

Current use of and future needs for soil invertebrate functional traits in community ecology

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1 **Current use of and future needs for soil invertebrate functional**
2 **traits in community ecology**

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52 **Abstract**

53 Soil invertebrates are assumed to play a major role in ecosystem dynamics, since they are
54 involved in soil functioning. Functional traits represent one of the main opportunities to bring
55 new insights into the understanding of soil invertebrate responses to environmental changes.
56 They are properties of individuals which govern their responses to their environment. As no
57 clear conceptual overview of soil invertebrate trait definitions is available, we first stress that
58 previously-described concepts of trait are applicable to soil invertebrate ecology after minor
59 modification, as for instance the inclusion of behavioural traits. A decade of literature on the
60 use of traits for assessing the effects of the environment on soil invertebrates is then reviewed.
61 Trait-based approaches may improve the understanding of soil invertebrate responses to
62 environmental changes as they help to establish relationships between environmental changes
63 and soil invertebrates. Very many of the articles are dedicated to the effect of one kind of
64 stress at limited spatial scales. Underlying mechanisms of assembly rules were sometimes
65 assessed. The patterns described seemed to be similar to those described for other research
66 fields (*e.g.* plants). The literature suggests that trait-based approaches have not been reliable
67 over eco-regions. Nevertheless, current work gives some insights into which traits might be
68 more useful than others to respond to a particular kind of environmental change. This review
69 also highlights methodological advantages and drawbacks. First, trait-based approaches
70 provide complementary information to taxonomic ones. However the literature does not allow
71 us to differentiate between trait-based approaches and the use of *a priori* functional groups. It
72 also reveals methodological shortcomings. For instance, the ambiguity of the trait names can
73 impede data gathering, or the use of traits at a species level, which can hinder scientific
74 interpretation as intra-specific variability is not taken into account and may lead to some
75 biases. To overcome these shortcomings, the last part aims at proposing some solutions and

76 prospects. It concerns notably the development of a trait database and a thesaurus to improve
77 data management.

78

79 **Keywords:** behaviour, community ecology, constraint, database management system,

80 disturbance, ecological preference, life-history trait, soil fauna, thesaurus

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81 Zusammenfassung

82 Man nimmt an, dass wirbellose Bodentiere eine wichtige Rolle bei der
83 Ökosystemdynamik spielen, da sie am Funktionieren der Böden beteiligt sind.
84 Funktionelle Merkmale bilden eine der wichtigsten Möglichkeiten für ein neues
85 Verständnis der Reaktion von Bodenwirbellosen auf Umweltänderungen. Es
86 handelt sich um Eigenschaften von Individuen, die deren Reaktion auf die
87 Umwelt bestimmen. Da es keinen klaren konzeptionellen Überblick über die
88 Merkmalsdefinitionen für Bodenwirbellose gibt, betonen wir zunächst, dass
89 existierende Konzepte nach geringen Modifikationen auf die Ökologie von
90 Bodenwirbellosen anwendbar sind, wie z.B. das Einbeziehen von
91 Verhaltensmerkmalen. Anschließend betrachten wir ein Jahrzehnt der Literatur
92 zum Gebrauch von Merkmalen bei der Abschätzung der Effekte der Umwelt auf
93 Bodenwirbellose. Merkmalsbasierte Ansätze können unser Verständnis der
94 Reaktionen von Bodenwirbellosen auf Umweltänderungen verbessern, da sie
95 helfen, Beziehungen zwischen Umweltänderungen und Bodenwirbellosen zu
96 etablieren. Sehr viele der Artikel widmen sich dem Effekt eines Stressfaktors auf
97 begrenzten räumlichen Skalen. Die zugrundeliegenden Mechanismen von
98 Vergemeinschaftungsregeln wurden manchmal bestimmt. Die beschriebenen
99 Muster scheinen denen von anderen Forschungsgebieten (z.B. Pflanzen) ähnlich
100 zu sein. Die Literatur legt nahe, dass merkmalsbasierte Ansätze über
101 Ökoregionen hinweg nicht zuverlässig sind. Nichtsdestotrotz lassen aktuelle
102 Arbeiten erkennen, welche Merkmale nützlicher als andere sein könnten, um auf
103 spezielle Umweltveränderungen zu reagieren. Diese Arbeit stellt auch
104 methodische Vor- und Nachteile heraus. Zuerst liefern merkmalsbasierte
105 Ansätze Informationen, die taxonomische ergänzen. Indessen erlaubt uns die
106 Literatur nicht, zwischen merkmalsbasierten Ansätzen und dem Gebrauch von a-
107 priori definierten funktionellen Gruppen zu unterscheiden. Sie zeigt auch
108 methodische Unzulänglichkeiten. So kann z.B. die Mehrdeutigkeit von
109 Merkmalsbezeichnungen das Sammeln von Daten behindern, oder der Gebrauch

110 von Merkmalen auf der Artebene, der die wissenschaftliche Interpretation
111 erschweren kann, da die intraspezifische Variabilität nicht berücksichtigt wird
112 und zu gewissen Verzerrungen führen kann. Um diese Unzulänglichkeiten zu
113 überwinden, hat der letzte Teil zum Ziel, einige Lösungen und Ausblicke
114 vorzuschlagen. Dies betrifft namentlich die Entwicklung einer
115 Merkmalsdatenbank und eines Thesaurus' um die Datenverwaltung zu
116 verbessern.

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120 **Introduction**

121 The current biodiversity estimation of soil fauna assumes that soil is the third biotic frontier
122 after tropical forest canopies and ocean abysses (Swift, Heal & Anderson 1979; André, Noti
123 & Lebrun 1994; Giller 1996; Wolters 2001). The soil fauna encompasses both the obligate
124 and facultative inhabitants of soil and soil annexes (Wolters 2001). Soil annexes are simple
125 structures which diversify the soil surface (*e.g.* tree stumps)(Gobat, Aragno & Matthey 1998).
126 The soil includes a variety of animals from almost all major taxa that compose the terrestrial
127 animal communities and may represent as one quarter of all currently described biodiversity
128 (Decaëns, Jimenez, Gioia, Measey & Lavelle 2006). Soil invertebrates are assumed to play a
129 major role in ecosystem dynamics, since they are involved in soil functioning (*e.g.* carbon
130 transformation and sequestration, regulation of microbial activity or community structure,
131 nutrient turnover, aggregation). Consequently, soil invertebrates contribute to the provision of
132 many ecosystem services such as nutrient cycling or soil structure maintenance (Lavelle,
133 Decaëns, Aubert, Barot, Blouin et al. 2006; Barrios 2007; Kibblewhite, Ritz & Swift 2008).
134 Studying soil invertebrate responses to environmental changes is of great interest. In various
135 research fields (*e.g.* plant ecology), functional components of communities have revealed
136 valuable insights into the understanding of organisms' responses to the environment (McGill,
137 Enquist, Weiher & Westoby 2006; Garnier & Navas 2012). Originally, taxa were grouped
138 into *a priori* functional groups based on certain “characteristics” which they shared. The
139 classification into such functional groups is based on subjective expert judgment. For
140 instance, several plant functional types existed, based on their life form or growth form
141 (Lavorel, McIntyre, Landsberg & Forbes 1997). Conclusions were drawn from these *a priori*
142 functional groups' richness (Villéger, Mason & Mouillot 2008). However these approaches
143 led to several limitations (Villéger et al. 2008) such as (i) a loss of information by imposing a
144 discrete structure on functional differences between taxa, which are usually continuous (Gitay

145 & Noble 1997; Fonseca & Ganade 2001), (ii) a non-robust way of obtaining results depending
146 on the choice of the functional group types in the analysis (Wright, Naeem, Hector, Lehman,
147 Reich et al. 2006) and sometimes (iii) a failure to take account of abundance (Díaz & Cabido
148 2001). As an alternative to the taxonomic and *a priori* functional group approaches, trait-
149 based approaches have been developed (Lavorel & Garnier 2002; McGill et al. 2006). Traits
150 can be divided into response and effect traits. An effect trait is an individual property which
151 affects an upper level of organization (*e.g.* ecosystem processes). Response traits, also called
152 functional traits, are properties of individuals which govern their responses to their
153 environment (Statzner, Hildrew & Resh 2001; Violle, Navas, Vile, Kazakou, Fortunel et al.
154 2007). In the following, traits will mean response traits. Unlike *a priori* functional groups,
155 trait-based approaches are based on objective relations between individual properties (= traits)
156 and the environment. In other research fields, notably for plants, trait-based approaches have
157 brought several new insights to the understanding of organisms' responses to environmental
158 changes, by improving predictability and reducing context dependence (Webb, Hoeting,
159 Ames, Pyne & LeRoy Poff 2010; Garnier et al. 2012). Prediction involves that a relationship
160 must be found between soil invertebrates and environmental changes through their traits. It
161 has been demonstrated that community assembly mechanisms are governed by rules. The
162 literature tends to support the existence of environmental filters which filter a sub-set of
163 individuals of the regional pool to form local communities (Keddy 1992; McGill et al. 2006).
164 Furthermore, environmental filters can be categorized according to the scale on which they
165 work. From larger scales to smaller ones, filters are (i) dispersal filters which select
166 individuals according to their dispersal capacity, (ii) abiotic filters which select individuals
167 according to their capacity to live under certain abiotic conditions and (iii) biotic filters which
168 represent the selection resulting from the interactions between individuals (Belyea &
169 Lancaster 1999; Garnier et al. 2012). Reducing context dependency implies that trait-based

170 approaches have to be: (i) generic over eco-regions and (ii) reliable whatever kind of
171 environmental change is considered. Enough trait-based approach studies have been made on
172 plants to associate one or more traits with one or more environmental changes in any eco-
173 region (Garnier *et al.* 2012). For instance, “leaf area” responds gradually to complex
174 environmental change such as climate change over eco-regions (Thuiller, Lavorel, Midgley,
175 Lavergne & Rebelo 2004; Moles, Warton, Warman, Swenson, Laffan *et al.* 2009).
176 To our knowledge, attempts to relate terrestrial invertebrate responses in terms of their
177 “characteristics” to environmental stress began at the end of the ninetieth century (Statzner *et*
178 *al.* 2001). In 1880, Semper (in Statzner *et al.* 2001) assessed the temperature-induced switch
179 from parthenogenetic to sexual reproduction in aphids. During the following years, authors
180 were convinced that environmental stress and “characteristics” of terrestrial insects were
181 linked (Shelford 1913; Buxton 1923; Hesse 1924; Pearse 1926 - all in Statzner *et al.* 2001).
182 For instance, Buxton (1923 - in Statzner *et al.* 2001) related “characteristics” of terrestrial
183 insects such as the presence of wings or the tolerance of larvae to a lack of food and water to
184 harsh environmental conditions of deserts (*e.g.* drought, torrential rain, whirlwinds).
185 Despite this early interest, no clear conceptual and methodological overview has been made
186 for such “characteristics” of soil invertebrates, which are now called traits. Originally, as for
187 plants, most previous studies assessed soil invertebrate responses to their environment using
188 taxonomic structure and/or composition of communities. As soil invertebrate taxonomic
189 diversity is huge, authors tried to simplify it by grouping together individuals by shared
190 properties. The grouping also dealt with the lack of knowledge of taxonomy. For instance,
191 eco-morphological groups, such as epigeic, anecic and endogeic groups of earthworms
192 (Bouché 1972), epiedaphic, hemiedaphic and euedaphic groups of springtails (Gisin 1943) or
193 terrestrial isopods (Schmallfuss 1984) and functional guilds such as the distinction between
194 ecosystem engineers, litter transformers and micropredators (Lavelle & Spain 2001) were

195 used. For instance, eco-morphological groups bring together individuals based on subjective
196 expert judgments of some of the ecological or biological “characteristics” they share. For
197 instance, epigeic earthworms are pigmented and live near the soil surface, whereas endogeic
198 earthworms are unpigmented and live deep in the soil. As for plants, all of these groupings
199 have been used as *a priori* functional groups and should present the same disadvantages (see
200 above). Experience in other research fields led us to think that using functional trait-based
201 approaches for soil invertebrates represents one of the main opportunities to bring new
202 insights into the understanding of soil invertebrate responses to the environment.

203 To our knowledge, no attempt has been made to clearly define functional trait concepts for
204 soil invertebrates. The concept already existed but was used in other research fields. As a
205 consequence, we first determine whether the actual definitions around the notion of traits are
206 applicable to soil invertebrates. Second, to summarise the current advances in the
207 understanding of soil invertebrate responses to the environment through their traits, a one-
208 decade literature review was made. It also aimed to focus on current methodological
209 advantages and drawbacks of soil invertebrate trait-based approaches. The last part envisages
210 solutions and prospects for overcoming current conceptual and methodological drawbacks. It
211 notably deals with the development of eco-informatics tools.

212

213 **Are existing trait definitions applicable to soil invertebrates?**

214 From work on terrestrial plants (Lavorel, Díaz, Cornelissen, Garnier, Harrison et al. 2007) or
215 aquatic invertebrates (Bonada, Prat, Resh & Stutzner 2006), traits are being defined as
216 properties of organisms measured at the individual level (Violle et al. 2007). Furthermore, a
217 trait is qualified as “functional” when it influences the organism’s performance and
218 consequently its fitness (Southwood 1977; Nylin & Gotthard 1998; Blanck, Tedesco &
219 Lamouroux 2007; Violle et al. 2007; Webb et al. 2010). Some authors distinguish the

220 performance traits from morphological, phenological and physiological traits (“M-P-P” traits).
221 Performance traits describe growth, reproduction and survival, considered as being the three
222 components of fitness (Arnold 1983; McGill et al. 2006; Violle et al. 2007). Three main
223 performance traits are recognized in plant ecology: vegetative biomass, reproductive output
224 and measured plant survival (Violle et al. 2007). Conversely, “M-P-P” traits are supposed to
225 influence fitness indirectly by influencing performance traits. In addition, plant abiotic
226 preferences are denominated “Ellenberg’s numbers” and reflect optima/ranges in
227 environmental gradients (Ellenberg 1988). In aquatic invertebrate ecology, traits are usually
228 split into biological and ecological traits (Dolédec, Statzner & Bournard 1999). Biological
229 traits include M-P-P and life-history traits, while ecological traits reflect behaviour and
230 ecological optima/ranges in environmental gradients.

231 Regarding soil fauna, many functional traits considered in the literature are related to
232 morphology, physiology or phenology (Ribera, Dolédec, Downie & Foster 2001; Barbaro &
233 van Halder 2009; Vandewalle, de Bello, Berg, Bolger, Dolédec et al. 2010; Pérès,
234 Vandenbulcke, Guernion, Hedde, Beguiristain et al. 2011) matching the definition proposed
235 by Violle et al. (2007). The literature used, for instance, carabid beetle eye diameter or wing
236 form for morphology, carabid beetle breeding season for phenology (Ribera et al. 2001;
237 Vandewalle et al. 2010) or springtail reproductive mode for physiology (Malmstrom 2012).

238 However, behaviour, such as “hunting strategy” (Langlands, Brennan, Framenau & Main
239 2011), is a crucial component in animal fitness that was not taken into account in Violle’s
240 definition as the definition was stated for plants. For animals other than soil invertebrates,
241 behaviour was semantically included (i) in a “biological traits” group, (ii) in an “ecological
242 traits” group or (iii) in a semantically dedicated “behavioural traits” group (Relya 2001;
243 Bonada, Dolédec & Statzner 2007; Frimpong & Angermeier 2010). Behaviour can be defined
244 as an organized and directed biological response to variations in the environment to suit the

245 individual's requirements (adapted from (Barnard 2004))). The environment refers both to the
246 biocenosis and the biotope. We propose to extend Violle et al.'s (2007) definition of a
247 functional trait for soil invertebrates as follows: "any morphological, physiological,
248 phenological or behavioural (MPPB) feature measurable at the individual level, from the cell
249 to the whole-organism level, without reference to any other level of organization" (Table 1).
250 Furthermore, as for plants, we can distinguish MPPB traits from performance traits. The
251 performance traits for soil invertebrates could be for instance: biomass, offspring output and
252 measured survival. Population parameters can be derived from the median, mean and/or
253 breadth of distribution of a trait (aggregated values of a MPPB or a performance trait, Table
254 1).

255 In addition, some of the functional traits used in the literature refer to properties of the
256 environment in which individuals of a given species live. For instance, authors used the term
257 "soil moisture preferences" (Makkonen, Berg, van Hal, Callaghan, Press et al. 2011) to
258 express the breadth of the occurrence distribution of individuals of a species along a soil
259 moisture gradient. We propose to call "ecological preference" any value which results from
260 the optimum and/or the breadth of distribution of a trait along an environmental gradient
261 (Table 1).

262 Finally, authors called "life-history traits" (Stearns 1992) or "life-cycle traits" a wide range of
263 data such as moisture preference (Bokhorst, Phoenix, Bjerke, Callaghan, Huyer-Brugman et
264 al. 2012), adult daily activity (Barbaro et al. 2009) or body size estimated for a species
265 (Malmstrom 2012). Life-history traits need to be renamed, depending on their nature. In our
266 examples, moisture preference will be classified as an "ecological preference", while adult
267 daily activity and body size estimated for a species are "population parameters derived from a
268 trait".

269 **Trait-based approaches for soil invertebrate community ecology**

270 *Methods for literature review*

271 A literature review was made from the ISI Web of Knowledge research platform using the
272 search terms “trait” and “soil” or “ground” with each vernacular or taxonomic name of four
273 groups: earthworms, ground beetles, spiders and springtails. The taxonomic groups were
274 chosen because they represent a wide range of biological strategies and were often used as
275 bio-indicators. Papers were selected according to several criteria described below. The term
276 “trait” must have directly concerned soil invertebrates. To keep the scope of our study as
277 restricted as possible, we only selected studies dealing with the effects of environmental
278 changes on soil invertebrates. We did not include approaches exclusively dealing with other
279 ecological questions or dedicated to evolutionary questions (*e.g.* adaptation, speciation).
280 However, we are aware that ecological and evolutionary questions can overlap, notably when
281 considering links between phylogeny and trait conservation (Cavender-Bares, Kozak, Fine &
282 Kembel 2009). Reviews (with no original data) and methodological papers were excluded.
283 Searches were limited to papers published since 2000 as the use of the term “trait” in soil
284 invertebrate ecological studies is quite recent. We may have failed to find some papers as the
285 word “trait” was not used in some papers even though a trait-based approach was used. This
286 highlights the fact that the trait concept suffers from semantic inconsistency for soil
287 invertebrates as stated in the previous section. However, we chose to look for literature on
288 measurable criteria (as mentioned above), especially by using the search word “trait”, rather
289 than on studies based on expert knowledge, even though this meant excluding a considerable
290 number of papers. For instance, some studies using a trait-based approach have not been
291 collected, *e.g.* for carabid beetles (Vanbergen, Woodcock, Koivula, Niemelä, Kotze et al.
292 2010), springtails (Ponge, Dubs, Gillet, Sousa & Lavelle 2006), earthworms (Jimenez,
293 Decaëns & Rossi 2012), spiders (Lambeets, Vandegheuchte, Maelfait & Bonte 2008; Le Viol,
294 Julliard, Kerbiriou, de Redon, Carnino et al. 2008; Lambeets, Vandegheuchte, Maelfait &

295 Bonte 2009; Cristofoli, Mahy, Kekenbosch & Lambeets 2010) and for multiple groups (Bell,
296 Mead, Skirvin, Sunderland, Fenlon et al. 2008; Jennings & Pocock 2009; Moretti & Legg
297 2009; De Lange, Lahr, Van der Pol & Faber 2010; Hedde, van Oort & Lamy 2012). However,
298 we are confident in the representativeness of the literature review, which found 4, 17, 4 and 6
299 papers for earthworms, ground beetles, spiders and springtails respectively (Table 2).

300 *Scientific advances and drawbacks*

301 All the literature showed, as for other research fields, that some environmental filters filter a
302 sub-set of individuals from a regional pool to form local communities according to some of
303 their traits. Most of the studies were dedicated to assess soil invertebrate response to some
304 kind of stress (Table 2). For instance, Barbaro et al. (2009), Driscoll et al. (2005) and Ribera
305 et al. (2001) assessed mechanisms of carabid beetle responses to habitat types according to
306 their traits (*e.g.* body size, wing development, Table 2). Underlying mechanisms of assembly
307 rules were sometimes assessed. For instance, Decaëns et al. (2008) demonstrated that some
308 abiotic environmental filters led to a trait convergence for earthworms. Decaëns et al. (2011)
309 revealed that the variability of morphological earthworm traits was lower in the regional
310 species pool and higher in the local species pool compared to what would have been expected
311 by chance. As very few examples were given, such patterns cannot be used as general patterns
312 for soil invertebrate assembly rules. However, the patterns described seemed to be similar to
313 those described in the introduction for other research fields. These results claimed that soil
314 invertebrate trait-based approaches help to improve predictability of community assembly in
315 relation to environmental changes as they materialise relationships between traits and
316 environmental changes.

317 Almost all of the studies assessed the responses of soil invertebrates in relation to only one
318 kind of environmental change. Some exceptions were found. For instance, Gobbi et al. (2010)
319 aimed to assess both the abiotic effect of deglaciation and the biotic effect of plant

320 communities on carabid beetle communities. While individual studies usually dealt with a
321 single change, environmental changes studied were diverse among studies. They included
322 “natural” changes such as habitat type, fire, flooding or climatic events and also “anthropic”
323 changes such as invasive tree species or human practices on cultivated fields or forests (Table
324 2). In addition, studies were geographically limited to the regional scale (sensu Belyea et al.
325 1999). Some exceptions occurred, *e.g.* Vandewalle et al. (2010) who sampled carabid beetles
326 in several European countries. They assumed that the responses of functional diversity indices
327 calculated from traits (*e.g.* Rao index of diversity, Botta-Dukat 2005) to habitat composition
328 and landscape heterogeneity were consistent across geographical regions.

329 To conclude, we cannot be confident in trait genericity over eco-regions, as this was rarely
330 studied (Vandewalle et al. 2010). Despite these shortcomings in reducing the context
331 dependence, the literature currently gives us some insights as to which traits might be more
332 useful than others to respond to a particular kind of environmental change. For instance, it has
333 been shown that ground beetle wing development varies with habitat type in different contexts
334 (Ribera et al. 2001; Driscoll & Weir 2005; Gobbi & Fontaneto 2008; Barbaro et al. 2009;
335 Gobbi, Caccianiga, Cerabolini, Bernardi, Luzzaro et al. 2010; Vandewalle et al. 2010). To
336 make the trait-based approaches reliable whatever the kind of environmental changes, we
337 have to establish relationships between each kind of environmental change with one or several
338 traits.

339 *Methodological advantages and drawbacks*

340 *Complementarity with other approaches*

341 From a methodological point of view, trait-based approaches bring new insights into the
342 understanding of soil invertebrate responses to stress, compared to taxonomic approaches
343 (Cole, McCracken, Dennis, Downie, Griffin et al. 2002; Gobbi et al. 2008; Langlands et al.
344 2011). First, inverse trends between results obtained by trait-based and taxonomic approaches

345 were reported. For example, Gerisch, Agostinelli, Henle & Dziock (2012) showed that the
346 species diversity of ground beetle communities increased whereas functional diversity
347 (functional evenness and divergence) decreased with increasing flooding disturbances. This
348 combined approach led the authors to conclude that flooding disturbance increased the
349 number of species but that species were functionally redundant. Otherwise, Gobbi et al.
350 (2008) showed that ground beetle traits such as wing morphology, diet and body size
351 responded to habitat diversity, while species richness and a taxonomic diversity index based
352 on phylogeny did not. The authors therefore claimed that trait-based approaches should be
353 favoured for assessing mechanisms of carabid beetle responses to habitat disturbance rather
354 than taxonomic approaches. In other cases, trait-based approaches complemented the
355 conclusions based on taxonomic approaches. For instance, in a study by Fournier, Samaritani,
356 Shrestha, Mitchell & Le-Bayon (2012), community-weighted means of earthworm traits (*e.g.*
357 body length and width, pH optimum and range) were more strongly correlated with
358 environmental variables (*e.g.* total carbon, gravel sizes, type of cover, such as mosses, woody
359 debris) than species composition and taxonomic diversity. However, no study aimed at
360 comparing approaches based on *a priori* functional groups (*e.g.* eco-morphological groups)
361 with trait-based approaches.

362 *Deficiencies in trait definitions, data treatment and gathering structure*

363 The literature review revealed semantic inconsistencies for trait names. For instance, the type
364 of materials eaten by soil invertebrates (*e.g.* carnivorous) and the way they feed on them (*e.g.*
365 as predators, *i.e.* by killing their preys). However, the literature revealed several categorical
366 traits whose attributes could describe several of the above concepts simultaneously. For
367 instance, “food of the adult” (Cole et al. 2002; Ribera et al. 2001) referred both to the type of
368 food eaten (*e.g.* plant, springtails) but also to the way it was eaten (*e.g.* generalist predators)
369 whereas “diet” (Barbaro et al. 2009) refers only to the first one. Such drawbacks occurred

370 within a taxon but also among taxa. They can hinder data gathering in so far as they can cast
371 doubt on a trait's scientific meaning.

372 At the moment, soil invertebrate trait-based approaches used traits at the species level. Such a
373 process can lead to two main biases. A first bias occurs when the trend of the relationship
374 between the mean trait of N species and an environmental gradient is in the opposite direction
375 to the relationships between this environmental gradient and individual trait values. The
376 second bias is that using traits at the species level hides individual heterogeneity.

377 Traits can be described in two formats, numerical data (*e.g.* eye diameter, (Ribera et al. 2001))
378 or by text (*e.g.* pigmentation, wing form, (Vandewalle et al. 2010)). Format heterogeneity and
379 the missing data impeded the use of traits. It has been suggested that traits should be encoded
380 into a limited number of subsets (Chevenet, Dolédec & Chessel 1994; Hedde et al. 2012). For
381 all of these reasons, some authors discretized data into attributes, *e.g.* by fuzzy coding
382 procedures (*e.g.* body size classes, (Jelaska, Jesovnik, Jelaska, Pirnat, Kucinic et al. 2010) or
383 diet, (Pérès et al. 2011)). When working on one or several taxonomic groups, it was crucial to
384 be able to deal with different data formats. However when this was done, the way data were
385 transformed by fuzzy coding was not clearly explained. This impedes the comparison between
386 studies using a trait shared by one or several groups but not necessarily using the same coding
387 procedure (*e.g.* different categories for the diet) (Barbaro et al. 2009; Gerisch 2011). It also
388 limits the reuse of an encoded trait from the literature as readers do not know exactly how the
389 trait was encoded.

390 Exploiting existing literature was preferred to time-consuming trait measurements on sampled
391 specimens. Whatever the methodology, the review of literature underlined the lack of a data-
392 compilation structure for soil invertebrate traits. Depending on the author, a trait could be
393 described from different literature sources. Cole et al. (2002) and Karen, O'Halloran, Breen,
394 Giller, Pithon et al. (2008) described body size trait values for *Nebria brevicollis* (Fabricius)

395 from two different literature sources. As a consequence, works do not benefit each other as no
396 data-compilation allows authors to have access on existing trait data.

397 A general shortcoming which is not often considered in the current literature is the fact that
398 traits used in a study can be inter-correlated (“trait syndromes”) (Poff, Olden, Vieira, Finn,
399 Simmons et al. 2006). Inter-correlation can therefore cause that traits appear decoupled from
400 environmental changes (Statzner, Dolédec & Hugueny 2004; Poff et al. 2006). Generally, trait
401 selection for analyses was *a priori* justified on the basis of the biological function they are
402 supposed to be linked with. For instance, (Langlands et al. 2011) selected the body shape of
403 spiders, as spiders with flattened bodies are supposed to shelter better from fire. Apart from
404 this view, no analysis has been described to identify “trait syndromes” before performing
405 linking traits to environmental variables. Exception was made for certain studies (Gobbi et al.
406 2008).

407 **Future needs: eco-informatics at a crossroad**

408 The following prospects are not limited to the four taxa used in the literature search. They are
409 suitable for all the soil invertebrate taxa. Large amounts of data from multiple data sources
410 need to be characterized and integrated into a unified corpus in order to improve soil
411 invertebrate trait-based approaches. Current eco-informatics literature provides a basis for a
412 global scheme to structure ecological data (Madin, Bowers, Schildhauer, Krivov, Pennington
413 et al. 2007; Garnier et al. 2012). Between non-robust data storage by scientists (*e.g.*
414 spreadsheets, relational database systems) (Jones, Schildhauer, Reichman & Bowers 2006)
415 and their exploitation by software tools (*e.g.* “R Statistical Package”) (R Development Core
416 Team 2010), an intermediate level is needed. It requires linking data with metadata, which are
417 information used to document and interpret data (Jones et al. 2006). Such a level would
418 greatly enhance data management (storage, integrating, querying, and analysing) by
419 producing robust traceability. One way is to construct a database management system

420 (DBMS) for soil invertebrate traits which could associate metadata with data. First are
421 “scientific” metadata describing scientific data (*e.g.* information usually provided in the
422 Materials and methods section). Scientific metadata provide all the necessary information for
423 acquiring, interpreting and using scientific data. Second are “computer” metadata required for
424 computerisation (*e.g.* metadata required for the database structure, semantic metadata). They
425 principally allow acquisition and automated input, analysis and processing of scientific data
426 by the computer (Michener 1997; Michener 2006). Associating data to metadata in a DBMS
427 provides several advantages. Data longevity (data history) and quality (control of the nature of
428 data) are increased. Data could be easily reused and integrated. Finally data sharing is
429 facilitated (Jones et al. 2006; Michener 2006). DBMS *per se* possesses sorting, indexing and
430 querying functions which increase data interpretation and use (Porter 1998). A few databases
431 for soil invertebrates already exist: for instance, Edaphobase (Russell, Vorwald, Franzke,
432 Höfer, Horak et al. 2012), Coltrait (Salmon & Ponge 2012), the Dutch soil invertebrate trait
433 database (from M.P. Berg) (Makkonen et al. 2011), Macrofauna (Lapied, personal
434 communication), and Ant Profiler (Bertelsmeier, Luque, Confais & Courchamp 2012).
435 Nevertheless, they do not always contain trait data or are not always in a format which allows
436 collaborative data sharing. Even if they fulfil such criteria, they tend to be concerned with a
437 small part of the whole diversity of soil invertebrates (usually a single group is concerned).
438 Computer science solutions currently exist to gather data from different sources (Jones et al.
439 2006; Michener 2006), so previous soil invertebrate databases should not be seen as isolated
440 islands (Jones et al. 2006) but as complementary bricks which can be combined to create new
441 soil invertebrate trait databases. However, combining data from different formats, especially
442 from spreadsheets, is not easy (Jones et al. 2006).
443 Among the existing solutions, semantic data integration is a promising way which preserves
444 the scientific meaning of data. Semantic approaches deal with the differences in the terms

445 used (terminology) and the scientific concepts formulated by soil invertebrate experts over
446 time (Madin et al. 2007; Laporte, Mougenot & Garnier 2012). To achieve this, the soil
447 invertebrate scientific community is required to standardize meaningful and precise terms that
448 cover their domain of interest. Trait names are especially concerned, taking a central position
449 in trait-based approaches in the context of the responses of soil invertebrates to their
450 environment. A thesaurus of a particular domain reflects a community agreement on a set of
451 terms established in a given area and its organization through a well-designed structure.
452 Furthermore, a thesaurus is recognized as a knowledge organization system and bypasses
453 ambiguity issues in natural language, controlling and clarifying the access and exchange of
454 information and facilitating communication. The main concern focuses on access, sharing and
455 dissemination of information within the soil invertebrate scientific community. First, a soil
456 invertebrate trait thesaurus can serve as a stable reference resource, specifically when
457 published in RDF (Resource Description Framework) language (Manola & Miller 2004) and
458 available as linked data on the web. A second prospect is to include such a thesaurus in soil
459 invertebrate trait databases to facilitate data management. A third, more long-term prospect,
460 involves the use of the thesaurus as a prerequisite for the construction of a soil invertebrate
461 trait ontology. To conclude, it would be of major assistance for the soil invertebrate scientist
462 community to have access to knowledge-based models enabling the efficient answering of
463 questions, which, for example, may require the data aggregation of different traits from
464 several taxa.

465 Effort on data management using eco-informatics tools will fill some gaps revealed by the
466 literature review. First, it will strengthen current scientific advances. By increasing the
467 collection of trait data and associated environmental parameters, it will offer the possibility of
468 considering the actions of several environmental filters on different spatial and temporal
469 scales (see section “Scientific advances and drawbacks”). It will also aim to establish

470 consistent “population parameters derived from traits” and “ecological preferences” (Table 1)
471 by increasing the number of literature sources informing trait values used to calculate them.
472 All of this will contribute to a better general understanding of soil invertebrate responses to
473 the environment from local to biogeographical scales, which was not always possible from
474 independent single studies. The data gathering structure should also improve knowledge of
475 soil invertebrate group interactions, since it will become possible to work on several groups
476 and taxa with several comparable traits.

477 Second, it will help with some methodological shortcomings. It will improve the possibility of
478 dealing with (i) inter-correlation of traits and (ii) bias when using traits on the species level
479 (see section “Deficiencies in trait definitions, data treatment and gathering structure”). On the
480 one hand (i), “trait syndromes” could be more easily revealed because the data gathering
481 structure should provide a large body of available documented traits. We recommend testing
482 for inter-correlation of traits before drawing conclusions (*e.g.* fuzzy correspondence analysis,
483 “ade4” R package, (Chessel, Dufour & Thioulouse 2004)). One other solution which has not
484 been tested for soil invertebrates since not enough trait data have yet been gathered, is the
485 screening method (Bernhardt-Römermann, Römermann, Nuske, Parth, Klotz et al. 2008).
486 This allows the best combination of traits to be found for an environmental change. On the
487 other hand (ii), with the increasing number of trait values measured on individuals rather than
488 compiled at species or higher taxonomic level, it will provide the opportunity to put much
489 more intraspecific variability into the assessment of functional diversity. It is a way to
490 overrule bias when using traits at a species level.

491 Although the data gathering structure will enable the collection of data documenting traits
492 from all sources (*e.g.* articles, books) and from all formats, *i.e.* numerical data (*e.g.* body size
493 distribution) and literal data (*e.g.* text descriptions of diets), it will not deal with the definition
494 of similar fuzzy coding protocols (see section “Deficiencies in trait definitions, data treatment

495 and gathering structure”). For instance, we propose two main protocols: one for traits
496 described by numerical values and another for traits described by textual data (see Appendix
497 A).

498

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505

505 **Tables**

506 Table 1. Definitions of trait concepts for soil invertebrates.

507

Concept	Definitions
<i>MPPB trait</i>	Any morphological, physiological, phenological or behavioural (MPPB) feature measurable at the individual level, from the cell to the whole-organism level, without reference to any other level of organization
<i>Performance trait</i>	Performance traits describe growth, reproduction and survival, considered as being the three components of fitness (Violle et al. 2007). For soil invertebrates there are for instance: biomass, offspring output and survival
<i>Ecological preference</i>	The optimum and/or the breadth of distribution of a trait on an environmental gradient.
<i>Population parameters derived from traits</i>	The median, mean and/or breadth of distribution of a trait (aggregated values of a MPPB or a performance trait).

508

509

510 Table 2. Results of the literature review and some of the properties of the selected articles. LIT: trait data from the literature, OMS: original
 511 measurements of traits. Without any specific information, we assumed that trait data had been derived from the literature.
 512

Reference	Soil invertebrate group	Environmental change	LIT or OMS	Traits
Decaëns et al. (2011)	Earthworms	Habitat (different aged pastures)	LIT	(Ecological category), body length, diameter, weight, epithelium type, pigmentation
Decaëns et al. (2008)	Earthworms	Habitat	LIT	Size, weight, pigmentation, (ecological categories, ecological features)
Fournier et al. (2012)	Earthworms	Flooding	LIT + OMS	Length, width, weight, segment number, pH optimum, pH range, prostomium type, (ecological type), C/N (soil) preference
Pérès et al. (2011)	Earthworms	Contamination and land use	LIT	Body pigmentation, body wall thickness, food, reproductive strategy, rarity
Bonte et al. (2006)	Spiders	Sand dynamics	LIT + OMS	Mean size, local activity-density, niche breath, ballooning, seasonal activity, generation time, diurnal activity
Buchholz (2010)	Spiders	Climate (drought)	/	/
Langlands et al. (2011)	Spiders	Fire	LIT + OMS	Burrowing, body size (length), cephalothorax heavy sclerotisation, abdominal scutes, ballooning, time to maturity, phenology, hunting strategy, diet specialization (ants), flattened body
Tropek et al. (2008)	Spiders	Stone quarry	/	/
Bokhorst et al. (2012)	Springtails	Climate (winter warming)	LIT + OMS	(Life form), biomass, body length, moisture preference, vertical stratification

Huebner et al. (2012)	Springtails	Fire	LIT	Dente shape, eye number, total body length, furcula, pigmentation, body scales, PAO, antennae length, antennal organ, sexual dimorphism
Lindberg & Bengtsson (2005)	Springtails	Climate (drought)	LIT + OMS	Depth distribution, reproductive mode, habitat specialization, (ecological category) Ocelli number, body size, body pigmentation level, body pigmentation pattern, modified hairs or scales, furca development, antenna/body, moisture preference, habitat width
Makkonen et al. (2011)	Springtails	Climate	LIT	Habitat (vertical stratification), body size, reproductive mode, dispersal traits
Malmstrom (2012)	Springtails	Fire	LIT + OMS	Ocelli, antenna length, furca, hairs/scales, pigmentation
Vandewalle et al. (2010)	Springtails	Invasive tree species	LIT	European trend, European rarity, regional rarity, biogeographic position, daily activity, diet, overwintering, body colour, breeding season, body size (mm), wing development, adult activity period
Barbaro et al. (2009)	Ground beetles	Habitat (fragmentation)	LIT	Size (length), overwintering, life cycle duration, adult food, daily activity, breeding season, emergence, main activity, wing morphology, locomotion
Cole et al. (2002)	Ground beetles	Habitat (agricultural management)	LIT	Flight, trophic group, adult primary position, size
Driscoll et al. (2005)	Ground beetles	Habitat (fragmentation)	LIT	Wing morphology, overwintering strategy (reproduction season), body size
Gerisch et al. (2012)	Ground beetles	Flooding	LIT	Body size, wing morphology, reproduction period, overwintering stage, daily activity, colour elytra,
Gerisch (2011)	Ground beetles	Flooding	LIT	

				body pubescence, food type
Gobbi et al. (2010)	Ground beetles	Deglaciated terrain and plants	/	Brachypterous, autumn-breeding, predators, average body length
Gobbi et al. (2008)	Ground beetles	Habitat	LIT	Wing morphology, body length, diet
Grimbacher & Stork (2009)	Ground beetles	Climate (seasonality)	LIT + OMS	Feeding ecology, body size, habitat strata, mean period of activity
Jelaska et al. (2010)	Ground beetles	Habitat (natural temperate forests)	LIT + OMS	Body size
Karen et al. (2008)	Ground beetles	Habitat (forest cycle plantation)	LIT	Broad habitat associations, body size, wing-type, microhabitat associations
Liu et al. (2012)	Ground beetles	Habitat (human practices on semi-natural habitats and cultivated fields)	LIT & OMS	Trophic status, body size
Ribera et al. (2001)	Ground beetles	Habitat (land disturbance)	LIT + OMS	Eye diameter, antenna length, pronotum maximum width, pronotum maximum depth, elytra maximum width, metafemur length, metatrochanter length, metatarsi length, metafemur maximum width, total length, leg color, body color, wing development, pronotum shape, overwintering, adult food, daily activity, breeding season, main period of adult emergence, main period of adult activity
Silva et al. (2011)	Ground beetles	Habitats (orchard and riparian)	LIT	Moisture preferences
Tropek et al. (2008)	Ground beetles	Stone quarry	/	/
Vandewalle et al. (2010)	Ground beetles	Habitat (composition and	LIT	Wing form, body pubescence, body length, elytra width, elytra

		landscape heterogeneity)		length, femora length, femora width, tibiae length, metatarsus length, pronotum height, pronotum length, eye diameter, antennae length, body black, body pale, legs black, legs pale, anthropic
Verhagen et al. (2008)	Ground beetles	Habitat (removal of topsoil on former agricultural fields)	LIT	Habitat preference (characterization and amplitude), dispersal capacity (flying), occurrence, size
Warnaffe & Dufrene (2004)	Ground beetles	Habitat (forest management)	LIT	Mean size, wing development

513

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- 783
- 784

1 **Appendix A. Supplementary data**

2

3 The heterogeneity of data informing trait (numeric, textual), the missing data and finally the
4 heterogeneity of individuals within and between taxa led authors to transform trait raw data to
5 (i) allow their comparison and (ii) reduce continuous data into a limited number of subsets.

6 The fuzzy coding is one of the techniques which allowed the synthesis of data informing trait
7 from different formats by their discretization into trait sub-classes called “categories”
8 (Chevenet, Dolédec & Chessel 1994).

9 In soil invertebrate ecology, the main aim of the fuzzy coding is to discretize data informing a
10 trait for a taxon into categories. Category choice is *a priori* done and must be thought out from
11 sound biological hypotheses and from the accuracy of data informing trait. For instance, the
12 “integument sclerotization” trait could be divided into 2 categories: unsclerotized or
13 sclerotized. The thesaurus described in our review can serve as a stable semantic reference
14 which fixes both trait names but also their category number and names (also category name
15 synonyms).

16

17 Once trait categories were defined, the information for a taxon obtained from a literature
18 source must be coded for each trait category by an affinity score. For instance, affinity scores
19 can range from 0 to 3, from no to very high affinity of the taxon to a trait category. Then,
20 affinity scores of several sources of a trait were converted to a percentage for building a trait
21 profile for the considered taxon.

22

23 The way an affinity score is attributed to the categories was generally not clearly explained in
24 the literature review. That is a point we want to fix in this review by proposing detailed
25 protocols depending on the data format informing the trait.

26

27 **Trait informed by numerical data**

28 Literature sources commonly proposed one or several values for a trait. We propose to only
29 use the minimum and the maximum values. Then, affinity scores are attributed to each *a*
30 *priori* category. For each category, it is done according to “the space of the interval between
31 the maximum and the minimum category values” occupied by “the interval between the
32 maximum and the minimum trait values”. For this, each category interval was divided into
33 three sub-categories:

- 34 • $[a ; a + (b-a)*1/3 [$ which represents the first 33% of the category interval
- 35 • $[a + (b-a)*1/3 ; a + (b-a)*2/3 [$ which represents the middle 33% of the category
36 interval
- 37 • $[a + (b-a)*2/3 ; b [$ which represents the last 33% of the category interval

38 where a and b are the minimum and the maximum values of the category.

39

40 Then if the interval between the maximum and the minimum trait values is included into

- 41 • No sub-category, then the affinity will be **0**.
- 42 • One sub-category, then the affinity score will be **1**.
- 43 • Two sub-categories, then the affinity score will be **2**.
- 44 • Three sub-categories, then the affinity score will be **3**.

45

46 Then, affinities scores of several sources for a trait were converted to percentages building a
47 trait profile for the considered taxon.

48

49 Example:

50 We took the maximum and minimum body length of *Lumbricus castaneus* from different
 51 literature sources (Table 1).

52 **Table 1. Examples of minimum and maximum body length values for *Lumbricus castaneus* from two literature sources**

Source	Minimum body length (mm)	Maximum body length (mm)
Bouché (1972)	25	60
Sims & Gerard (1985)	30	45

53
 54 We proposed to divide the body length trait into 6 categories: [20;35[, [35;50[, [50;100[,
 55 [100;150[, [200;400[. Then we attribute the affinity scores by category following the rules
 56 above described (Table 2). For instance, the Bouché's interval (25-60) is not included into the
 57 first sub-category [20;25[but is included into the two other sub-categories [25;30[and [30;35[
 58 of the first category [20;35[. As a consequence, affinity score for the first category for Bouché
 59 is 2. The second category [35;50[is completely filled by the Bouché's interval (25-60). That
 60 is why the affinity score is 3.

61 **Table 2. Affinity scores for *Lumbricus castaneus* from two literature sources**

Source	[20;35[[35;50[[50;100[[100;150[[200;400[
Bouché (1972)	2	3	1	0	0
Sims et al. (1985)	1	3	0	0	0

62
 63 Finally, affinity scores of several sources were converted to percentages to create a trait
 64 profile (Table 3). For instance, for the first category, the percentage is calculated as being the
 65 ratio between the sum of affinity scores for this category (2+1) and the sum of all the affinity
 66 scores (10).

67 **Table 3. Trait profile for *Lumbricus castaneus***

Taxon	[20;35[[35;50[[50;100[[100;150[[200;400[
<i>Lumbricus castaneus</i>	0.3	0.6	0.1	0	0

68
 69 **Trait informed by textual data**

70 The text informing a trait generally contains two kinds of information: (i) some words which
 71 correspond to category names or their synonyms and (ii) adjectives which qualify categories.

72 For instance, the diet description for *Amara aenea* from (Brandmayr 1972) “Italy, in the field:
73 mostly seeds” contains the word “seed” which corresponds to a category of the “diet” trait and
74 “mostly”, an adverb. An affinity score must be attributed to each *a priori* category. We
75 propose to do this according to (i) the number of categories embodied in a given literature
76 source and (ii) the strength of adverbs characterizing each category. To do this, we first build
77 a correspondence table (Table 4) between the frequently found adverbs in the literature and
78 their strength.

79 **Table 4. Correspondence table between adjectives and their strength**

Strong	Medium	Weak
absolutely	almost	absent
almost entirely	common(ly)	accidentally
almost exclusively	frequently	episodically
always	generally	exceptionally
constantly	moderately	few
continually	moderately	infrequently
decidedly	more (in, during)	less frequently
definitely	mostly	maybe
entirely	often frequent	mentioned
especially	particularly numerous	missing
essentially	preferably	more or less
exceptionally	quite often	never
fully	regularly	occasionally
mainly	to like	optionally
majority	to prefer	partially
maximum	to require	possibly
numerically dominant in	usually	presumed to be
overwhelmingly	well known	probably
particularly		rarely
persistently		scarcely
predilection for		slightly
predominantly		sometimes
purely		sometimes
significantly		somewhat
specialist		sporadically
specially		to seem to
specifically		to tolerate
strictly		transiently
strong		only
strongly favoured		
strongly influenced by		

surely
systematically
to avoid
typical

80

81 Then, we develop rules to determine affinity scores:

82 • If there is no adverb:

83 ○ and words of a given literature source correspond to more (>) than 2
84 categories, then the category will receive an affinity score of **2**

85 ○ and words of a given literature source corresponds to 1 or 2 categories, then the
86 category will receive an affinity score of **3**

87 • If there are adverbs whose:

88 ○ strength is “weak”, then the category will receive an affinity score of **1**

89 ○ strength is “medium”, then the category will receive an affinity score of **3**

90 ○ strength is “strong”

91 ▪ and words of a given literature source correspond to more (>) than 2
92 categories, then the category will receive an affinity score of **3**

93 ▪ and words of a given literature source correspond to 1 or 2 categories,
94 then the category will receive an affinity score of **4**

95

96 Example:

97 The diet of *Loricera pilicornis* is described in different literature sources (Table 5).

98 **Table 5. Examples of diet description for *Amara aenea* from two literature sources**

Source	Diet description
Davies (1953)	England, in the field: food of adults: collembola, spiders and pollen
Ribera, Doledec, Downie & Foster (2001)	Mostly collembola

99

100 We proposed to divide the diet trait into 5 categories: detritivore, microbivore-
 101 microphytophagous, phytophagous, geophagous, zoophagous. Then we attribute the affinity
 102 scores by category following the rules above described (Table 6). In the first source, the
 103 sentence contains the words corresponding to 2 categories: “collembolan” and “spiders” for
 104 the zoophagous category and “pollen” for the phytophagous category. As there are no adverb,
 105 affinity scores are 3 for both categories. In the second source, the sentence contains a word
 106 “collembola” corresponding to the zoophagous category. A “strong” adjective is present. The
 107 affinity score is therefore 4.

108 **Table 6. Affinity scores for *Loricera pilicornis* from two literature sources**

Source	Detritivore	Microbivore	Phytophagous	Geophagous	Zoophagous
Davies (1953)	0	0	3	0	3
Ribera et al. (2001)	0	0	0	0	4

109

110 Finally, affinity scores of several sources were converted to percentages to create a trait
 111 profile (Table 7). For instance, for the zoophagous category, the percentage is calculated as
 112 the ratio between the sum of affinity scores for this category (3+4) and the sum of all the
 113 affinity scores (10).

114 **Table 7. Trait profile for *Lumbricus castaneus***

Taxon	Detritivore	Microbivore	Phytophagous	Geophagous	Zoophagous
<i>Loricera pilicornis</i>	0	0	0.3	0	0.7

115

116

117

118 **References for the Appendix**

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