression approach was taken to predict scores under each

index using a combination of traits. We selected linear parametric modelling

because it gives more readily interpretable results. Furthermore, our literature

review gave no reason to believe that trait relationships would be non-linear. All

analyses were performed in R 3.2.3 (R Core Team, 2015). Goodness-of-fit was

assessed for several sets of models. The first three sets ('global' models) included

all taxa for which scores were available under the respective indices: (i) the

global 'all traits' model using all 63 traits; (ii) the global model 'pruned' using

stepwise selection in both directions (*stepAIC* function, MASS package; Venables

& Ripley, 2002); and (iii) the global 'literature' model using only the subset of 35

traits drawn from the literature (Table A1). For each index, nested global models

were compared using the *anova* function. We did not explore literature-based

models for WHPT.

Due to the bias introduced by inequalities in the number of scoring taxa for each

index, we generated another set of model results by taking 1000 random

samples of 90 taxa: (v) the 'all traits minimum' model; (vi) the 'pruned minimum'

model; and (vii) the 'literature minimum' model. Finally, to assess the sensitivity

of WHPT models to trait averaging at the family level, modelling for the all traits

minimum and pruned minimum scenarios was repeated for 100 random

samples of sub-family level (genus or species) traits within WHPT families, with

50 samples of 90 taxa for each set of sub-family level traits (5000 samples in

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218   total). All sampling was performed without replacement using the *sample*

219   function. In all cases we used R^2 as a measure of goodness-of-fit.

220

221   **Results**

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223   The global 'all traits' and 'pruned' models for WHPT had a higher goodness-of-fit

224   than equivalent models for the fine sediment indices (Table 1). In turn, the

225   goodness-of-fit for global EPSI and $EPSI_{mixed}$ models was substantially lower than

226   for CoFSI, OFSI and ToFSI. However, these results do not allow direct comparison

227   between indices due to variations in the number of scoring taxa, which affects

228   statistical power (Cohen, 1992). When offering only the literature-based traits as

229   explanatory variables the performance of global models for the fine sediment

230   indices was greatly reduced. The global 'all traits' model did not improve

231   predictions significantly ($p > 0.05$), except in the case of the EPSI literature model

232   ($p < 0.02$), *i.e.* in most cases the fit of more parsimonious 'pruned' models was not

233   significantly different to that of the more complex 'all traits' models (Table 1).

234   Thus, we focus primarily on the global 'pruned' models to assess trait-index

235   relationships (Figure 2).

236

237   The WHPT global 'pruned' model retained significant explanatory variables in

238   several trait categories, including aquatic stages, respiration and feeding modes,

239   diet and voltinism (Figure 2a). The global 'pruned' models for EPSI and $EPSI_{mixed}$

240   retained similar sets of traits (Figure 2b-c). The traits most strongly driving

241   species sensitivity under these indices were 'AttachedTemp', 'Shredder', and

242   'Scraper'. Those most strongly indicating tolerance were 'Adult' and 'Flier',

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243   although the latter was not significant (p>0.05). The CoFSI global 'pruned' model

244   retained a different set of coefficients, including several diet-, feeding mode-,

245   locomotion- and resistance- related traits (Figure 2d). The OFSI and ToFSI global

246   'pruned' models shared significant coefficients for traits describing voltinism,

247   ovoviviparity, tegumental respiration and feeding modes, yet the sign of

248   coefficients for these traits was opposite under each index (Figure 2e-f). In

249   general, the OFSI model was more strongly related to traits describing

250   respiration modes.

251

252   No traits were consistently associated with tolerance under all fine sediment

253   indices. Only 'Shredder' was consistently associated with sensitivity. CoFSI and

254   the PSI-related indices also shared strong and significant positive coefficients for

255   'AttachedTemp' and 'Crawler'. 'Scraper' indicated sensitivity in all cases except

256   ToFSI. There were opposite signs in trait-stressor relationships between the two

257   groups of fine sediment indices for 'Small', 'AerialActive', 'Ovoviviparity',

258   'Cocoons', 'Perren' (life cycle duration >1 year), 'OpenWaterSwimmer', 'Parasite',

259   'Predator', 'DeadAnimal' and 'DiapauseDormancy'.

260

261   With regards to the global 'literature' models, several literature-based traits

262   were significant predictors of EPSI and $EPSI_{mixed}$ weightings (p<0.05), whereas

263   relatively few of the traits purported to be important in determining sensitivity

264   or tolerance to fine sediment in the literature were significant predictors of OFSI

265   or ToFSI scores (Table 2, Table A2-A6). There were a number of inconsistencies

266   in the sign of relationships expected from the literature review and those

267   observed in the global literature models (Table 2).

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269   Figure 3 shows goodness-of-fit for the 'minimum' models. These results are

270   directly comparable between indices as they are not biased by variations in the

271   number of scoring taxa. The minimum 'all traits' (Figure 3a) and 'pruned' (Figure

272   3b) WHPT models, which were robust to trait averaging at the family level,

273   performed better than the fine sediment indices. When only traits drawn from

274   the literature review were included as explanatory variables, the goodness-of-fit

275   for all fine sediment indices was again greatly reduced (Figure 3c). After

276   controlling for the number of scoring taxa, the fit of models for alternative fine

277   sediment indices was similar.

278

279   **Discussion**

280

281   A large body of literature is forming around the response of macroinvertebrates

282   to fine sediment (see reviews by Wood & Armitage, 1997; Bilotta & Brazier,

283   2008; Jones et al., 2012). This includes several studies focusing explicitly on

284   species traits (Gayraud & Phillipe, 2001; Wagenhoff et al., 2012; Buendia et al.,

285   2013; Descloux et al., 2014), which have been employed to good effect in a range

286   of other applications, including flow intermittence (Datry et al., 2014),

287   insecticides (Rico & Van den Brink, 2015) and multiple agricultural stressors

288   (Lange et al., 2014). In Europe, these traits are typically drawn from the database

289   of Tachet et al. (2010), which is limited to 63 true traits in 11 categories.

290

291   The aforementioned literature has the potential to contribute towards progress

292   in biomonitoring. However, in the case of fine sediment, our findings

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293 demonstrate the need for more integration of the available trait data, the a priori

294 expectations from the literature, and the scores assigned to taxa under currently

295 available pressure-specific indices. This is evidenced by the relatively poor fit of

296 trait-based models for fine sediment indices, especially when only traits drawn

297 from the literature review were entered as explanatory variables. It is further

298 reinforced by the differences in significant traits retained in models for

299 alternative fine sediment indices.

300

301 Taxon scores under WHPT were strongly related to traits conferring tolerance or

302 sensitivity to organic pollution (Tomanova et al., 2008; Archaimbault et al., 2010;

303 Feio & Dolédec, 2012). WHPT scores were negatively related to taxa with

304 tegumental respiration and aquatic lives strongly skewed towards adult life-

305 stages (*e.g.* Acroloxidae, Dugesiidae) and positively to univoltine shredders (*e.g.*

306 Lepidostomatidae) and taxa with a range of aquatic life stages, including eggs

307 (*e.g.* Gyrinidae). In contrast, few traits with strong and significant coefficients in

308 the models for fine sediment indices could be related to the extant literature on

309 trait-fine sediment relationships. Some traits had coefficients with conflicting

310 signs between the two sets of indices. This is surprising given that both were

311 designed for biomonitoring of the same stressor. Before discussing these

312 differences in detail, it is worth noting two important nuances of the findings

313 reported.

314

315 Firstly, CoFSI, OFSI and ToFSI had a substantially higher R^2 than EPSI and

316 EPSI$_{mixed}$ for the global models (Table 1) but marginally lower for the 'minimum'

317 models (Figure 3). The CoFSI-related indices also had fewer significant variables

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318 than the PSI-related indices in the global literature-based models (Table 2),

319 despite a better fit. This is because the much lower number of scoring taxa under

320 CoFSI meant that the resulting models had a higher type II error rate (Cohen,

321 1992). Secondly, some traits with significant coefficients in the global pruned

322 models (Figure 2) did not have significant coefficients in the global literature

323 models (Table 2). This is because the significance of each coefficient is assessed

324 in the presence of all other independent variables, and the pruned models

325 retained traits that were not included in the literature models.

326

327 Only a single trait ('Shredder') was consistently associated with sensitivity

328 across all five fine sediment indices (PSI- and CoFSI- related). Both Buendia et al.

329 (2013) and Descloux et al. (2014) also found shredders to be relatively sensitive.

330 The mechanism for this may be the burial of leaf litter and/or a reduction in its

331 nutritional quality through inhibition of fungal growth (Febra, 2013). This is

332 similar to the mechanism posited for the sensitivity of scrapers (Brookes, 1986;

333 Suren, 2005; Kent & Stelzer, 2008; Jones et al., 2012; Relyea et al., 2012), which

334 were also consistently associated with sensitivity in all pruned models except

335 ToFSI. The next strongest association with sensitivity across the majority of fine

336 sediment indices was for temporarily attached organisms. However, Descloux et

337 al. (2014) reported this trait to be indicative of tolerance across three rivers in

338 Germany. Buendia et al. (2013) found that temporarily attached taxa were

339 present in sediment-laden tributaries of the River Isábena in the Central

340 Pyrenees but reported no significant correlation. Finally, crawlers were also

341 associated with sensitivity under CoFSI, EPSI and $EPSI_{mixed}$. This is consistent

342 with Buendia et al. (2013), who reported a significant negative correlation

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343   between the prevalence of crawling as a trait and the rank of sites increasingly

344   affected by fine sediment deposition. On the other hand, Descloux et al. (2014)

345   found a consistently significant positive correlation between the relative

346   occurrence of crawlers and colmation.

347

348   Several further traits were inconsistently associated with sensitivity or

349   tolerance, having coefficients with opposite signs under the various indices.

350   These included small taxa (2.5-5 mm), aerial (active) dispersers, ovoviviparous

351   reproducers, parasites, predators, perennial organisms and those with strong

352   resistance traits for cocoons and diapause or dormancy. Some of these

353   inconsistencies may be explained by the use of different calibration techniques

354   under the two sets of indices, i.e. visually assessed surficial sediments under PSI-

355   related indices but quantitative superficial and surficial sediments under the

356   CoFSI-related indices. However, the lack of support for trait-index associations

357   from the literature suggests that this explanation is only partial at best. Instead,

358   such equivocal results suggest that there is a problem in the trait-literature-

359   biomonitoring nexus. The problem may lie with the literature, with the way that

360   traits are described, or with the development of the biotic indices. It is most

361   likely to be a combination of these factors. This likelihood is further reinforced

362   by the fact that our models lacked significant coefficients for a range of other

363   traits purported to important in fine sediment response in the literature (Table

364   A1).

365

366   *Body size*

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368   Small-bodied taxa (<5 mm) are expected to be strongly sensitive to fine sediment

369   due to smothering and restricted dispersal in reduced pore space (Gayraud &

370   Phillipe, 2001; Wood et al., 2001; Wagenhoff et al., 2012; Descloux et al., 2014).

371   However, body size did not feature strongly in our models.

372

373   *Life cycle duration and voltinism*

374

375   Based on the literature, we expected perennial and uni- or semi-voltine taxa to

376   be sensitive and ephemeral and multivoltine taxa to be relatively tolerant

377   (Larsen et al., 2011; Buendia et al., 2013). Semivoltine and perennial taxa were

378   tolerant according to the pruned models for EPSI, $EPSI_{mixed}$ and CoFSI but

379   voltinism traits were associated with either sensitivity (OFSI) or tolerance

380   (ToFSI) under the CoFSI sub-indices, indicating that the combination of axes

381   describing organic matter and total fine sediment under CoFSI may cancel out

382   distinct mechanisms of the fine sediment impact. Only ToFSI had a significant

383   coefficient for any life-history trait (semivoltine, tolerant) among the literature-

384   based models. Ephemeral or multivoltine taxa were not found to be tolerant

385   under any of our models, with the exception of ToFSI. On the contrary, these

386   traits were strongly linked with sensitivity under OFSI.

387

388   *Aquatic life-stages*

389

390   Life-stage can affect an organism's ability to avoid burial and excavate itself,

391   although there is much variability between taxa for a given life-stage (Wood et

392   al., 2001; 2005). Certainly, immotile eggs are expected to be negatively impacted

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393   by fine sediment (Jones et al., 2012) and this was supported in literature-based

394   models for EPSI and EPSI$_{mixed}$. Models for CoFSI and ToFSI indicated that taxa

395   with strong larval life-stages are tolerant, whilst models for EPSI, EPSI$_{mixed}$ and

396   ToFSI indicated the same for adult life-stages. However, the picture is far from

397   clear because of the way fuzzy coded traits are organised, which is a problem

398   when focusing on life-stage. For example, a taxon which is aquatic as an egg,

399   larva, pupa and adult would receive equal fuzzy codes across all four trait

400   modalities. The results for life-stages, therefore, must be seen as representing

401   the level of aquatic specialism rather than the sensitivity of a given life-stage *per*

402   *se*. Advances in trait-based biomonitoring would benefit from ontogenetic

403   information (Statzner & Běche, 2010).

404

405   *Reproduction and resistance*

406

407   There is little information in the literature as to how reproduction and resistance

408   traits are expected to respond to fine sediment. Descloux et al. (2014) found that

409   ovoviviparity was less prevalent at impacted sites and that cocoons and asexual

410   reproduction varied significantly across the gradient of colmation, although the

411   sign of these relationships was not consistent among three rivers. In the pruned

412   models there were significant coefficients for 'cocoons' (EPSI, tolerant),

413   'DiapauseDormancy' (ToFSI, sensitive) and asexual reporoduction (EPSI$_{mixed}$,

414   sensitive). The EPSI and OFSI pruned models indicated that ovoviviparous taxa

415   are tolerant, whereas the equivalent ToFSI model indicated sensitivity for the

416   same trait, again suggesting that the combination of organic matter and total fine

417   sediment gradients under CoFSI may obscure discrete processes.

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Diet and feeding mode

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421   The literature contains a relative richness of information upon which to base a

422   priori expectations for traits describing diet and feeding mode. The majority of

423   this information points to sensitivity of shredders and scrapers due to burial and

424   dilution of food resources and reductions in nutritional quality (Brookes, 1986;

425   Suren, 2005; Kent & Stelzer, 2008; Relyea et al., 2012; Febra, 2013; Doretto et al.,

426   2015), and of filter-feeders due to the clogging of feeding apparatus (Kurtak,

427   1978; Lemly, 1982; Edington & Hildrew, 1995; Strand & Merrit, 1997) as well as

428   a decline in nutritional quality (Nuttall & Bielby, 1973), although the empirical

429   evidence from recent work focusing explicitly on traits is often equivocal on this

430   (Buendia et al., 2013; Descloux et al., 2014). As discussed above, the sensitivity of

431   shredders and scrapers was supported by our findings, but no other consistent

432   relationships between taxon scores and diets or feeding modes were evident.

433

Respiration

435

436   Of the respiration traits available, we expected to find significant associations

437   between taxon scores and tegumental and gill respiration modes. Descloux et al.

438   (2014) reported a significant reduction in tegumental respiration and a

439   significant increase in gill respiration across a gradient of colmation. Buendia et

440   al. (2013) also found that gills conferred tolerance. However, this is

441   counterintuitive as organisms with tegumental respiration are typically

442   associated with tolerance to oxygen depletion, which is characteristic of fine

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443   sediment stress (Tomanova et al., 2008; Larsen et al., 2011; Von Bertrab et al.,

444   2013). On the other hand, organisms with gills have previously been reported as

445   sensitive (Townsend et al., 2008; Larsen et al., 2011) due to abrasion and

446   clogging of the breathing apparatus (Lemly, 1982; Culp et al., 1986; Jones et al.,

447   2012). Gills did not feature strongly in any of our models but tegumental

448   respiration was a significant indicator of tolerance in the literature-based model

449   for EPSI and the pruned model for OFSI. The latter also included spiracle

450   respiration. This reflects the closer association of OFSI with the content of

451   organic matter (Murphy et al., 2015), which is linked to the important role of

452   oxygen availability and sediment quality (Von Bertrab et al., 2013). Tegumental

453   respiration was indicated as sensitive in the ToFSI pruned model, again

454   suggesting that the invertebrate response to organic matter and total fine

455   sediment may be discrete.

456

457   *Locomotion and relation to the substrate*

458

459   Given that locomotion traits describe an organism's habitat use, they should be

460   strongly linked to fine sediment. Indeed, both Buendia et al. (2013) and Descloux

461   et al. (2014) consistently found that open water swimmers, burrowers and

462   interstitial organisms were sensitive. Interstitial organisms in particular are

463   expected to be susceptible to smothering and restrictions to movement with

464   increasing fine sediment (Wood et al., 2005; Jones et al., 2012), yet this was only

465   supported by pruned and literature-based models for CoFSI and ToFSI. Crawlers

466   are not identified in the literature as either sensitive or tolerant, but pruned

467   models for EPSI, EPSImixed and CoFSI strongly indicated sensitivity for this trait.

20

468   Evidence for other locomotion traits in our results and in the wider literature is

469   equivocal.

470

471   *Refining traits for fine sediment biomonitoring*

472

473   Both of our main findings - that (i) the performance of trait-based models for fine

474   sediment indices was inferior to those for WHPT and (ii) that traits retained in

475   the models were inconsistent and difficult to reconcile with the literature - may

476   be partly attributable to the lack of relevant traits in the trait database of Tachet

477   et al. (2010). Our findings suggest the need to build upon the excellent work of

478   Tachet et al. (2010) in the context of fine sediment. We therefore recommend a

479   refined set of traits specifically for fine sediment biomonitoring.

480

481   There is a difference between species that actively forage by swimming in open

482   water (e.g. *Notonecta*) and those that use swimming as an escape strategy but

483   would potentially be impacted by fine sediment deposition (e.g. *Cloeon*), yet both

484   receive fuzzy scores for 'OpenWaterSwimmer' in the trait database. The

485   sensitivity of taxa with fixed eggs (*e.g*. 'IsolatedEggsCemented') depends on what

486   the eggs are fixed to (stones, wood, plants) and where (shallow zone, margin,

487   hyporheic zone). The sensitivity of filter-feeders depends on their ability to

488   excrete excess fines: insect filter feeders (e.g. Simuliidae, Hydropsychidae) are

489   likely to be sensitive whereas lower taxa that able to excrete inert fine matter

490   (e.g. Unionidae, Sphaeriidae) are likely to be tolerant. Crawlers could be

491   sensitive, such as certain Ephemeroptera (Ciborowski et al., 1977; Corkum et al.,

492   1977; cf. Jones et al., 2012) or tolerant, for example Chironomidae and Caenidae,

21

493 who burrow into fine sediment (Jones et al., 2012). Burrowers could also be

494 sensitive or tolerant depending on what they burrow into. Some taxa burrow

495 into fine sediment (e.g. Caenidae, some Sialidae), others in coarser substrata (e.g.

496 Ephemeridae). The same argument applies to other traits describing relation to

497 substrate. Finally, some gills are easily clogged (e.g. Potamanthidae, *Serratella*),

498 others (e.g. Caenidae) are not (Corbin & Goonan, 2010). Physical adaptation in

499 the latter and behavioural adaptation in others (e.g. *Baetis*) confers tolerance to

500 colmation (Buffagni et al., 2009).

501

502 Thus, we recommend the following refinements to the trait database: (i) split

503 open water swimmers into two categories (active foraging, escape); (ii)

504 consolidate several reproduction traits into fixed versus free eggs and include

505 more information on preferred oviposition sites; (iii) split filter-feeder trait into

506 those able and unable to excrete excess fines; (iv) a split involving anatomical

507 and/or behavioural adaptations allowing gill respiration in highly sedimented

508 environments and (v) combine traits describing locomotion and relation to

509 substrate with information on substrate preference. The latter suggestion risks

510 criticism due to the circular nature of using substrate preference to indicate fine

511 sediment stress. However, we argue that these traits do not make sense in the

512 absence of such information, and without sufficient and relevant data on 'true'

513 biological traits (*e.g.* excavation capacity; Wood et al., 2005) substrate preference

514 is the only alternative.

515

516 Our study did not explicitly consider trait interactions, trait combinations and

517 context (*e.g.* ontogenetic, environmental) dependency (Poff et al., 2006). Verberk

22

518 et al. (2013) have suggested that trait-based approaches to biomonitoring should

519 recognise the important trait linkages driven by evolutionary trade-offs (where

520 investment in one trait leaves fewer resources for another), spin-offs (where

521 investment in one trait decreases the cost or increases the benefit of another)

522 and body plan constraints due to fundamental physical and biological

523 developmental limits. Further progress may lie in the search for sets of traits

524 underlying life-history strategies adapted for coping with fine sediment stress.

525

526 **Conclusions**

527

528 Our findings point to a problem in the trait-literature-biomonitoring nexus

529 within the context of fine sediment. This is evidenced by a relatively poor fit of

530 trait-based models for fine sediment indices compared to WHPT, a lack of

531 consistency in the traits indicating sensitivity and tolerance under CoFSI- and

532 PSI- related biomonitoring tools, and equivocality between our results and

533 evidence from the extant literature. We suggest that progress may lie in the

534 refinement of traits for fine sediment applications, building on the valuable

535 compilations of traits previously published.

536

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538

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542

23

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35

837 **Table 1** Goodness-of-fit and ANOVA results for global models. The test evaluates
838 the null hypothesis that the fit of the global 'all traits' model is no better than the
839 fit of the more parsimonious model ('pruned', 'literature').

840

All traits model	n	Pruned model			Literature model		
		R^2	F (*df*)	*p*	R^2	F (*df*)	*p*
WHPT (R^2=0.90)	106	0.88	0.24 (*26*)	0.99	NA	NA	NA
EPSI (R^2=0.36)	421	0.34	0.32 (*32*)	0.99	0.28	1.73 (*26*)	0.02
EPSI$_{mixed}$ (R^2=0.35)	348	0.32	0.44 (*33*)	0.99	0.27	1.46 (*26*)	0.08
CoFSI (R^2=0.70)	95	0.65	0.17 (*31*)	1.00	0.46	1.09 (*25*)	0.40
OFSI (R^2=0.74)	95	0.68	0.24 (*27*)	0.99	0.43	1.58 (*25*)	0.11
ToFSI (R^2=0.66)	95	0.61	0.18 (*25*)	1.00	0.39	1.04 (*25*)	0.45

841

36

842 **Table 2** Expected and observed relationships between traits and taxon sensitivity (↑) or tolerance (↓). (-) denotes non-significant
843 result. Green arrows represent agreement, red disagreement and black where inconsistent results were found in the literature (†).
844 Observed relationships taken from global literature models. See Table A1 for details of the traits and expectations included.
845

Category	Modality	Expected	EPSI	EPSI$_{mixed}$	CoFSI	OFSI	ToFSI
Maximum length (mm)	VSmall	↑	-	-	-	-	-
	Small	↑	↓***	-	-	-	-
	SmallMed	↓	-	-	-	-	-
	Med	↓	-	-	-	-	-
	MedLarge	↑	-	-	-	-	-
	Large	↑	-	-	-	-	-
Life cycle duration	Ephem	↓	-	-	-	-	-
	Perren	↑	↑***	-	-	-	-
Voltinism (number of generations per year)	Semivoltine	↑	-	-	-	-	↓*
	Univoltine	↑	-	-	-	-	-
	Multivoltine	↓	-	-	-	-	-
Aquatic stages	Egg	↑	↑***	↑**	-	-	-
	Larva	↑	-	-	↓*	-	↓*
	Nymph	↓	-	-	-	-	-
	Adult	↓	↓***	↓*	↓*	-	↓*
Reproduction	Oviparity	↑	-	-	-	-	-
	Asexual	↑/↓†	-	-	-	-	-
Resistance forms	Cocoons	↑/↓†	-	-	-	-	-
Type of food	Microorganisms	↑/↓†	-	-	-	-	-
	FineDetritus	↓	-	-	-	-	-
	DeadPlant	↑/↓†	-	-	-	-	-
	Microphytes	↑/↓†	-	-	-	-	-
	Microinvs	↑	-	-	-	-	-

37

Feeding mode	DepsoitFeeder	↑/↓†	-	-	-	-	-
	Shredder	↑	-	↑*	-	-	-
	Scraper	↑/↓†	↑*	↑*	-	-	-
	Filterer	↑	-	-	-	-	-
Respiration	Tegument	↑/↓†	↓*	-	-	-	-
	Gill	↑/↓†		-	-	-	-
Mode of locomotion and relation to substrate	OpenWaterSwimmer	↑	-	-	-	-	-
	Crawler	↑/↓†	-	-	-	-	-
	Burrower	↑	↑*	↑*	-	-	-
	Interstitial	↑	-	-	↑*	-	↑*
	Attached (temporary)	↓	↑***	↑*	↑*	-	-
	Attached (permanent)	↓	-	-	-	-	-

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847   Significance levels: ≤0.05(*); ≤0.01 (**); ≤0.001(***).

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848 **Table A1** Traits used as independent variables. Trait modes in bold indicate
849 inclusion in the subset of traits selected from a review of the literature.
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Category	Mode	Short name
Maximum length (mm)	<2.5	**VSmall[1]**
	2.5-5	**Small[1]**
	5-10	**SmallMed[1]**
	10-20	**Med[1]**
	20-40	**MedLarge[1]**
	40-80	**Large[1]**
	>80	VLarge
Life cycle duration (years)	≤1	**Ephem[2]**
	>1	**Perren[2]**
Voltinism (generations per year)	<1	**Semivoltine[2]**
	1	**Univoltine[2]**
	>1	**Multivoltine[2]**
Aquatic stages	Egg	**Egg[3]**
	Larva	**Larva[3]**
	Nymph	**Nymph[3]**
	Adult	**Adult[3]**
Reproduction	Ovoviviparous and care for young	**Ovoviviparity[4]**
	Free single eggs	IsolatedEggsFree
	Fixed single eggs	IsolatedEggsCemented
	Cemented or fixed clutches	ClutchesFixed
	Free clutches	ClutchesFree
	Endophytic clutches	ClutchesVeg
	Terrestrial clutches	ClutchesTerr
	Asexual reproduction	**Asexual[5]**
Dispersal	Water passive	AquaticPassive
	Water active	AquaticActive
	Areial passive	AerialPassive
	Aerial active	AerialActive
Resistance forms	Eggs, statoblasts	EggsStatoblasts
	Cocoons	**Cocoons[6]**
	Protection against dessication	Housing
	Diapause/dormancy	DiapauseDormancy
	None	NoResistance
Type of food	Fine sediment and microrganisms	**Microorganisms[7]**
	Detritus <1mm	**FineDetritus[7]**
	Plant detritus >1mm	**DeadPlant[8]**
	Living microphytes	**Microphytes[9]**
	Living macrophytes	Macrophytes
	Dead animals >1mm	DeadAnimal

	Living microinvertebrates	**Microinvs[10]**
	Living macroinvertebrates	Macroinvs
	Vertebrates	Vertebrates
Feeding mode	Absorber	Absorber
	Collector-gatherer	**DepositFeeder[7]**
	Shredder	**Shredder[8]**
	Scraper	**Scraper[9]**
	Filterer	**Filterer[11]**
	Piercer	Piercer
	Predator	Predator
	Parasite	Parasite
Respiration	Tegument	**Tegument[12]**
	Gills	**Gill[13]**
	Plastron	Plastron
	Spiracle	Spiracle
	Hydrostatic vesicle	Hydrostatic
Mode of locomotion and relationship to substrate	Flight	Flier
	Surface swimmers	SurfaceSwimmer
	Open water swimmer	**OpenWaterSwimmer[14]**
	Crawling	**Crawler[14]**
	Burrowing	**Burrower[14]**
	Within interstices	**Interstitial[14,15]**
	Attached (temporary)	**AttachedTemp[14]**
	Attached (permanent)	**AttachedPerm[14]**

[1]Small-bodied taxa more sensitive to fine sediment due to restricted dispersal in reduced pore space (Gayraud & Phillipe, 2001; Wagenhoff et al., 2012; Descloux et al., 2014). Larger taxa may also be relatively sensitive (Buendia et al., 2013)

[2]Voltinism reflects ability to recover from disturbance due to fine sediment; ephemeral and multivoltine taxa are tolerant compared to perennial and uni- and semi-voltine taxa (Buendia et al., 2013; Larsen et al., 2011)

[3]Life-stage affects ability to avoid burial (Wood et al., 2001; Jones et al., 2012)

[4]Oviviparity was less prevalent at sites impacted by colmation (Descloux et al., 2014)

[5]Prevalence of asexual reproduction exhibited a significant response to colmation but sign of relationship was inconsistent among three sites (Descloux et al., 2014)

[6]Prevalence of cocoons as a resistance form exhibited a significant response to colmation but sign of relationship was inconsistent among three sites (Descloux et al., 2014)

[7]Diets and feeding modes associated with fine sediment (e.g. Buendia et al., 2013), although effect was not consistent among three sites for fine sediment and microorganisms diet and collector-gather feeding mode (Descloux et al., 2014)

[8]Deposited sediment may limit consumption of plant detritus by shredders (Febra, 2013). Both Buendia et al. (2013) and Descloux et al. (2014) found that shredders were relatively sensitive. However, Descloux et al/ (2014) also found that the prevalence of dead plant diets increased with colmation. Doretto et al. (2015) also found that the abundance of shredders and the availability of coarse particulate organic matter declined with sedimentation in alpine streams.

[9]Fine sediment may bury and dilute algal resources for scrapers (grazers) (Brookes, 1986; Suren, 2005; Kent & Stelzer, 2008; Relyea et al., 2012) yet both Buendia et al. (2013) and Descloux et al. (2014) found that scrapers were relatively tolerant of fine sediment

[10]Prevalence of living microinvertebrate diets decreased with colmation (Descloux et al., 2014)

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876 [11]Filtering apparatus can become clogged, interrupting feeding and possibly causing
877 abandonment (Edington & Hildrew, 1995; Strand & Merrit, 1997). Buendia et al. (2013) found
878 that filterers were sensitive to fine sediment
879 [12]Prevalence of tegumental respiration decreased with colmation in three rivers (Descloux et al.,
880 2014). However, Larsen et al. (2011) found that organisms with tegumental respiration were
881 tolerant of sand addition.
882 [13]Gills can become clogged and abraded (Lemly, 1982; Jones et al., 2012). Townsend et al. (2008)
883 and Larsen et al. (2011) both found that organisms with gills were sensitive to fine sediment.
884 However, both Buendia et al. (2013) and Descloux et al. (2014) found that the prevalence of gills
885 as a respiration mode increased with colmation.
886 [14]Locomotion traits all exhibited significant associations with fine sediment (Buendia et al., 2013;
887 Descloux et al., 2014)
888 [15]Interstitial organisms are susceptible to smothering and hypoxia (Wood et al., 2005).
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891 **Table A2** Results of the 'global literature' model for EPSI.
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	Estimate	**SE**	***t***	***p***
(Intercept)	0.000	0.043	0.00	1.00
VSmall	0.056	0.047	1.19	0.23
Small	-0.222	0.098	-2.27	0.02
SmallMed	-0.045	0.077	-0.59	0.55
Med	0.011	0.075	0.15	0.88
MedLarge	-0.139	0.074	-1.89	0.06
Large	0.019	0.061	0.32	0.75
Ephem	0.145	0.101	1.43	0.15
Perren	0.420	0.125	3.35	0.00
Semivoltine	-0.143	0.087	-1.65	0.10
Univoltine	-0.042	0.089	-0.47	0.64
Multivoltine	-0.065	0.105	-0.62	0.54
Egg	0.189	0.061	3.08	0.00
Larva	-0.053	0.080	-0.66	0.51
Nymph	-0.074	0.086	-0.85	0.39
Adult	-0.514	0.121	-4.26	0.00
Ovoviviparity	-0.095	0.076	-1.25	0.21
Asexual	0.062	0.052	1.17	0.24
Cocoons	-0.049	0.066	-0.73	0.46
Microorganisms	-0.025	0.056	-0.44	0.66
FineDetritus	0.058	0.088	0.66	0.51
DeadPlant	-0.099	0.076	-1.31	0.19
Microphytes	-0.089	0.069	-1.29	0.20
Microinvs	-0.116	0.072	-1.60	0.11
DepositFeeder	-0.060	0.098	-0.61	0.54
Shredder	0.170	0.088	1.94	0.05
Scraper	0.181	0.076	2.37	0.02
Filterer	-0.081	0.131	-0.61	0.54
Tegument	-0.025	0.078	-0.33	0.75
Gill	-0.065	0.077	-0.85	0.39
OpenWaterSwimmer	0.016	0.094	0.17	0.87
Crawler	0.059	0.102	0.58	0.56
Burrower	0.186	0.082	2.26	0.02
Interstitial	0.068	0.059	1.15	0.25
AttachedTemp	0.442	0.144	3.06	0.00
AttachedPerm	-0.078	0.049	-1.59	0.11

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895 **Table A3** Results of the 'global literature' model for EPSI$_{mixed}$.

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	Estimate	**SE**	**t**	**p**
(Intercept)	0.000	0.048	0.00	1.00
VSmall	0.031	0.053	0.57	0.57
Small	-0.187	0.124	-1.51	0.13
SmallMed	0.001	0.091	0.02	0.99
Med	0.014	0.094	0.15	0.88
MedLarge	-0.092	0.081	-1.13	0.26
Large	0.092	0.060	1.53	0.13
Ephem	0.067	0.117	0.58	0.57
Perren	0.086	0.137	0.63	0.53
Semivoltine	0.144	0.100	1.44	0.15
Univoltine	0.051	0.102	0.50	0.62
Multivoltine	0.118	0.113	1.04	0.30
Egg	0.174	0.066	2.64	0.01
Larva	-0.060	0.095	-0.63	0.53
Nymph	-0.007	0.092	-0.08	0.94
Adult	-0.275	0.128	-2.15	0.03
Ovoviviparity	-0.037	0.072	-0.51	0.61
Asexual	0.104	0.059	1.76	0.08
Cocoons	-0.039	0.078	-0.50	0.61
Microorganisms	-0.100	0.064	-1.56	0.12
FineDetritus	0.012	0.085	0.14	0.89
DeadPlant	-0.107	0.075	-1.44	0.15
Microphytes	-0.044	0.081	-0.54	0.59
Microinvs	-0.091	0.081	-1.12	0.26
DepositFeeder	-0.025	0.094	-0.27	0.79
Shredder	0.257	0.092	2.78	0.01
Scraper	0.243	0.089	2.74	0.01
Filterer	0.098	0.112	0.88	0.38
Tegument	-0.101	0.094	-1.07	0.29
Gill	-0.020	0.095	-0.21	0.83
OpenWaterSwimmer	0.058	0.124	0.47	0.64
Crawler	0.193	0.112	1.72	0.09
Burrower	0.154	0.074	2.07	0.04
Interstitial	0.055	0.063	0.87	0.38
AttachedTemp	0.330	0.140	2.36	0.02
AttachedPerm	-0.101	0.057	-1.76	0.08

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900 **Table A4** Results of the 'global literature' model for CoFSI.
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	Estimate	**SE**	*t*	*p*
(Intercept)	0.000	0.096	0.00	1.00
Small	-0.182	0.262	-0.69	0.49
SmallMed	-0.431	0.305	-1.41	0.16
Med	-0.056	0.237	-0.24	0.81
MedLarge	-0.356	0.270	-1.31	0.19
Large	-0.290	0.205	-1.42	0.16
Ephem	0.233	0.251	0.93	0.36
Perren	0.288	0.333	0.86	0.39
Semivoltine	-0.502	0.257	-1.95	0.06
Univoltine	-0.303	0.215	-1.41	0.16
Multivoltine	-0.322	0.262	-1.23	0.22
Egg	0.171	0.173	0.99	0.33
Larva	-0.446	0.209	-2.13	0.04
Nymph	-0.251	0.223	-1.13	0.26
Adult	-0.680	0.331	-2.06	0.04
Ovoviviparity	-0.253	0.213	-1.19	0.24
Asexual	0.201	0.175	1.15	0.25
Cocoons	0.112	0.174	0.64	0.52
Microorganisms	0.241	0.145	1.67	0.10
FineDetritus	0.170	0.240	0.71	0.48
DeadPlant	-0.182	0.165	-1.11	0.27
Microphytes	-0.166	0.195	-0.85	0.40
Microinvs	0.051	0.202	0.25	0.80
DepositFeeder	-0.226	0.259	-0.87	0.39
Shredder	0.140	0.219	0.64	0.52
Scraper	-0.238	0.250	-0.95	0.34
Filterer	-0.376	0.297	-1.27	0.21
Tegument	-0.052	0.216	-0.24	0.81
Gill	0.104	0.175	0.59	0.56
OpenWaterSwimmer	-0.038	0.170	-0.22	0.82
Crawler	0.145	0.266	0.55	0.59
Burrower	0.128	0.175	0.73	0.47
Interstitial	0.359	0.170	2.12	0.04
AttachedTemp	0.735	0.358	2.05	0.04
AttachedPerm	-0.181	0.130	-1.39	0.17

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904   **Table A5** Results of the 'global literature' model for OFSI.
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	Estimate	SE	t	p
(Intercept)	0.000	0.098	0.00	1.00
Small	0.014	0.268	0.05	0.96
SmallMed	-0.038	0.312	-0.12	0.90
Med	0.044	0.242	0.18	0.86
MedLarge	-0.084	0.277	-0.30	0.76
Large	0.024	0.209	0.11	0.91
Ephem	0.490	0.257	1.91	0.06
Perren	0.006	0.341	0.02	0.99
Semivoltine	0.232	0.263	0.88	0.38
Univoltine	0.183	0.220	0.83	0.41
Multivoltine	0.306	0.268	1.14	0.26
Egg	0.053	0.177	0.30	0.77
Larva	-0.064	0.214	-0.30	0.77
Nymph	-0.164	0.228	-0.72	0.48
Adult	0.110	0.338	0.33	0.75
Ovoviviparity	-0.347	0.218	-1.59	0.12
Asexual	0.025	0.179	0.14	0.89
Cocoons	-0.003	0.178	-0.02	0.99
Microorganisms	0.063	0.148	0.42	0.67
FineDetritus	-0.031	0.245	-0.13	0.90
DeadPlant	-0.291	0.169	-1.73	0.09
Microphytes	-0.136	0.199	-0.68	0.50
Microinvs	0.067	0.207	0.32	0.75
DepositFeeder	0.073	0.265	0.27	0.79
Shredder	0.143	0.224	0.64	0.53
Scraper	0.225	0.256	0.88	0.38
Filterer	-0.238	0.304	-0.78	0.44
Tegument	0.012	0.221	0.06	0.96
Gill	0.342	0.179	1.91	0.06
OpenWaterSwimmer	-0.104	0.174	-0.60	0.55
Crawler	-0.093	0.272	-0.34	0.73
Burrower	-0.079	0.179	-0.44	0.66
Interstitial	-0.084	0.174	-0.48	0.63
AttachedTemp	0.192	0.367	0.52	0.60
AttachedPerm	-0.071	0.133	-0.54	0.59

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907   **Table A6** Results of the 'global literature' model for ToFSI.
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	Estimate	**SE**	**_t_**	**_p_**
(Intercept)	0.000	0.101	0.00	1.00
Small	-0.210	0.276	-0.76	0.45
SmallMed	-0.457	0.322	-1.42	0.16
Med	-0.087	0.250	-0.35	0.73
MedLarge	-0.348	0.285	-1.22	0.23
Large	-0.335	0.216	-1.55	0.13
Ephem	-0.016	0.265	-0.06	0.95
Perren	0.316	0.351	0.90	0.37
Semivoltine	-0.689	0.271	-2.54	0.01
Univoltine	-0.440	0.227	-1.94	0.06
Multivoltine	-0.530	0.276	-1.92	0.06
Egg	0.161	0.182	0.88	0.38
Larva	-0.460	0.221	-2.08	0.04
Nymph	-0.187	0.235	-0.80	0.43
Adult	-0.818	0.349	-2.35	0.02
Ovoviviparity	-0.086	0.225	-0.38	0.70
Asexual	0.210	0.184	1.14	0.26
Cocoons	0.126	0.183	0.69	0.50
Microorganisms	0.233	0.153	1.53	0.13
FineDetritus	0.207	0.253	0.82	0.42
DeadPlant	-0.039	0.174	-0.23	0.82
Microphytes	-0.108	0.205	-0.53	0.60
Microinvs	0.020	0.213	0.09	0.93
DepositFeeder	-0.292	0.273	-1.07	0.29
Shredder	0.075	0.230	0.33	0.74
Scraper	-0.392	0.264	-1.49	0.14
Filterer	-0.285	0.313	-0.91	0.37
Tegument	-0.065	0.228	-0.29	0.78
Gill	-0.077	0.185	-0.42	0.68
OpenWaterSwimmer	0.016	0.179	0.09	0.93
Crawler	0.213	0.280	0.76	0.45
Burrower	0.186	0.185	1.01	0.32
Interstitial	0.446	0.179	2.49	0.02
AttachedTemp	0.710	0.378	1.88	0.07
AttachedPerm	-0.161	0.137	-1.17	0.25

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916   **Figure legends**

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918   **Figure 1** Comparison of taxon scores under CoFSI and taxon weightings under

919   EPSI for 71 taxa that score under both indices.

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921   **Figure 2** Coefficients for 'global pruned' models: WHPT (a); EPSI (b); EPSI mixed

922   (c); CoFSI (d); OFSI (e); and ToFSI (f). Note that positive coefficients denote traits

923   associated with sensitivity under each index.

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925   **Figure 3** Goodness-of-fit for 'minimum' models using all traits (a), traits retained

926   after stepwise selection (b) and literature-based traits (c). Symbols indicate

927   means and whiskers show 95% confidence intervals from random sampling.

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929   **Figure A1** Coefficients for 'global pruned' models: WHPT presence-absence (a);

930   the mean of abundance-weighted WHPT scores for each scoring taxon (b); and

931   the high abundance WHPT score for each scoring taxon (c).EPSI (c). Note that

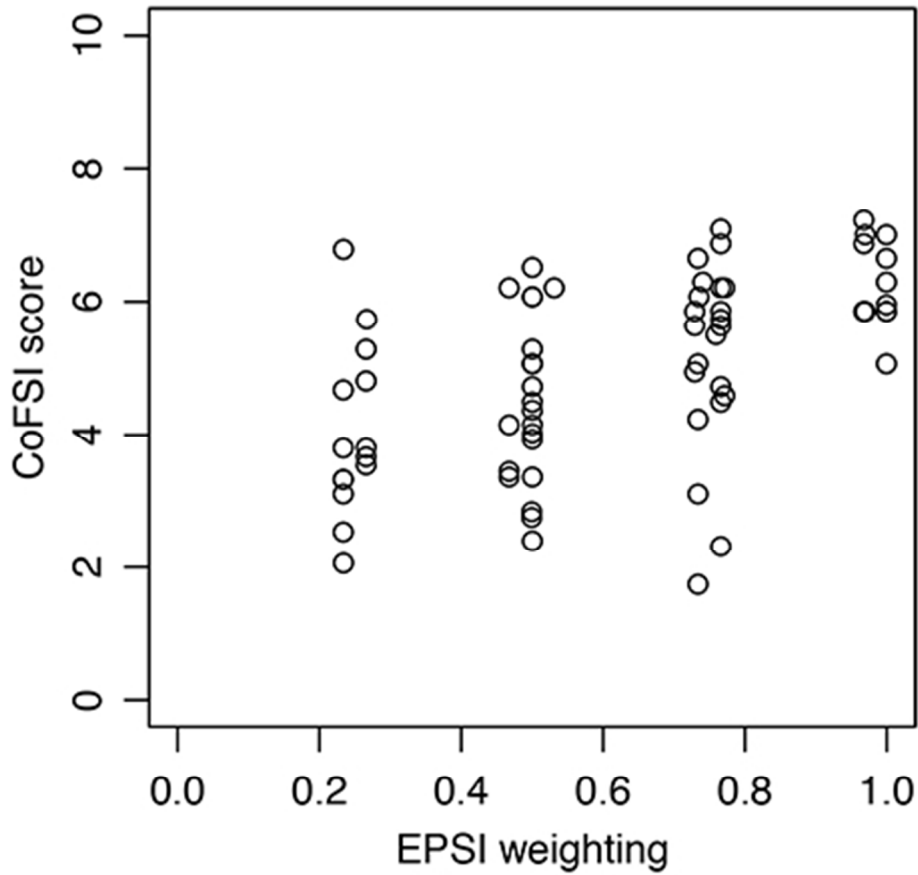932   positive coefficients denote traits associated with sensitivity.

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Figure 1 Comparison of taxon scores under CoFSI and taxon weightings under EPSI for 71 taxa that score under both indices.
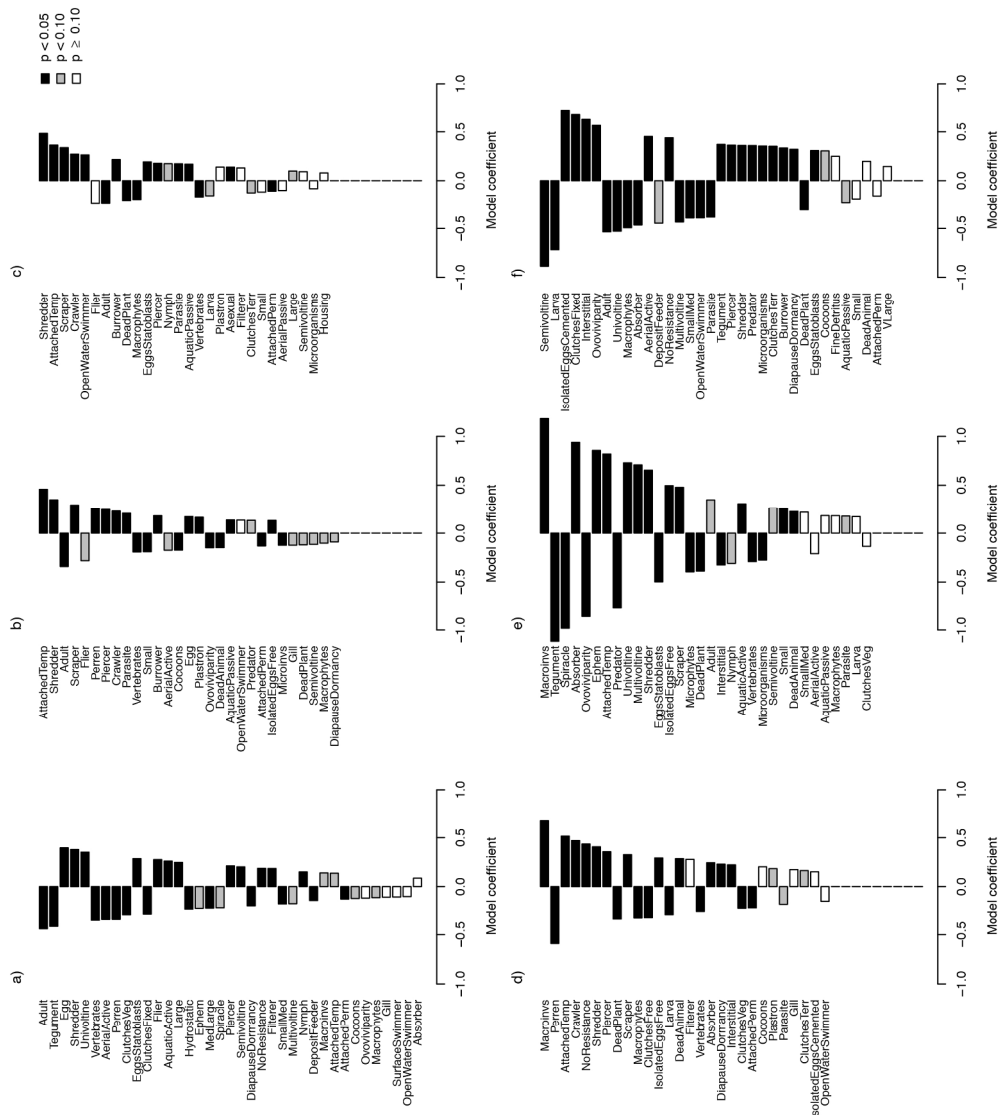
39x38mm (300 x 300 DPI)

Figure 2 Coefficients for 'global pruned' models: WHPT (a); EPSI (b); EPSI mixed (c); CoFSI (d); OFSI (e); and ToFSI (f). Note that positive coefficients denote traits associated with sensitivity under each index.
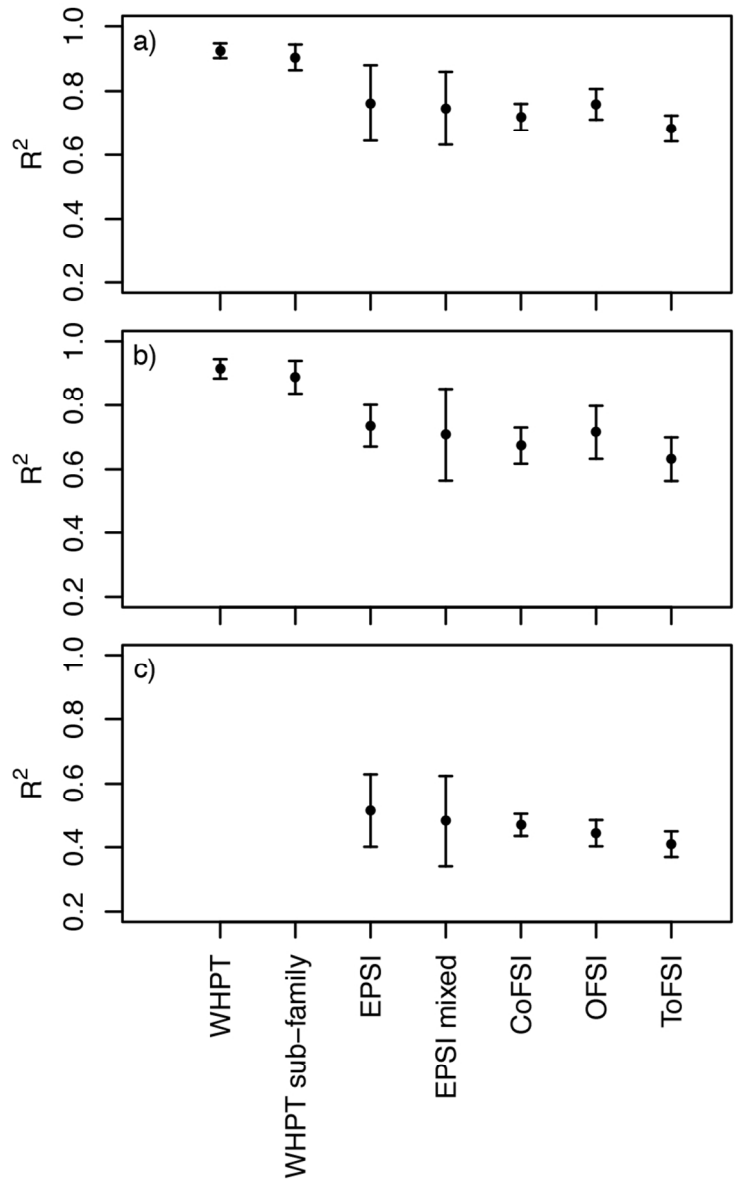
215x244mm (300 x 300 DPI)

Figure 3 Goodness-of-fit for 'minimum' models using all traits (a), traits retained after stepwise selection (b) and literature-based traits (c). Symbols indicate means and whiskers show 95% confidence intervals from random sampling.
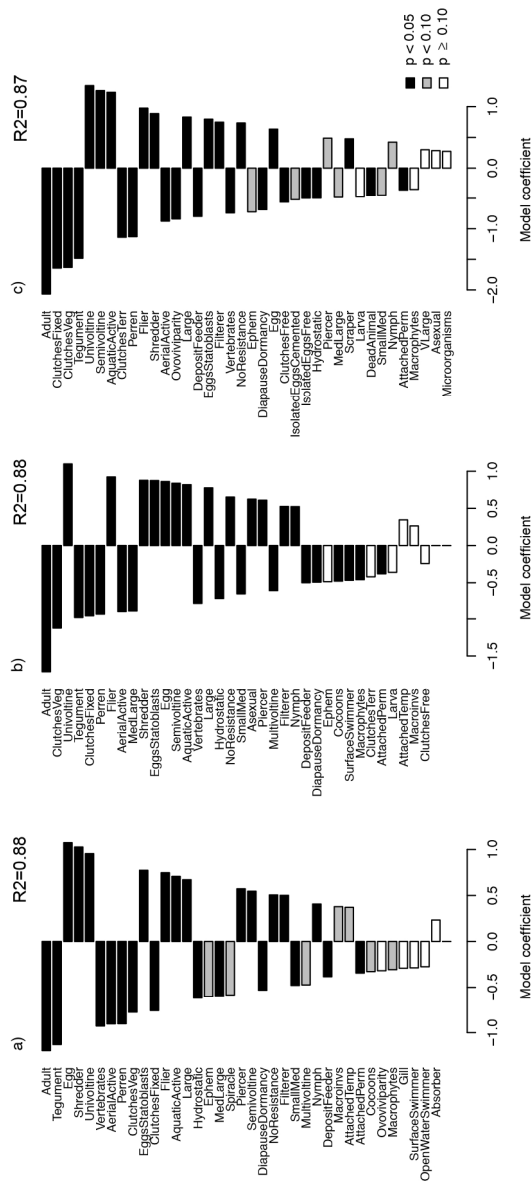
74x121mm (300 x 300 DPI)

Figure A1 Coefficients for 'global pruned' models: WHPT presence-absence (a); the mean of abundance-weighted WHPT scores for each scoring taxon (b); and the high abundance WHPT score for each scoring taxon (c).EPSI (c). Note that positive coefficients denote traits associated with sensitivity.

107x241mm (300 x 300 DPI)