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

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3 1 **Assessing the mechanistic basis for fine sediment**
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6 2 **biomonitoring: Inconsistencies among the literature,**
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9 3 **traits and indices**
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37 15 **Keywords**
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39 16 Biomonitoring; fine sediment; macroinvertebrates; traits; colmation.
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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 ($0.68 < \text{mean } R^2 < 0.76$). 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 ($0.27 < \text{mean } R^2 < 0.46$). 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.

For Peer Review

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3 43 **Introduction**
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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.

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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 Nieuwenhuysen 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

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3 68 to indirect impacts related to prey abundance (Sear et al., 1993; Kemp et al.,
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5 69 2011; Relyea et al., 2012). It is now a primary research area for many freshwater
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7 70 ecology and environmental engineering groups around the world. In Europe, this
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10 71 is partly a result of the focus brought by the implementation of the Water
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12 72 Framework Directive (WFD), leading to the realisation that fine sediment is an
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14 73 important and widespread cause of ecological deterioration linked to drivers as
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16 74 diverse as agriculture, urbanisation, flood management and flow regulation
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19 75 (Collins & Anthony, 2008; Taylor & Owens, 2009; Acreman & Ferguson, 2010).
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23 77 Authorities in the United Kingdom use a macroinvertebrate community index
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25 78 known as Walley Hawkes Paisley Trigg (WHPT) for WFD status classification.
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28 79 WHPT scores taxa based on their occurrence (presence-absence) or assigns a log
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30 80 abundance-weighted score in one of four categories (1-9; 10-99; 100-999; and
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32 81 >999 individuals). WHPT evolved from the Biological Monitoring Working Party
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34 82 (BMWP) method, in which taxa were attributed organic pollution sensitivity
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36 83 scores based on expert judgement (Armitage et al., 1983). The index has been
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38 84 refined since the inception of BMWP, most recently by using data-driven
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40 85 optimisation (Paisley et al., 2014). WHPT is among the most well developed
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42 86 biomonitoring tools in the world. This is evidenced by its long history of
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44 87 optimisation and the adoption of the method in many parts of the world (e.g.
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46 88 Diaz et al., 2004; Herman & Nejadhashemi, 2015). This history demonstrates the
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48 89 pioneering role that the United Kingdom has played in index development,
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50 90 something which it continues to do in the context of fine sediment
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52 91 biomonitoring.
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3 93 Whilst WHPT is a central pillar of WFD classification in the UK, diagnosing the
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5 94 cause of ecological degradation and classifying ecological status more accurately
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7 95 requires the use of a range of pressure-specific indicators. In the United Kingdom
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10 96 there are currently two such groups of indices for fine sediment: those related to
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12 97 the Proportion of Sediment-sensitive Invertebrates (PSI) index; and those
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14 98 comprising the Combined Fine Sediment Index (CoFSI). In the development of
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16 99 the PSI scoring system taxa were subjectively assigned to one of four Fine
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19 100 Sediment Sensitivity Rating (FSSR) categories: (A) highly sensitive; (B) sensitive;
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21 101 (C) tolerant; and (D) highly tolerant, based on a review of existing empirical
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23 102 information primarily published in ecological monographs and identification
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25 103 keys (Extence et al., 2011). Weightings for each taxon were later computed using
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27 104 extensive monitoring data by Turley et al. (2015) at the genus and species levels
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29 105 (EPSI), and by Turley et al. (2016) at mixed taxonomic levels (EPSI_{mixed}), to
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31 106 enhance the empirical basis for PSI. However, the resulting scores (%) still
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33 107 remain constrained by the original FSSR categories.
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39 109 CoFSI was developed more recently using a highly statistical approach (Murphy
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41 110 et al., 2015) whereby a number of environmental gradients, determined from
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43 111 extensive fieldwork, were reduced to two axes using partial Canonical
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45 112 Correspondence Analysis (pCCA). The resulting axes, describing gradients of
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47 113 total fine sediment (Total Fine Sediment Index; ToFSI) and organic matter
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49 114 (Organic Fine Sediment Index; OFSI), were then used to derive species scores
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51 115 based on their projected position along each axis, followed by calculation of a
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53 116 combined score at the community level. Thus the procedure was entirely data-
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55 117 driven, leaving no room for the use of extensive prior knowledge from the
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3 118 literature. As a result of differences in their development, the two tools (EPSI and
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5 119 CoFSI) often assign different scores to the same taxa (e.g. Figure 1).
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10 121 Direct comparison of the two sets of indices (PSI- and CoFSI- related) is
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12 122 challenging due to differences in the methods used in their development. The
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14 123 original PSI index was calibrated using visual estimates of surface fine sediment
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16 124 cover (Turley et al., 2014). In contrast, CoFSI was calibrated using the sediment
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18 125 resuspension technique (Duerdoth et al., 2015). We avoid the pitfalls of direct
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20 126 comparisons by focusing on the mechanistic basis for fine sediment
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22 127 biomonitoring using data on species traits.
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28 129 Trait-based approaches to freshwater biomonitoring have been growing in
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30 130 popularity (Menezes et al., 2010; Statzner & Běche, 2010). This is due to
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32 131 methodological advances (Cornwell et al., 2006; Poff et al., 2006; Villéger et al.,
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34 132 2008; Laliberte & Legendre, 2010; Schleuter et al., 2010) and the availability of
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36 133 fuzzy coded data describing species traits (e.g. Tachet et al., 2010). However,
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38 134 attempts to develop robust predictive tools based on trait-environment
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40 135 relationships have been met with frustration (Verberk et al., 2013), and many
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42 136 trait-based approaches to the development of biomonitoring tools are informed
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44 137 by expert interpretation of primary literature rather than any published trait
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46 138 databases (e.g. Extence et al., 2011).
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52 140 We assessed the degree to which taxon scores under EPSI and CoFSI are related
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54 141 to species traits drawn from the widely used trait database of Tachet et al.
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56 142 (2010). We considered linear models for each index using a series of traits
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3 143 describing life-history, morphology, physiology and behaviour as independent
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5 144 variables. As the most well-developed biomonitoring index, we compare the
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7 145 results with models for WHPT. Our objectives were to (i) test the relative
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9 146 performance of the two fine sediment biomonitoring tools with respect to trait
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11 147 associations and against a benchmark provided by WHPT and (ii) test the
12
13 148 absolute power of currently available traits to predict taxon scores under these
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15 149 tools. Objective (ii) also included a secondary aim to assess the predictive power
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17 150 of a subset of traits drawn from the literature. We hypothesised that traits would
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19 151 be a better fit to taxon scores under WHPT due to its long history of
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21 152 development, followed by EPSI due to its origin as a trait-driven index, then
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23 153 finally CoFSI as the most empirically-based tool.
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30 **Methods**

31 32 33 34 35 157 *Index scores and trait values*

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39 159 Taxon scores for WHPT (UKTAG, 2014), empirical weightings for EPSI (Turley et
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41 160 al., 2015) and EPSI_{mixed} (Turley et al., 2016) and taxon scores under CoFSI
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43 161 (Murphy et al., 2015) were taken from their respective sources. We considered
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45 162 models for OFSI and ToFSI scores as well as the combined CoFSI score for each
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47 163 individual scoring taxon (see equation 2 in Murphy et al., 2015). For WHPT we
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49 164 explored separate models predicting scores for presence-absence, the mean of
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51 165 abundance-weighted scores for each scoring taxon, and the high abundance
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53 166 score for each scoring taxon. The results of these alternative models were very
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57 167 similar (Figure A1). We therefore focused on WHPT presence-absence scores for
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3 168 simplicity in the remainder of our modelling. Prior to the modelling all index
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5 169 scores were centred and standardised in order to aid interpretation of model
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7 170 coefficients.
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12 172 Where possible, taxon scores were matched with fuzzy coded trait values from
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14 173 Tachet et al. (2010) as alternative databases were largely incomplete (e.g.
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16 174 Schmidt-Kloiber & Hering, 2015) for 'true' traits, *i.e.* not those reflecting
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18 175 ecological preferences (Statzner & Bêche, 2010; Verberk et al., 2013). In
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20 176 instances where index scores were available at a coarser taxonomic level than
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22 177 traits, fuzzy values were averaged across genera or species. This resulted in a
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24 178 total number of taxa for which matched trait data were available of 106 (WHPT),
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26 179 421 (EPSI), 348 (EPSI_{mix}) and 95 (CoFSI, OFSI, ToFSI) for the respective indices.
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28 180 Taxonomic resolution for WHPT was family level, whereas fine sediment indices
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30 181 were generally at species level (see supplementary material).
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36 183 The complete trait dataset encompassed 63 trait modalities (hereafter referred
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38 184 to as 'traits' for brevity) in 11 trait categories (Table A1). After compiling lists of
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40 185 scoring taxa and their traits separately for each index, individual trait modalities
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42 186 were centred and standardised within a trait category to give equal weights
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44 187 across all trait categories. As some traits describing type of food and feeding
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46 188 mode were moderately correlated ($0.6 < r < 0.75$) we considered removing the
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48 189 correlated food types. However, since variance inflation factors (VIFs) were low
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50 190 (< 2), it was decided to keep the full set of food types. Finally, a subset of traits
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52 191 that are purported to be instrumental in conferring tolerance or sensitivity to
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54 192 fine sediment was selected based on a review of the literature (Table A1).
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7 194 *Modelling approach*
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11 196 A multiple linear regression approach was taken to predict scores under each
12 197 index using a combination of traits. We selected linear parametric modelling
13 198 because it gives more readily interpretable results. Furthermore, our literature
14 199 review gave no reason to believe that trait relationships would be non-linear. All
15 200 analyses were performed in R 3.2.3 (R Core Team, 2015). Goodness-of-fit was
16 201 assessed for several sets of models. The first three sets ('global' models) included
17 202 all taxa for which scores were available under the respective indices: (i) the
18 203 global 'all traits' model using all 63 traits; (ii) the global model 'pruned' using
19 204 stepwise selection in both directions (*stepAIC* function, MASS package; Venables
20 205 & Ripley, 2002); and (iii) the global 'literature' model using only the subset of 35
21 206 traits drawn from the literature (Table A1). For each index, nested global models
22 207 were compared using the *anova* function. We did not explore literature-based
23 208 models for WHPT.
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210 Due to the bias introduced by inequalities in the number of scoring taxa for each
211 index, we generated another set of model results by taking 1000 random
212 samples of 90 taxa: (v) the 'all traits minimum' model; (vi) the 'pruned minimum'
213 model; and (vii) the 'literature minimum' model. Finally, to assess the sensitivity
214 of WHPT models to trait averaging at the family level, modelling for the all traits
215 minimum and pruned minimum scenarios was repeated for 100 random
216 samples of sub-family level (genus or species) traits within WHPT families, with
217 50 samples of 90 taxa for each set of sub-family level traits (5000 samples in

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3 218 total). All sampling was performed without replacement using the *sample*
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5 219 function. In all cases we used R^2 as a measure of goodness-of-fit.
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10 221 **Results**
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14 223 The global 'all traits' and 'pruned' models for WHPT had a higher goodness-of-fit
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16 224 than equivalent models for the fine sediment indices (Table 1). In turn, the
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18 225 goodness-of-fit for global EPSI and EPSI_{mixed} models was substantially lower than
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20 226 for CoFSI, OFSI and ToFSI. However, these results do not allow direct comparison
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22 227 between indices due to variations in the number of scoring taxa, which affects
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24 228 statistical power (Cohen, 1992). When offering only the literature-based traits as
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26 229 explanatory variables the performance of global models for the fine sediment
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28 230 indices was greatly reduced. The global 'all traits' model did not improve
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30 231 predictions significantly ($p > 0.05$), except in the case of the EPSI literature model
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32 232 ($p < 0.02$), *i.e.* in most cases the fit of more parsimonious 'pruned' models was not
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34 233 significantly different to that of the more complex 'all traits' models (Table 1).
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36 234 Thus, we focus primarily on the global 'pruned' models to assess trait-index
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38 235 relationships (Figure 2).
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46 237 The WHPT global 'pruned' model retained significant explanatory variables in
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48 238 several trait categories, including aquatic stages, respiration and feeding modes,
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50 239 diet and voltinism (Figure 2a). The global 'pruned' models for EPSI and EPSI_{mixed}
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52 240 retained similar sets of traits (Figure 2b-c). The traits most strongly driving
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54 241 species sensitivity under these indices were 'AttachedTemp', 'Shredder', and
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56 242 'Scraper'. Those most strongly indicating tolerance were 'Adult' and 'Flier',
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3 243 although the latter was not significant ($p>0.05$). The CoFSI global ‘pruned’ model
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5 244 retained a different set of coefficients, including several diet-, feeding mode-,
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7 245 locomotion- and resistance- related traits (Figure 2d). The OFSI and ToFSI global
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9 246 ‘pruned’ models shared significant coefficients for traits describing voltinism,
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11 247 ovoviviparity, tegumental respiration and feeding modes, yet the sign of
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13 248 coefficients for these traits was opposite under each index (Figure 2e-f). In
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15 249 general, the OFSI model was more strongly related to traits describing
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17 250 respiration modes.
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21 252 No traits were consistently associated with tolerance under all fine sediment
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23 253 indices. Only ‘Shredder’ was consistently associated with sensitivity. CoFSI and
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25 254 the PSI-related indices also shared strong and significant positive coefficients for
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27 255 ‘AttachedTemp’ and ‘Crawler’. ‘Scraper’ indicated sensitivity in all cases except
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29 256 ToFSI. There were opposite signs in trait-stressor relationships between the two
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31 257 groups of fine sediment indices for ‘Small’, ‘AerialActive’, ‘Ovoviviparity’,
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33 258 ‘Cocoons’, ‘Perren’ (life cycle duration >1 year), ‘OpenWaterSwimmer’, ‘Parasite’,
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35 259 ‘Predator’, ‘DeadAnimal’ and ‘DiapauseDormancy’.
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39 261 With regards to the global ‘literature’ models, several literature-based traits
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41 262 were significant predictors of EPSI and EPSI_{mixed} weightings ($p<0.05$), whereas
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43 263 relatively few of the traits purported to be important in determining sensitivity
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45 264 or tolerance to fine sediment in the literature were significant predictors of OFSI
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47 265 or ToFSI scores (Table 2, Table A2-A6). There were a number of inconsistencies
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49 266 in the sign of relationships expected from the literature review and those
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51 267 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.

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279 Discussion

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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 & Phillippe, 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.

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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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3 293 demonstrate the need for more integration of the available trait data, the a priori
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5 294 expectations from the literature, and the scores assigned to taxa under currently
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7 295 available pressure-specific indices. This is evidenced by the relatively poor fit of
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9 296 trait-based models for fine sediment indices, especially when only traits drawn
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11 297 from the literature review were entered as explanatory variables. It is further
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13 298 reinforced by the differences in significant traits retained in models for
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15 299 alternative fine sediment indices.
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21 301 Taxon scores under WHPT were strongly related to traits conferring tolerance or
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23 302 sensitivity to organic pollution (Tomanova et al., 2008; Archambault et al., 2010;
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25 303 Feio & Dolédec, 2012). WHPT scores were negatively related to taxa with
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27 304 tegumental respiration and aquatic lives strongly skewed towards adult life-
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29 305 stages (*e.g.* Acroloxidae, Dugesiidae) and positively to univoltine shredders (*e.g.*
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31 306 Lepidostomatidae) and taxa with a range of aquatic life stages, including eggs
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33 307 (*e.g.* Gyrinidae). In contrast, few traits with strong and significant coefficients in
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35 308 the models for fine sediment indices could be related to the extant literature on
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37 309 trait-fine sediment relationships. Some traits had coefficients with conflicting
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39 310 signs between the two sets of indices. This is surprising given that both were
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41 311 designed for biomonitoring of the same stressor. Before discussing these
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43 312 differences in detail, it is worth noting two important nuances of the findings
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45 313 reported.
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52 315 Firstly, CoFSI, OFSI and ToFSI had a substantially higher R^2 than EPSI and
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54 316 $EPSI_{\text{mixed}}$ for the global models (Table 1) but marginally lower for the 'minimum'
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56 317 models (Figure 3). The CoFSI-related indices also had fewer significant variables
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3 318 than the PSI-related indices in the global literature-based models (Table 2),
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5 319 despite a better fit. This is because the much lower number of scoring taxa under
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7 320 CoFSI meant that the resulting models had a higher type II error rate (Cohen,
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9 321 1992). Secondly, some traits with significant coefficients in the global pruned
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11 322 models (Figure 2) did not have significant coefficients in the global literature
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13 323 models (Table 2). This is because the significance of each coefficient is assessed
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15 324 in the presence of all other independent variables, and the pruned models
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17 325 retained traits that were not included in the literature models.
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21 327 Only a single trait ('Shredder') was consistently associated with sensitivity
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23 328 across all five fine sediment indices (PSI- and CoFSI- related). Both Buendia et al.
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25 329 (2013) and Descloux et al. (2014) also found shredders to be relatively sensitive.
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27 330 The mechanism for this may be the burial of leaf litter and/or a reduction in its
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29 331 nutritional quality through inhibition of fungal growth (Febra, 2013). This is
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31 332 similar to the mechanism posited for the sensitivity of scrapers (Brookes, 1986;
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33 333 Suren, 2005; Kent & Stelzer, 2008; Jones et al., 2012; Relyea et al., 2012), which
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35 334 were also consistently associated with sensitivity in all pruned models except
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37 335 ToFSI. The next strongest association with sensitivity across the majority of fine
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39 336 sediment indices was for temporarily attached organisms. However, Descloux et
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41 337 al. (2014) reported this trait to be indicative of tolerance across three rivers in
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43 338 Germany. Buendia et al. (2013) found that temporarily attached taxa were
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45 339 present in sediment-laden tributaries of the River Isábena in the Central
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47 340 Pyrenees but reported no significant correlation. Finally, crawlers were also
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49 341 associated with sensitivity under CoFSI, EPSI and EPSI_{mixed}. This is consistent
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51 342 with Buendia et al. (2013), who reported a significant negative correlation
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3 343 between the prevalence of crawling as a trait and the rank of sites increasingly
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5 344 affected by fine sediment deposition. On the other hand, Descloux et al. (2014)
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7 345 found a consistently significant positive correlation between the relative
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9 346 occurrence of crawlers and colmation.
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13 348 Several further traits were inconsistently associated with sensitivity or
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15 349 tolerance, having coefficients with opposite signs under the various indices.
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17 350 These included small taxa (2.5-5 mm), aerial (active) dispersers, ovoviviparous
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19 351 reproducers, parasites, predators, perennial organisms and those with strong
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21 352 resistance traits for cocoons and diapause or dormancy. Some of these
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23 353 inconsistencies may be explained by the use of different calibration techniques
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25 354 under the two sets of indices, i.e. visually assessed surficial sediments under PSI-
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27 355 related indices but quantitative superficial and surficial sediments under the
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29 356 CoFSI-related indices. However, the lack of support for trait-index associations
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31 357 from the literature suggests that this explanation is only partial at best. Instead,
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33 358 such equivocal results suggest that there is a problem in the trait-literature-
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35 359 biomonitoring nexus. The problem may lie with the literature, with the way that
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37 360 traits are described, or with the development of the biotic indices. It is most
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39 361 likely to be a combination of these factors. This likelihood is further reinforced
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41 362 by the fact that our models lacked significant coefficients for a range of other
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43 363 traits purported to important in fine sediment response in the literature (Table
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45 364 A1).
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54 366 *Body size*
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3 368 Small-bodied taxa (<5 mm) are expected to be strongly sensitive to fine sediment
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5 369 due to smothering and restricted dispersal in reduced pore space (Gayraud &
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7 370 Phillipe, 2001; Wood et al., 2001; Wagenhoff et al., 2012; Descloux et al., 2014).
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10 371 However, body size did not feature strongly in our models.

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14 373 *Life cycle duration and voltinism*

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19 375 Based on the literature, we expected perennial and uni- or semi-voltine taxa to
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21 376 be sensitive and ephemeral and multivoltine taxa to be relatively tolerant
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23 377 (Larsen et al., 2011; Buendia et al., 2013). Semivoltine and perennial taxa were
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25 378 tolerant according to the pruned models for EPSI, EPSI_{mixed} and CoFSI but
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27 379 voltinism traits were associated with either sensitivity (OFSI) or tolerance
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29 380 (ToFSI) under the CoFSI sub-indices, indicating that the combination of axes
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31 381 describing organic matter and total fine sediment under CoFSI may cancel out
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33 382 distinct mechanisms of the fine sediment impact. Only ToFSI had a significant
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35 383 coefficient for any life-history trait (semivoltine, tolerant) among the literature-
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37 384 based models. Ephemeral or multivoltine taxa were not found to be tolerant
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39 385 under any of our models, with the exception of ToFSI. On the contrary, these
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41 386 traits were strongly linked with sensitivity under OFSI.
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48 388 *Aquatic life-stages*

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53 390 Life-stage can affect an organism's ability to avoid burial and excavate itself,
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55 391 although there is much variability between taxa for a given life-stage (Wood et
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57 392 al., 2001; 2005). Certainly, immotile eggs are expected to be negatively impacted

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3 393 by fine sediment (Jones et al., 2012) and this was supported in literature-based
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5 394 models for EPSI and EPSI_{mixed}. Models for CoFSI and ToFSI indicated that taxa
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7 395 with strong larval life-stages are tolerant, whilst models for EPSI, EPSI_{mixed} and
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9 396 ToFSI indicated the same for adult life-stages. However, the picture is far from
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11 397 clear because of the way fuzzy coded traits are organised, which is a problem
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13 398 when focusing on life-stage. For example, a taxon which is aquatic as an egg,
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15 399 larva, pupa and adult would receive equal fuzzy codes across all four trait
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17 400 modalities. The results for life-stages, therefore, must be seen as representing
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19 401 the level of aquatic specialism rather than the sensitivity of a given life-stage *per*
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21 402 *se*. Advances in trait-based biomonitoring would benefit from ontogenetic
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23 403 information (Statzner & Běche, 2010).
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30 405 *Reproduction and resistance*
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35 407 There is little information in the literature as to how reproduction and resistance
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37 408 traits are expected to respond to fine sediment. Descloux et al. (2014) found that
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39 409 ovoviviparity was less prevalent at impacted sites and that cocoons and asexual
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41 410 reproduction varied significantly across the gradient of colmation, although the
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43 411 sign of these relationships was not consistent among three rivers. In the pruned
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45 412 models there were significant coefficients for 'cocoons' (EPSI, tolerant),
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47 413 'DiapauseDormancy' (ToFSI, sensitive) and asexual reproduction (EPSI_{mixed},
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49 414 sensitive). The EPSI and OFSI pruned models indicated that ovoviviparous taxa
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51 415 are tolerant, whereas the equivalent ToFSI model indicated sensitivity for the
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53 416 same trait, again suggesting that the combination of organic matter and total fine
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55 417 sediment gradients under CoFSI may obscure discrete processes.
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419 *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.

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434 *Respiration*

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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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3 443 sediment stress (Tomanova et al., 2008; Larsen et al., 2011; Von Bertrab et al.,
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5 444 2013). On the other hand, organisms with gills have previously been reported as
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7 445 sensitive (Townsend et al., 2008; Larsen et al., 2011) due to abrasion and
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10 446 clogging of the breathing apparatus (Lemly, 1982; Culp et al., 1986; Jones et al.,
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12 447 2012). Gills did not feature strongly in any of our models but tegumental
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14 448 respiration was a significant indicator of tolerance in the literature-based model
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16 449 for EPSI and the pruned model for OFSI. The latter also included spiracle
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18 450 respiration. This reflects the closer association of OFSI with the content of
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20 451 organic matter (Murphy et al., 2015), which is linked to the important role of
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22 452 oxygen availability and sediment quality (Von Bertrab et al., 2013). Tegumental
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24 453 respiration was indicated as sensitive in the ToFSI pruned model, again
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26 454 suggesting that the invertebrate response to organic matter and total fine
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28 455 sediment may be discrete.
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34 457 *Locomotion and relation to the substrate*

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39 459 Given that locomotion traits describe an organism's habitat use, they should be
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41 460 strongly linked to fine sediment. Indeed, both Buendia et al. (2013) and Descloux
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43 461 et al. (2014) consistently found that open water swimmers, burrowers and
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45 462 interstitial organisms were sensitive. Interstitial organisms in particular are
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47 463 expected to be susceptible to smothering and restrictions to movement with
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49 464 increasing fine sediment (Wood et al., 2005; Jones et al., 2012), yet this was only
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51 465 supported by pruned and literature-based models for CoFSI and ToFSI. Crawlers
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53 466 are not identified in the literature as either sensitive or tolerant, but pruned
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55 467 models for EPSI, EPSImixed and CoFSI strongly indicated sensitivity for this trait.
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3 468 Evidence for other locomotion traits in our results and in the wider literature is
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5 469 equivocal.

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9 471 *Refining traits for fine sediment biomonitoring*

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14 473 Both of our main findings - that (i) the performance of trait-based models for fine
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16 474 sediment indices was inferior to those for WHPT and (ii) that traits retained in
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18 475 the models were inconsistent and difficult to reconcile with the literature - may
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20 476 be partly attributable to the lack of relevant traits in the trait database of Tachet
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22 477 et al. (2010). Our findings suggest the need to build upon the excellent work of
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24 478 Tachet et al. (2010) in the context of fine sediment. We therefore recommend a
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26 479 refined set of traits specifically for fine sediment biomonitoring.

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31 481 There is a difference between species that actively forage by swimming in open
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33 482 water (e.g. *Notonecta*) and those that use swimming as an escape strategy but
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35 483 would potentially be impacted by fine sediment deposition (e.g. *Cloeon*), yet both
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37 484 receive fuzzy scores for 'OpenWaterSwimmer' in the trait database. The
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39 485 sensitivity of taxa with fixed eggs (e.g. 'IsolatedEggsCemented') depends on what
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41 486 the eggs are fixed to (stones, wood, plants) and where (shallow zone, margin,
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43 487 hyporheic zone). The sensitivity of filter-feeders depends on their ability to
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45 488 excrete excess fines: insect filter feeders (e.g. Simuliidae, Hydropsychidae) are
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47 489 likely to be sensitive whereas lower taxa that able to excrete inert fine matter
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49 490 (e.g. Unionidae, Sphaeriidae) are likely to be tolerant. Crawlers could be
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51 491 sensitive, such as certain Ephemeroptera (Ciborowski et al., 1977; Corkum et al.,
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53 492 1977; cf. Jones et al., 2012) or tolerant, for example Chironomidae and Caenidae,
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3 493 who burrow into fine sediment (Jones et al., 2012). Burrowers could also be
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5 494 sensitive or tolerant depending on what they burrow into. Some taxa burrow
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7 495 into fine sediment (e.g. Caenidae, some Sialidae), others in coarser substrata (e.g.
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10 496 Ephemeraeidae). The same argument applies to other traits describing relation to
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12 497 substrate. Finally, some gills are easily clogged (e.g. Potamanthidae, *Serratella*),
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14 498 others (e.g. Caenidae) are not (Corbin & Goonan, 2010). Physical adaptation in
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16 499 the latter and behavioural adaptation in others (e.g. *Baetis*) confers tolerance to
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19 500 colmation (Buffagni et al., 2009).

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23 502 Thus, we recommend the following refinements to the trait database: (i) split
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25 503 open water swimmers into two categories (active foraging, escape); (ii)
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27 504 consolidate several reproduction traits into fixed versus free eggs and include
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29 505 more information on preferred oviposition sites; (iii) split filter-feeder trait into
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31 506 those able and unable to excrete excess fines; (iv) a split involving anatomical
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33 507 and/or behavioural adaptations allowing gill respiration in highly sedimented
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35 508 environments and (v) combine traits describing locomotion and relation to
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37 509 substrate with information on substrate preference. The latter suggestion risks
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39 510 criticism due to the circular nature of using substrate preference to indicate fine
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41 511 sediment stress. However, we argue that these traits do not make sense in the
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43 512 absence of such information, and without sufficient and relevant data on 'true'
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45 513 biological traits (e.g. excavation capacity; Wood et al., 2005) substrate preference
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47 514 is the only alternative.

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55 516 Our study did not explicitly consider trait interactions, trait combinations and
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57 517 context (e.g. ontogenetic, environmental) dependency (Poff et al., 2006). Verberk

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3 518 et al. (2013) have suggested that trait-based approaches to biomonitoring should
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5 519 recognise the important trait linkages driven by evolutionary trade-offs (where
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7 520 investment in one trait leaves fewer resources for another), spin-offs (where
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9 521 investment in one trait decreases the cost or increases the benefit of another)
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11 522 and body plan constraints due to fundamental physical and biological
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13 523 developmental limits. Further progress may lie in the search for sets of traits
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15 524 underlying life-history strategies adapted for coping with fine sediment stress.
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20 21 526 **Conclusions**

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25 528 Our findings point to a problem in the trait-literature-biomonitoring nexus
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27 529 within the context of fine sediment. This is evidenced by a relatively poor fit of
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29 530 trait-based models for fine sediment indices compared to WHPT, a lack of
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31 531 consistency in the traits indicating sensitivity and tolerance under CoFSI- and
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33 532 PSI- related biomonitoring tools, and equivocality between our results and
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35 533 evidence from the extant literature. We suggest that progress may lie in the
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37 534 refinement of traits for fine sediment applications, building on the valuable
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39 535 compilations of traits previously published.
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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

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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	Oviviparity	↑	-	-	-	-	-
	Asexual	↑/↓†	-	-	-	-	-
Resistance forms	Cocoons	↑/↓†	-	-	-	-	-
Type of food	Microorganisms	↑/↓†	-	-	-	-	-
	FineDetritus	↓	-	-	-	-	-
	DeadPlant	↑/↓†	-	-	-	-	-
	Microphytes	↑/↓†	-	-	-	-	-
	Microinvs	↑	-	-	-	-	-

Feeding mode	DepositFeeder	↑/↓†	-	-	-	-	-
	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(***)

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
Life cycle duration (years)	>80	VLarge
	≤1	Ephem ²
Voltinism (generations per year)	>1	Perren ²
	<1	Semivoltine ²
	1	Univoltine ²
Aquatic stages	>1	Multivoltine ²
	Egg	Egg ³
	Larva	Larva ³
	Nymph	Nymph ³
Reproduction	Adult	Adult ³
	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
Dispersal	Asexual reproduction	Asexual ⁵
	Water passive	AquaticPassive
	Water active	AquaticActive
	Aerial passive	AerialPassive
Resistance forms	Aerial active	AerialActive
	Eggs, statoblasts	EggsStatoblasts
	Cocoons	Cocoons ⁶
	Protection against dessication	Housing
	Diapause/dormancy	DiapauseDormancy
Type of food	None	NoResistance
	Fine sediment and microorganisms	Microorganisms ⁷
	Detritus <1mm	FineDetritus ⁷
	Plant detritus >1mm	DeadPlant ⁸
	Living microphytes	Microphytes ⁹
	Living macrophytes	Macrophytes
	Dead animals >1mm	DeadAnimal

	Living microinvertebrates	Microinvs¹⁰
	Living macroinvertebrates	Macroinvs
	Vertebrates	Vertebrates
Feeding mode	Absorber	Absorber
	Collector-gatherer	DepositFeeder⁷
	Shredder	Shredder⁸
	Scraper	Scraper⁹
	Filterer	Filterer¹¹
	Piercer	Piercer
	Predator	Predator
	Parasite	Parasite
Respiration	Tegument	Tegument¹²
	Gills	Gill¹³
	Plastron	Plastron
	Spiracle	Spiracle
	Hydrostatic vesicle	Hydrostatic
Mode of locomotion and relationship to substrate	Flight	Flier
	Surface swimmers	SurfaceSwimmer
	Open water swimmer	OpenWaterSwimmer¹⁴
	Crawling	Crawler¹⁴
	Burrowing	Burrower¹⁴
	Within interstices	Interstitial^{14,15}
	Attached (temporary)	AttachedTemp¹⁴
Attached (permanent)	AttachedPerm¹⁴	

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

²Voltinism 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)

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

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

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

⁶Prevalence 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)

⁷Diets 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)

⁸Deposited 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.

⁹Fine 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

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

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3 876 ¹¹Filtering apparatus can become clogged, interrupting feeding and possibly causing
4 877 abandonment (Edington & Hildrew, 1995; Strand & Merrit, 1997). Buendia et al. (2013) found
5 878 that filterers were sensitive to fine sediment
6 879 ¹²Prevalence of tegumental respiration decreased with colmation in three rivers (Descloux et al.,
7 880 2014). However, Larsen et al. (2011) found that organisms with tegumental respiration were
8 881 tolerant of sand addition.
9 882 ¹³Gills can become clogged and abraded (Lemly, 1982; Jones et al., 2012). Townsend et al. (2008)
10 883 and Larsen et al. (2011) both found that organisms with gills were sensitive to fine sediment.
11 884 However, both Buendia et al. (2013) and Descloux et al. (2014) found that the prevalence of gills
12 885 as a respiration mode increased with colmation.
13 886 ¹⁴Locomotion traits all exhibited significant associations with fine sediment (Buendia et al., 2013;
14 887 Descloux et al., 2014)
15 888 ¹⁵Interstitial 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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3 916 **Figure legends**
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7 918 **Figure 1** Comparison of taxon scores under CoFSI and taxon weightings under
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9 919 EPSI for 71 taxa that score under both indices.
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13 921 **Figure 2** Coefficients for 'global pruned' models: WHPT (a); EPSI (b); EPSI mixed
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15 922 (c); CoFSI (d); OFSI (e); and ToFSI (f). Note that positive coefficients denote traits
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17 923 associated with sensitivity under each index.
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21 925 **Figure 3** Goodness-of-fit for 'minimum' models using all traits (a), traits retained
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23 926 after stepwise selection (b) and literature-based traits (c). Symbols indicate
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25 927 means and whiskers show 95% confidence intervals from random sampling.
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29 929 **Figure A1** Coefficients for 'global pruned' models: WHPT presence-absence (a);
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31 930 the mean of abundance-weighted WHPT scores for each scoring taxon (b); and
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33 931 the high abundance WHPT score for each scoring taxon (c).EPSI (c). Note that
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35 932 positive coefficients denote traits associated with sensitivity.
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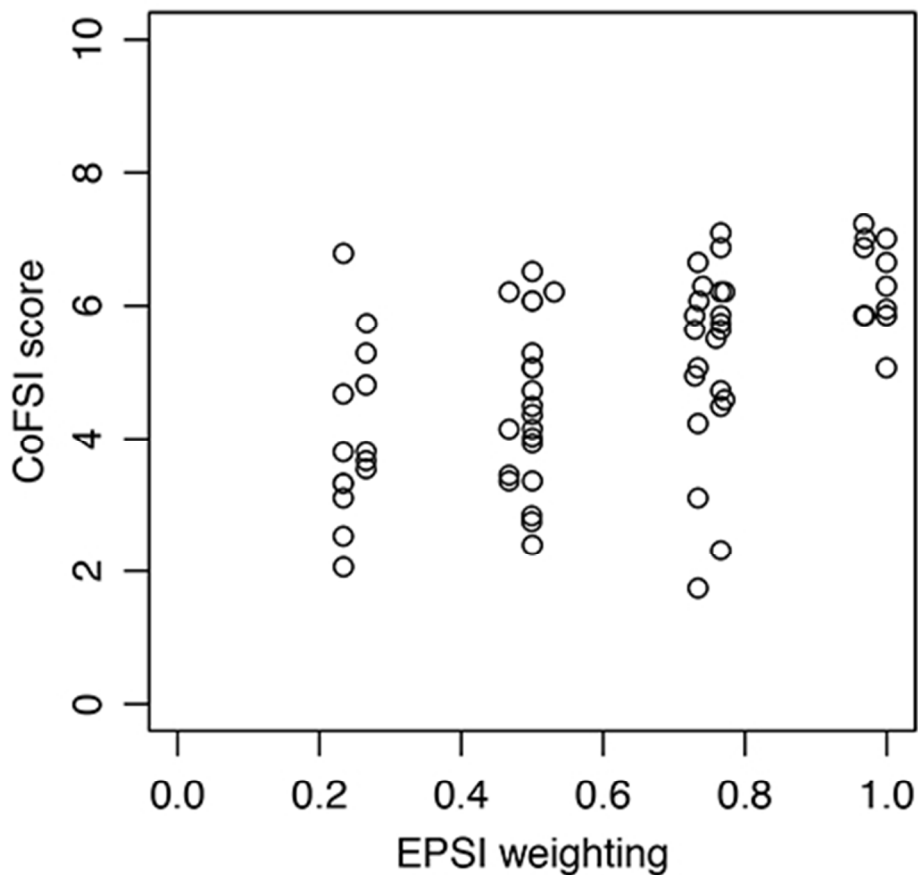


Figure 1 Comparison of taxon scores under CoFSI and taxon weightings under EPSI for 71 taxa that score under both indices.

39x38mm (300 x 300 DPI)



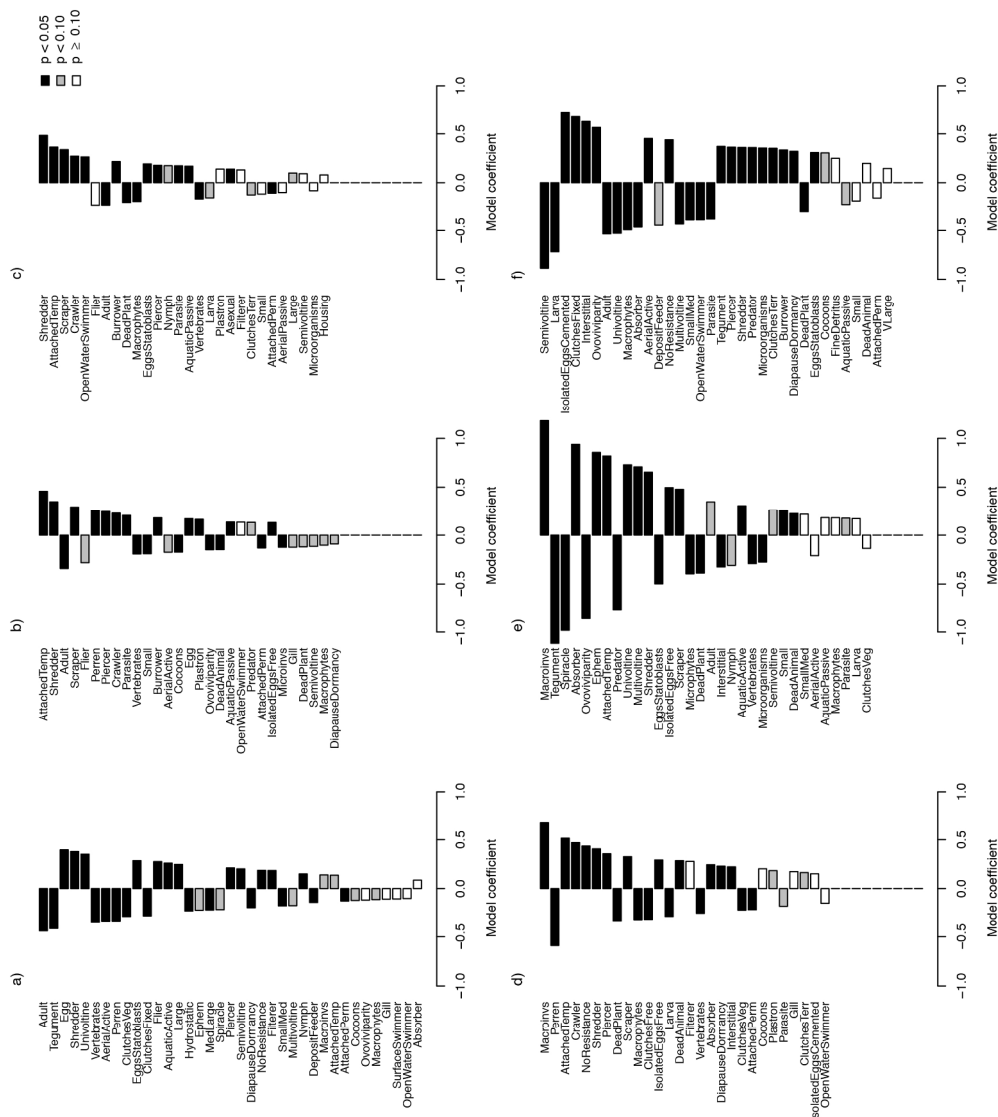


Figure 2 Coefficients for 'global pruned' models: WHPT (a); EPSI (b); EPSI mixed (c); CoFSI (d); OFSI (e); and ToFSI (f). Note that positive coefficients denote traits associated with sensitivity under each index.

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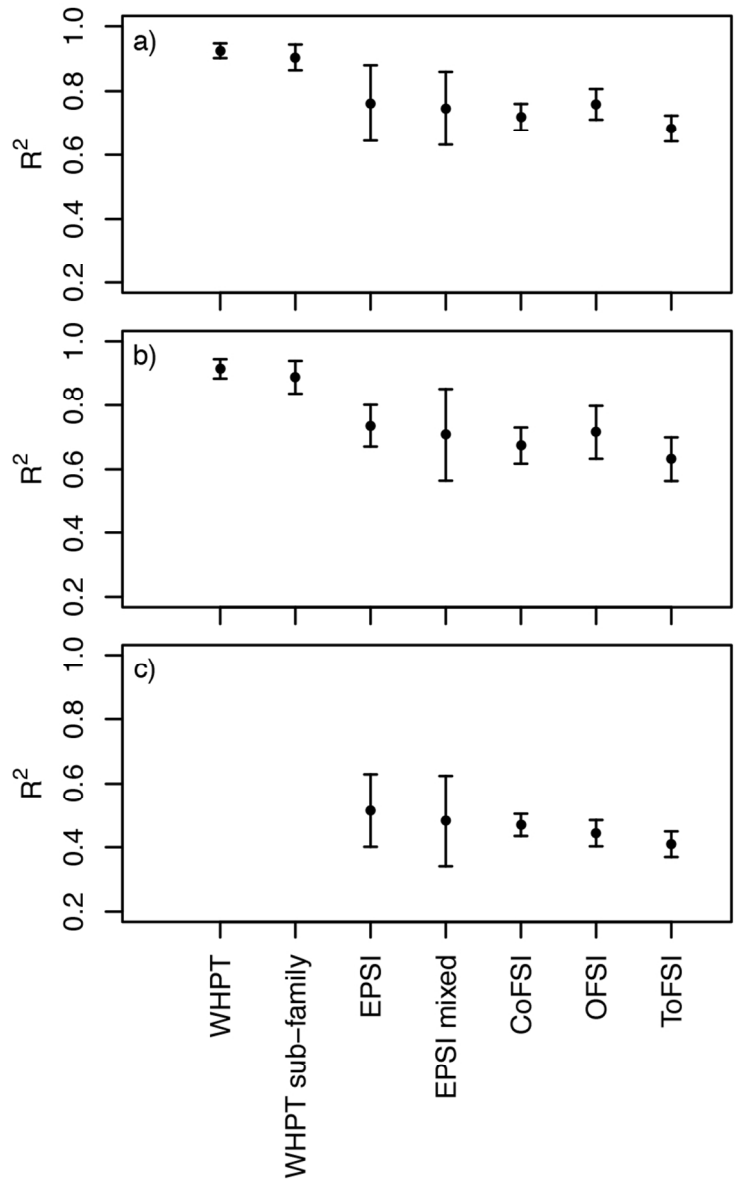


Figure 3 Goodness-of-fit for 'minimum' models using all traits (a), traits retained after stepwise selection (b) and literature-based traits (c). Symbols indicate means and whiskers show 95% confidence intervals from random sampling.

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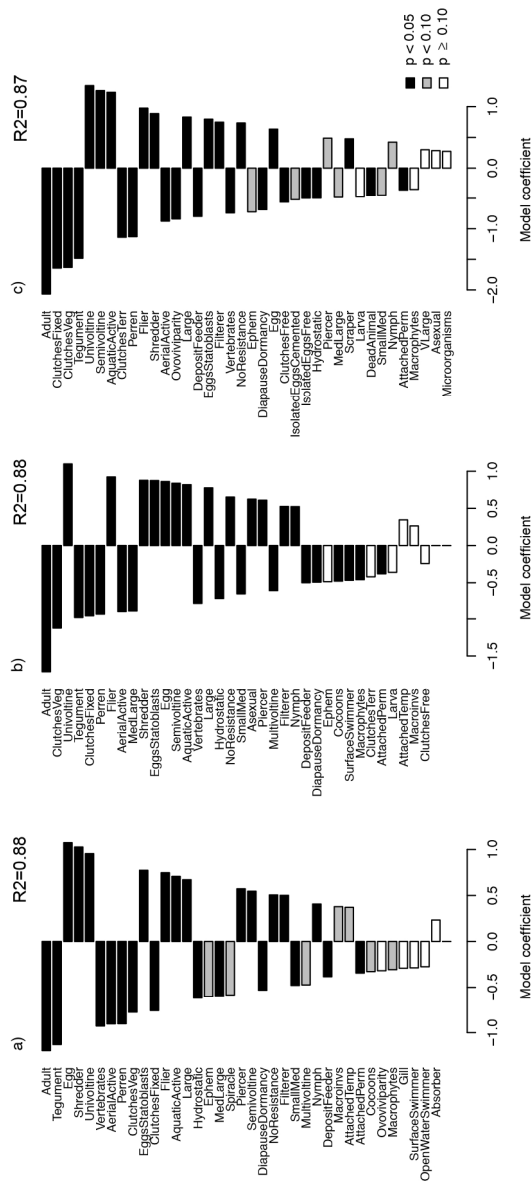


Figure A1 Coefficients for 'global pruned' models: WHPT presence-absence (a); the mean of abundance-weighted WHPT scores for each scoring taxon (b); and the high abundance WHPT score for each scoring taxon (c).EPSI (c). Note that positive coefficients denote traits associated with sensitivity.

107x241mm (300 x 300 DPI)