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## **A common framework for developing robust soil fauna classifications**

Mickael Hedde, Olivier Blight, Maria J.I. Briones, Jonathan Bonfanti, Alain A. Brauman, Margot Brondani, Irene Calderón Sanou, Julia Clause, Erminia Conti, Jérôme Cortet, et al.

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1 **Title:** A common framework for developing robust soil fauna classifications

2

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29 **Abstract**

30 Classifying organisms has a wide use and a long history in ecology. However, the meaning of  
31 a 'group of organisms' and how to group organisms is still the subject of much theoretical and  
32 empirical work. Achieving this long quest requires simplifying the complexity of species niches  
33 for which relevant morphological, behavioural, biochemical or life-history traits are often used  
34 as relevant proxies. Soil fauna is highly diverse and many classifications have been proposed  
35 to synthesize both the response of soil organisms to their environment and their effect on soil  
36 functioning. Here, we provide a critical overview of the characteristics and limitations of the  
37 existing classifications in soil ecology, and propose clarifications and alternatives to current  
38 practices. We summarise the similarities and differences in how classifications have been  
39 created and used in soil ecology. We propose a harmonization of the current concepts by  
40 properly defining 'guilds', 'functional groups' and 'trophic groups' as subcategories of  
41 'ecological groups', with different purposes and distinguishing criteria. Finally, based on these  
42 concepts, we suggest a common framework to define classifications based on functional traits  
43 that allows a better and unified understanding of changes in soil biodiversity and ecosystem  
44 functioning.

45

46 **Keywords:** guilds; functional groups; ecological groups; trait-based approach; soil  
47 invertebrates

## 48 1. Introduction

49 Classifying organisms has a long history in ecology (MacArthur and Levins, 1964) because  
50 defining groups is a common practice that “allows a context-specific simplification of the real  
51 world” (Gitay and Noble, 1997). Species sharing certain morphological, ecological or life history  
52 similarities are likely to play comparable functional roles (Pigot et al., 2020; Winemiller et al.,  
53 2015).

54 However, the objectives for creating a group of organisms and how to assemble organisms  
55 into homogenous groups are still the subject of much theoretical and empirical work in ecology  
56 (e.g. Simberloff and Dayan, 1991; Wilson, 1999; Jaillard et al., 2018; Bottinelli and Capowiez,  
57 2021). Clustering species into groups with similar response to the environment or similar  
58 impact on ecosystem functioning implies identifying the degree of overlap in at least one  
59 dimension of their ecological niche, defined as an  $n$ -dimensional hypervolume (Hutchinson,  
60 1957). Achieving this goal requires simplifying the complexity of the niche into synthetic axes.  
61 Organism traits are often taken as proxies for such niche axes (Violle and Jiang, 2009). For  
62 instance, in plant ecology, species are generally classified on the basis of their similarity of  
63 traits (Grime, 1977). This approach could be applied to any kind of organisms, and is relevant  
64 to describe cryptic underexplored organisms, such as soil fauna.

65 Soil organisms strongly influence soil processes and hence the functioning of terrestrial  
66 ecosystems (Lavelle et al., 2006; Dignac et al., 2017). With the world’s ecosystems  
67 experiencing ongoing global changes, the maintenance of ecosystem functionality urgently  
68 requires an understanding of how changes in soil invertebrate diversity could affect soil  
69 functioning (Eisenhauer et al., 2019). However, studying soil fauna remains a challenge (i) due  
70 to the huge diversity of soil organisms, (ii) because only a tiny fraction of the actual diversity  
71 has been identified (Decaëns, 2010), and (iii) we know little about the biology of most taxa  
72 (Orgiazzi et al., 2016). Realizing that some organisms share similar features, clustering species

73 into groups has been a regular practice for monitoring and predicting the response of soil fauna  
74 to natural and anthropogenic disturbances as well as their effects on soil functioning (Gisin,  
75 1943; Lavelle, 1997; Bouché, 1977; Bongers and Bongers, 1998; Brussaard, 2012; Briones,  
76 2014).

77 When considering the soil fauna as a whole, organisms are often classified (i) by taxonomy  
78 (hereafter called 'clades', e.g. Lumbricidae, Collembola, or Nematoda), (ii) according to their  
79 body size (i.e. macro-, meso- and micro-fauna; Swift et al., 1979; Gobat et al., 1998; Gongalsky  
80 et al., 2021), (iii) into trophic groups to aid the analysis of food webs (e.g. predatory mites,  
81 bacterivorous nematodes; de Ruiter et al., 1996; Sechi et al., 2015; Bloor et al., 2021), or (iv)  
82 according to their functional role, for example the soil ecosystem engineers (i.e., organisms  
83 that directly or indirectly modulate the availability of resources to other species, by causing  
84 physical state changes in biotic or abiotic materials) (Lavelle et al., 1997). Some classifications  
85 are widely used, such as the earthworm ecological categories (Bouché, 1977), terrestrial  
86 isopod groups (Schmalfuss, 1984), Collembola life forms (Gisin, 1943), nematode functional  
87 guilds (Bongers and Bongers, 1998), the 'cp' and 'pp' nematode groups (Bongers 1990,  
88 1999), ant functional groups (Andersen, 1995), termite feeding guilds (Donovan et al., 2001)  
89 or the soil functional groups defined by Lavelle and Spain (2001). These groups have been  
90 defined to summarize similar responses to their environment (e.g. Gisin, 1943) or effects on  
91 soil functioning (Lavelle et al., 2007).

92 However, there is a lack of an overarching framework for classifying the soil fauna traditionally  
93 operated with very broad groups, such as 'litter transformers', 'ecosystem engineers' and  
94 'micropredators' (Wardle, 2002), ignoring diversity of responses and functions within these  
95 groups. Only recently, a more detailed overarching classification that merged existing group-  
96 specific classifications using a hybrid taxonomic-and-trait approach was suggested (Potapov  
97 et al. 2022). However, the definition of groups in the classifications listed above depends on

98 the appreciation by specialists of the main role of the organisms. For example, Lavelle (1997)  
99 included macroinvertebrates as ecosystem engineers, whereas Brussaard (2012) added fungi  
100 to this group. This is an example to underline that the definition of functional groups  
101 dramatically depends on the knowledge and point of view we have on soil organisms. In  
102 addition, mixing groups that have been defined for a different clade would be meaningful if  
103 these groups were initially defined using similar traits or ecological preferences, hence  
104 representing the same axes of the niche. In practice though, mixing such groups in multi-taxa  
105 or multi-trophic approaches is not rare (Henneron et al., 2015; Ohlmann et al., 2018). For  
106 example, drawing conclusions from similar responses to an environmental constraint or  
107 disturbance for Collembola life forms and nematode trophic guilds may have feet of clay since  
108 they do not inform the same part of their respective niche (i.e. habitat and trophic dimensions,  
109 respectively). In multi-taxa or food web approaches, species attribution to a group may vary  
110 between studies (Henneron et al., 2015; Martinez-Almoyna et al., 2019; Sechi et al., 2015;  
111 Bloor et al., 2021), limiting our ability to draw clear conclusions across studies. As far as we  
112 know, the robustness of the results to classification methodology, i.e. to what extent the results  
113 would change if the classification was changed, has not yet been systematically tested.  
114 Finally, the low number of traits properly defined, the low level of knowledge on trait trade-offs  
115 at organism level and the lack of a common ontology that delineates the relationships between  
116 environmental pressures, soil organism trait and ecological functions impedes fluent  
117 communication among soil ecologists and with stakeholders (e.g. public authorities, NGOs,  
118 conservation ecology experts). Since there is a risk of making policy decisions on the  
119 quicksand of inaccurate knowledge, more attention needs to be devoted to effective  
120 communication of research data and results and thus validation of the scientific knowledge  
121 accumulated (Bouma, 2019). This includes rethinking our way of interpreting and  
122 communicating studies on soil fauna based on 'functional groups' (Briones, 2014).

123 In the present paper, we give a critical overview of the characteristics of main classifications  
124 currently used in soil ecology, and propose clarifications and alternatives to current practices.  
125 In the following, we summarize the similarity/differences in how classifications have been  
126 created and used in soil fauna ecology. We propose a harmonization of the current concepts  
127 and their applications and suggest a common framework to define classifications that allows a  
128 more consistent understanding of changes in soil biodiversity and ecosystem functioning.

129

## 130 2. Existing classifications were not built on the same grounds

131 Early work was mostly based on species natural history and expert knowledge (Table 1). Many  
132 classifications are the valuable heritage of work done in the 1930s up to the 1980s on the  
133 biology and ecology of soil organisms (Gisin, 1943; Lee, 1959; Bouché, 1977; Perel, 1975;  
134 Halffter and Matthews, 1966; Yeates et al., 1993; Bongers, 1990; Greenslade, 1978;  
135 Schmalfluss, 1984). Broadly, differences between these classifications arise from the type and  
136 the number of traits, and the organism's life stages that are taken into account to cluster  
137 species (Figure 1). Most classifications only consider adults and not juveniles. Certain  
138 classifications are based on non-mating individuals whereas others consider sexual ones  
139 (Figure 1). All these points are detailed in the following paragraphs.

140

### 141 2.1. Criteria used to cluster species

142 Soil ecologists have used a large number of traits related to behaviour, morphology, physiology  
143 or phenology to cluster species (Table 1). Some classifications rely on life-history traits and  
144 abiotic tolerances. Some others take into account indirect characteristics, such as the  
145 properties of biogenic structures created by the soil organisms (casts, mounds, nests, burrows,  
146 etc.). The number of traits used for clustering species depends on the authors and the clade.  
147 For instance, dung beetles are mostly assigned according to one type of trait (nesting



148 behaviour) whereas earthworm species are usually clustered by a combination of several types  
149 of traits (e.g. behaviour, morphology, physiology). Behaviour is the most common type of trait  
150 used to classify soil organisms, in particular foraging and/or reproductive behaviours (e.g.  
151 Yeates et al., 1993; Andersen, 1995; Halffter and Matthews, 1966; Savolainen and  
152 Vepsäläinen, 1988; Doube, 1990). Regarding morphology, traits commonly used to cluster soil  
153 organisms include body size, shape, color, number of ocelli, etc. (Bouché, 1977; Malcicka et  
154 al., 2017; Pessôa et al., 2017; Sosiak and Barden, 2020). There are classifications that use so  
155 many different traits that they are very difficult to apply since one rarely has information on all  
156 traits. Presumably, it may explain why the microarthropod classification of Gisin (1943), which  
157 relies on morphology, is more widely used than the one of Siepel (1994), which mostly relies  
158 on behaviour and life-history traits not well documented for many species. Moreover, large part  
159 of this particular classification seems to be non-published and not publicly available.

160

## 161 2.2. Number of groups in classifications

162 The number of within-clade groups differs from one clade to another, which makes  
163 classification resolution not easily comparable (Table 1). A low number of groups has the  
164 potential advantage of high genericity, meaning that the classification can be more easily  
165 extrapolated to different contexts, e.g., the Bornemissza (1976) classification for dung beetles  
166 (Figure 1, Table 1). However, oversimplifying the functional heterogeneity of soil organisms  
167 can lead to significant loss of essential information. Conversely, more detailed classifications  
168 have higher probability not to be transposable to new contexts. In a given geographic region,  
169 it is more likely that a classification derives from particular traits that are adapted to local  
170 environmental constraints, linked to particular taxa, etc. Finer classifications based on criteria  
171 adapted to local environments usually show increased accuracy as more ecological strategies  
172 are described, and highlight rare or specific combinations of traits that can reveal vulnerability  
173 of species or functional roles. To build a more universal approach, Sosiak and Barden (2020)

174 have recently provided two options for predicting the ecomorph of a given ant species: a  
175 simplified set of ecomorph syndromes (10 ecomorphs), or for more granular analysis,  
176 classifications of worker functional role (8 groups), foraging niche (5 groups) and nesting niche  
177 (5 groups). Hierarchical classifications of groups can be efficient to aid scalability of the  
178 approach and compatibility across different studies (Potapov et al., 2022).

179

### 180 2.3. Classifications do not describe all individuals of the species

181 Most existing classifications only consider adults because it is difficult to identify immature life  
182 stages for most soil animals. However, many invertebrates can spend at least as much time in  
183 their immature stages as in their adult stage, and juveniles often dominate in numbers and thus  
184 represent functionally important components of soil communities and food webs (Mulder and  
185 Vonk, 2011; Cohen and Mulder, 2014; Gongalsky, 2021; Potapov et al., 2021). Immature life  
186 stages are also exposed to environmental filtering and may play a different role on their  
187 environment (Buckingham et al., 2019). In addition, trophic interactions may change over the  
188 life cycle of soil organisms, e.g. cannibalism, predation, etc., like for holometabolous insects  
189 such as ground or rove beetles (Rainford and Mayhew, 2015) or some nematode taxa  
190 (juveniles are bacterial feeding, adults are predators; Yeates et al., 1993).

191 Within each species, classifications do not consider all types of individuals. For example,  
192 classifications of social insects usually focus on non-reproductive individuals that raise the  
193 offspring, build biogenic structures (e.g., mounds and sheeting) and forage, but ignore the few  
194 individuals dedicated to reproduction. Moreover, there is a strong dimorphism between castes  
195 (queens, males, workers and soldiers), and within the worker caste, the morphology and  
196 behaviour of individuals vary according to their size (i.e., small vs. large) and age. This  
197 complexity is likely to induce that natural selection and environmental filtering take place at  
198 both the individual and colony levels in eusocial insects (Keller, 1995). These two levels are  
199 important to characterize the response of species to environmental changes and their effect

200 on soil properties. For instance, soil porosity is associated with the size of mandibles of ants  
201 and termites which determines the size of soil particles that workers move (individual level;  
202 Dostal et al., 2005; Martin-Perea et al., 2019), and with the size, depth and type of nest (colony  
203 level; Cammerrat and Rish, 2008). To account for heterogeneity, one thus needs to quantify  
204 traits of workers and sexual individuals at the individual and colony scale (Parr et al., 2017).

205

### 206 3. Misuses limit the meaningfulness of classifications

#### 207 3.1. May local classification be universal in scope?

208 More than half of the classifications listed in Table 1 arose from local knowledge or experiments  
209 (Figure 2), and are mainly built on knowledge coming from the European region, and/or  
210 temperate and continental climates. For example, the classification from Bouché (1977) on  
211 French Lumbricidae, the one from Greenslade (1978) on Australian ants, and the one from  
212 Bongers et al. (1990) on Dutch nematodes are widely used with the strong assumption that  
213 they are universal in scope, though derived from regional knowledge (see Appendix for more  
214 details). Using a classification defined for a given biogeographical scope in another  
215 biogeographical area or at a larger scale can lead to several problems. For example, trophic  
216 differentiation among Collembola life forms is less pronounced in tropical than in temperate  
217 forests (Potapov et al., 2016; Susanti et al., 2021). A local classification system would have  
218 over-described local variability or would not fully describe the global organisms' traits variability,  
219 making it inoperative at other scales and/or irrelevant at other scales or in other contexts. Some  
220 studies tried to validate or adapt these classifications across borders, such as Lee (1985) for  
221 the Bouché's (1977) classification, or Horgan (2008) for the Doube's (1990) classification.  
222 Similarly, effects of such groups on soil function(s) are context-dependent and need to be  
223 tested at a larger scale, see e.g. Hedde et al. (2005) in Colombian savannahs, Blanchart et al.  
224 (1999) on neo- and afro-tropical soils.

225

### 226 3.2. Classifications are not stable in time

227 Classifications are subjected to changes after their initial description (Figure 3). Drivers of  
228 modifications include difficulties in data acquisition, the addition of new data, or changing  
229 contexts and objectives of classification in more recent studies. Over time, changes in  
230 classifications may decrease or increase their precision as compared to the initial description.  
231 For example, the classification of Andersen (1995) developed for Australian ant communities  
232 (9 ecological groups) was reduced to four groups by Moranz et al. (2013) to analyze the ants'  
233 response to grassland management. By contrast, other classifications were progressively  
234 complexified. According to their vertical position in soils, Collembola were initially grouped in  
235 three life forms (atmo-, hemi-, eu-edaphic; Gisin 1943). Although still used nowadays (e.g.  
236 Malcicka, 2017), a series of more precise classifications have also been proposed. For  
237 example, accounting for criteria on species micro-habitat, Christiansen (1964) and Thibaud  
238 and D'Haese (2010) considered up to six additional groups, and Stebaeva (1970) and Rusek  
239 (1989) distinguished epiedaphic from atmobiontic species. Thereafter, Potapov et al. (2016)  
240 linked species taxonomy to life forms to improve the prediction of springtail trophic niches. By  
241 doing so, they modified the principles and purpose of the classification.

242

### 243 3.3. Inconsistent naming of classifications

244 Many examples show that a large number of different terms can refer to one single  
245 classification. Representative examples of this problem are related to misuses of the  
246 classifications by Bouché's (1977) and Gisin's (1943) on earthworms and springtails,  
247 respectively. The classes defined by Bouché (1977) are alternatively referred to as ecological  
248 categories/groups/types (Bottinelli et al., 2020; Jégou et al., 1998; Asshoff et al., 2010;  
249 Bastardie et al., 2005), morpho-ecological or eco-morphological groups (Marriet et al., 2020;  
250 Pey et al., 2013), ecophysiological groups (Richardson et al., 2020), functional groups (Milcu

251 et al., 2006), feeding guilds/strategies (Depkat-Jakob et al., 2010; Huang et al., 2010) or  
252 ecotypes (Zhang et al., 2018). Similarly, the life forms (*Lebensformen*) defined by Gisin (1943)  
253 are alternatively called eco-morphological life-forms (Rusek, 2007; Hopkin, 1997; Joimel et al.,  
254 2017), ecological categories (Ponge, 1993), or feeding/functional guilds (Hopkin, 1997).

255

#### 256 3.4. Phenotypic plasticity precludes assigning species to one single group

257 Individuals of the same species may have high trait variation which may create conflicts with  
258 classifications. For example, Aphodiinae dung beetles are classified in three groups, namely  
259 soil- and dung-ovipositing endocoprids, and small paracoprids (Finn and Gittings, 2003). But it  
260 is recognized that some species choose to oviposit in the soil beneath dung pads or directly  
261 inside the dung, and thus could be alternatively classified as soil-ovipositing or dung-ovipositing  
262 endocoprids. Along the same line, it has been shown that even spider hunting guilds, that were  
263 initially defined at the family level, can differ among individuals of one single species (Suter  
264 and Benson, 2014). In the same vein, several earthworm species show an intermediate  
265 burrowing and feeding behaviour between surface dwellers (feeding on fresh organic matter)  
266 and horizontal burrowers of the mineral soils (epi-endogeics *sensu* Bouché, 1977). These  
267 intermediate categories can be dominant in tropical soils (Fragoso, 1999) and could be an  
268 indication of their wider environmental plasticity. Similarly, ecomorphs of the same species  
269 adapted to particular habitats and showing contrasted morphological features have also been  
270 reported, as e.g. for some Oligochaeta species. For example, (i) the pink and green forms of  
271 *Allolobophora chlorotica* (Savigny, 1826), or (ii) the taxa *Cognettia sphagnetorum* (Vejdovský,  
272 1878) and *C. pseudosphagnetorum* (Martinsson, Rota & Erséus, 2015 which) are two  
273 examples of morpha/taxa often lumped together in the literature. Furthermore, environmental  
274 stressors, such as land-use change, drought spells, soil amendments, or contamination events  
275 force some species to switch to a different diet (Krause et al., 2021) a “feeding flexibility” *sensu*

276 Briones, 2010), microhabitat or reproductive strategies and hence, change their position in the  
277 classification.

278

### 279 3.5. Misuses of concepts behind classifications

280 From an ecosystem ecology point of view, a functional group gathers individuals that contribute  
281 similarly to an environmental function (Blondel, 2003). Therefore, the concept of 'functional  
282 group' is tightly interlinked to the concept of 'functional trait', despite the latter being adapted  
283 to soil ecology only recently (Pey et al., 2014). For an individual, a trait is functional if it  
284 contributes to its fitness (Violle et al., 2007). Functional traits are involved in the response of  
285 individuals to their environment but they also influence their environment. The applications of  
286 these concepts in soil fauna ecology are far from clear and often blurred by misuses (Pey et  
287 al., 2014) with a persistent lack of consistency in concepts and terminology in soil ecology  
288 (Blondel, 2003; Lavorel and Garnier, 2002; Pey et al., 2014). To simplify the semantics in soil  
289 ecology and to conform with other fields of ecology, we propose to clarify definitions of  
290 ecological groups, guilds, functional groups and trophic groups (Box 1). The guild concept  
291 refers to resource sharing by species in a competitive way whereas the functional group  
292 concept essentially corresponds to the way individuals act on resources to provide an  
293 ecological function (Blondel, 2003; Wilson, 1999).

294

295 Box1/ Proposed definitions

296 **Ecological group:** group of individuals that show similar environmental tolerances and similar  
297 effects on their environment. This is the overarching concept that includes guilds, functional  
298 groups and trophic groups as sub-concepts.

299 **Guild:** group of species that largely overlap in their niche requirements (Grinnell, 1917; Root  
300 1967).

301 **Functional group:** group of individuals that similarly contribute to a specific ecological function  
302 (Díaz and Cabido, 2001). An ecological function is a change in matter and/or energy flows in  
303 an ecosystem, resulting from interactions between organisms or between organisms and their  
304 physical environment.

305 **Trophic group:** group of individuals that feed on the same food sources and have the same  
306 consumers (O'Connor et al., 2020; Bloor et al., 2021). For instance, plant feeding nematodes  
307 and weevil larvae do not belong to the same trophic group as they do not share the same  
308 predators, although they belong to the same trophic level (both feed on plant roots). Therefore,  
309 trophic groups can be perceived both as guilds and/or as functional groups (but the converse  
310 is not necessarily true).

311

## 312 4. Creating meaningful classifications

### 313 4.1. Criteria for a meaningful classification

314 We plea for rethinking classification procedures that should provide at least the following  
315 advantages. A classification:

- 316 ● must specify what it intends to predict or synthesize;
- 317 ● must specify its domain of use (the scope);
- 318 ● has to clearly define groups of individuals so that there is no room for doubt or confusion;
- 319 ● must be comprehensive, no individual should be left out;
- 320 ● should clearly explain the criteria or decision rules by which each and every taxon belongs  
321 to one (discrete clustering) or several categories (e.g. through fuzzy coding);
- 322 ● should have the capacity to accommodate a new situation (e.g. new taxa being described,  
323 extrapolation to another country or biome, etc.);
- 324 ● should therefore be such that it can incorporate all these changes while maintaining its  
325 stability.

326 To avoid confusion, we underline the importance to properly name, describe and cite any given  
327 classification. It is important to refrain from twisting the classification's meaning to  
328 accommodate it to a new research question.

329

#### 330 4.2. Clearly stating the objective of the classification

331 Basically, clustering soil fauna species into groups can help to understand (i) the responses of  
332 communities to their environment through guild analysis, (ii) the effect of communities on soil  
333 functioning through functional group analysis, and (iii) soil interaction networks. These three  
334 main goals may overlap when looking at how the effect of the environment on soil functioning  
335 is mediated by soil fauna and/or soil fauna interactions. In addition, such questions may arise  
336 within a clade (e.g. nematodes or Collembola), across clades and across trophic levels. When  
337 comparing several and very different taxonomic groups, it is important to build groups of  
338 individuals that are similar in scope: guilds referring to the same axes of the niche (e.g.  
339 resistance to drought), functional groups involved in the same soil function(s) (e.g. soil organic  
340 matter dynamics, formation and maintenance of soil physical structure) or trophic groups  
341 representing meaningful nodes and types of energy fluxes (Potapov, 2022) in the food web.

342

#### 343 4.3. Trait-based approaches as a playground

344 In the overview presented above, few soil fauna classifications have accounted for trait  
345 relationships when building groups. However, successful combinations of traits may be  
346 constrained by tradeoffs across or within niche dimensions (Ellers et al., 2018). The choice of  
347 the traits is then crucial to correctly represent the tradeoffs. Reducing the vast amount of soil  
348 fauna organisms to a limited number of groups that share similar traits (morphology,  
349 physiology, phenology, behaviour or life history) has both theoretical and operational  
350 advantages. For instance, classifying soil fauna into groups of similar traits could help to  
351 identify backbones in redundancy (many species with a similar combination of traits) and



352 vulnerability due to uniqueness (species with a unique combination of traits) over realms,  
353 ecosystems and environmental constraints (Boulangeat et al., 2012; McLean et al., 2021; Pigot  
354 et al., 2020).

355

#### 356 4.4. Why and how to cluster soil fauna species into groups?

357 There is an overwhelming demand for knowledge on threats on soil and potential contribution  
358 of soil to global change scenarios. For this, we need a comparable level of knowledge for each  
359 clade (e.g. nematodes, earthworms, Collembola...) as for traditionally more extensively studied  
360 organisms (e.g. vascular plants, fish). To go further, soil fauna ecologists must adopt a  
361 common consistent framework of faunal classifications that allows to integrate all taxa. While  
362 development of such overarching classification requires collection and harmonization of trait  
363 data, here we propose a repeatable procedure to cluster species into hierarchical groups based  
364 on existing knowledge, and to use a trait-based approach to describe and assign species to a  
365 specific group. The proposed approach is ambitious because it requires unified trait definitions  
366 (Pey et al., 2004), consistent protocols to measure traits (Moretti et al., 2017), and open  
367 databases to share and reuse trait values (for example, Betsi <https://portail.betsi.cnrs.fr/> or  
368 Ecotaxonomy <http://ecotaxonomy.org/>). To (i) study the response of soil fauna to environmental  
369 gradients or its effect on ecosystem functioning, and (ii) to define guilds or functional groups,  
370 we propose to follow the seven-steps protocol described below (Figure 4).

371 - (1) The first step consists of identifying which dimensions of the individual's niche is  
372 under consideration. To do so, one needs to describe the environmental gradient, such as the  
373 soil temperature, N content, trophic resources or the bioavailability of soil contaminant, or the  
374 targeted function(s), such as the organic matter dynamics, water infiltration, or formation and  
375 maintenance of the soil physical structure.

376 - (2) In the second step, we suggest identifying the traits that reflect the corresponding  
377 part of the niche. Traits selection can derive from expertise, published evidence and/or from

378 statistical detection of trait-environment relationships, e.g. through fourth-corner analysis (Dray  
379 and Legendre, 2008). In multi-taxa studies (i.e. those including organisms across clades), a  
380 challenge is to draw trait-niche links for organisms that are phylogenetically distant and for  
381 which different trait trade-offs have resulted from different evolutionary processes.

382 - (3) The third step requires assessing the availability of trait data in the soil fauna  
383 databases. Unfortunately, the current state of knowledge is highly heterogeneous with a small  
384 number of soil fauna species that show correctly-informed data for a large number of traits,  
385 and many other species that present data for only a little number of traits, if any (Brousseau et  
386 al., 2017). This unbalanced distribution of trait data in soil databases emphasizes the need to  
387 share structured trait data across taxa at the global scale (Gallagher et al., 2020).

388 - (4) The fourth step is to create a “trait per species matrix”. To do so, one needs to pay  
389 specific attention to the necessary trade-offs between trait space quality, described by the  
390 number of traits and the quality of the data, and the usefulness of the matrix. It requires carefully  
391 selecting relevant traits and avoiding omissions that have a strong impact on the construction  
392 of trait space (Mouillot et al., 2021). In multi-taxa studies, we suggest creating one matrix per  
393 clade to account for evolutionary constraints on trait trade-offs. In the case of trophic groups,  
394 Gravel et al. (2016) proposed to investigate three types of traits: (i) topological traits that  
395 determine whether a given consumer can feed on a given resource, (ii) consumption traits that  
396 determine the rate at which trophic interactions harm the resource population and benefit the  
397 consumer, and (iii) life history traits that are characteristics of consumer and resources that  
398 affect their demography.

399 - (5) The fifth step consists of quantifying dissimilarity between species using distance-  
400 based measures based on the trait matrix described in step four. The interplay of trade-offs  
401 between traits shapes species phenotypic diversity, and the degree of interdependence among  
402 traits may be highlighted e.g. by a PCoA. The choice of distance metric is important (Laliberté  
403 and Legendre, 2010). The Gower distance (Gower, 1971) could be preferred to combine

404 quantitative and categorical traits (Botta-Dukát, 2005; de Bello et al., 2021). The Gower  
405 distance focuses on the dissimilarity in species-level average traits, but it is also possible to  
406 integrate trait overlap between species by accounting for within-species trait variability (De  
407 Bello et al., 2013). In multi-taxa studies when evolutionary constraints on trait trade-offs differ  
408 widely, it is usually preferred to quantify dissimilarity within clades.

409 - (6) The sixth step is to identify groups of species that share more similar traits values  
410 than others using a clustering algorithm. The clustering method is important (Laliberté and  
411 Legendre, 2010). To create a generic ecological classification and make the clustering as  
412 universal as possible, we advise to cluster species from a large species pool covering a highest  
413 possible diversity of biomes at a geographic scale similar or broader than the scale of the  
414 planned research. Under such conditions clustering will integrate a large part of the intra- and  
415 inter-species variability. Hierarchical clustering defines several grains of classification, and  
416 enables choosing smaller or broader groups according to the scientific questions and  
417 geographic coverage. In a broad study spanning across various taxa and spatial scales,  
418 Mouillot et al. (2021) identified invariant scaling relationships between (i) the number of  
419 clusters, the number of species in the dominant cluster and the number of unique species, and  
420 (ii) the total species richness. Functional uniqueness is represented by species that have no  
421 neighbors in the trait space owing to their unique combination of traits. When the number of  
422 species increases, the number of “single-species” groups tends to saturate, and species tend  
423 to pack disproportionately into the richest cluster, being more redundant than expected  
424 (Mouillot et al., 2014). Unique species can play key and irreplaceable functional roles, and  
425 represent unique responses to environmental constraints (Violle et al., 2017).

426 - (7) The last step is to validate the trait-based classification by confronting it to previous  
427 knowledge. In general, trait-based guilds are expected to reflect available data on species  
428 distribution along ecological gradients. Similarly, trait-based functional groups should  
429 correspond to published information on the effects of species on a given ecological function.

430 To validate trait-based trophic groups, one could compare them to trophic groups previously  
431 defined by isotopic or other dietary tracers (Potapov et al., 2019, 2021). An alternative strategy  
432 is to compare trait-based trophic groups to groups obtained by stochastic block modelling of  
433 an adjacency matrix of known trophic relationships (O'Connor et al., 2020; Bloor et al., 2021).  
434 Once validated, and if the clustering includes a large proportion of species of the targeted clade  
435 that come from various biomes, we expect that adding new species will not drastically change  
436 the species clustering.

437 Soils are multifunctional and some functions are closely related (e.g. carbon storage and  
438 nutrient cycling) whereas others appear more independent (e.g. water infiltration and pesticide  
439 degradation). Studying the relationships between soil fauna and soil multifunctionality requires  
440 to define functional groups that reflect common effects on the investigated functions. The  
441 relationship between numerous ecological functions and emergent functional groups has to be  
442 tested using strong scientific assumptions derived from validated trait-based approaches. As  
443 well in multi-trophic studies, this framework allows testing for top-down or bottom-up effects of  
444 inferred groups. Additionally, machine learning techniques make it possible to create  
445 probabilistic graphs of emergent functional groups, and reclassify and validate new entries. For  
446 example, Random forest analysis can validate species classification into ecological groups  
447 from morphological trait data (Sosiak and Barden 2020). The relationships between soil fauna  
448 and soil multifunctionality must be studied in the light of such emergent functional groups  
449 (Potapov, 2022). More precisely, understanding the interplay between soil multifunctionality  
450 and the network of interactions between the functional groups is probably the crux of the  
451 problem.

452

453 **5. Conclusions**

454 Despite their widespread applications, we depicted several limitations and misuses of the  
455 current classifications used in soil fauna ecology. The design of a common framework that  
456 could be generalizable across the entire soil fauna community has been considered before,  
457 yet not implemented (Briones, 2014). We now have both established trait databases and  
458 mathematical tools that should allow us to elaborate more accurate soil fauna classifications  
459 which will be applicable across geographical regions and scales. This is especially important  
460 considering rapidly developing global initiatives of soil animal biodiversity assessments and  
461 their potential policy impacts (FAO et al. 2021; Guerra et al., 2021; Potapov et al., 2022). To  
462 go a step further, we suggest harmonizing the terminology and the underlying concepts of  
463 classification. We described a way to build sounder classifications, whether composed of  
464 guilds, functional groups or trophic groups. This framework should become more and more  
465 relevant with the advent of massive datasets associated with molecular characterization of soil  
466 fauna (e.g. environmental DNA metabarcoding) that contain genetic information on hundreds  
467 of interacting species involved in many soil functions. However, to reach its full potential, this  
468 framework requires more knowledge on effect traits in functional trait databases. Our  
469 framework would also allow to cross the soil's borders and integrate soil fauna into wider  
470 approaches, like aboveground-belowground or soil-water continuums using trait-based  
471 approaches (Gallagher et al., 2020). Transparent and stable classifications should promote  
472 accurate meta-analyses in the future. Finally, classification is a particularly important step in  
473 ecosystem modelling as it identifies the basic parameters that become the inputs of models,  
474 thus making the outputs more interpretable and reliable.

475

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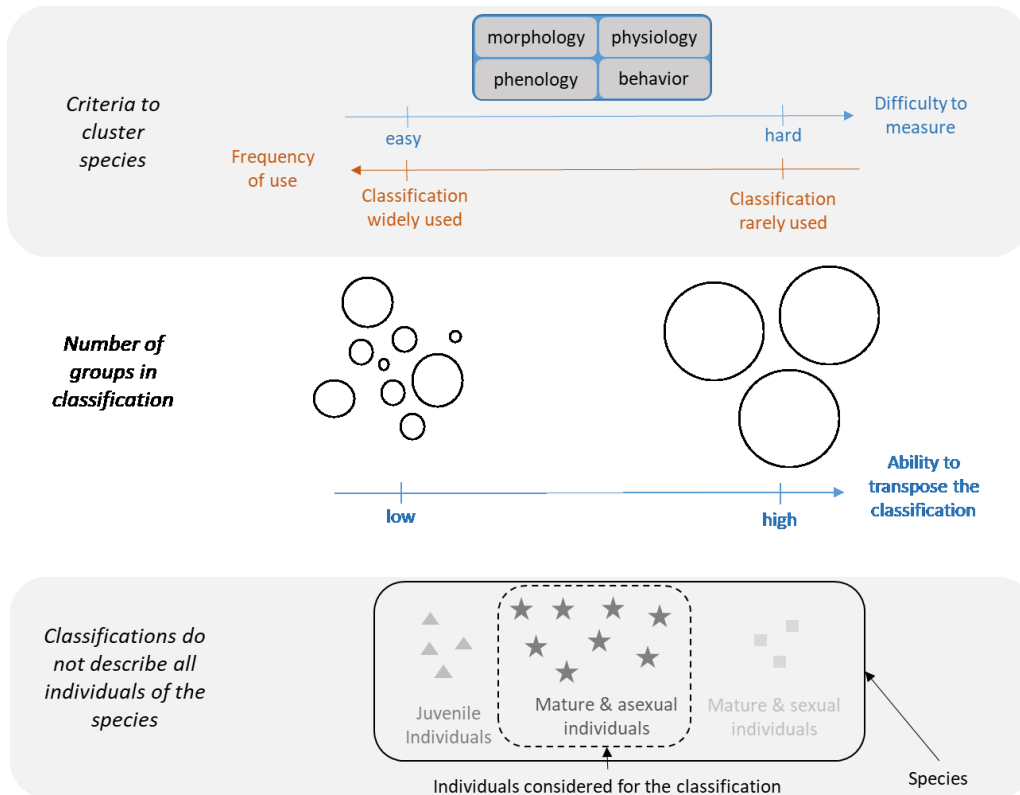


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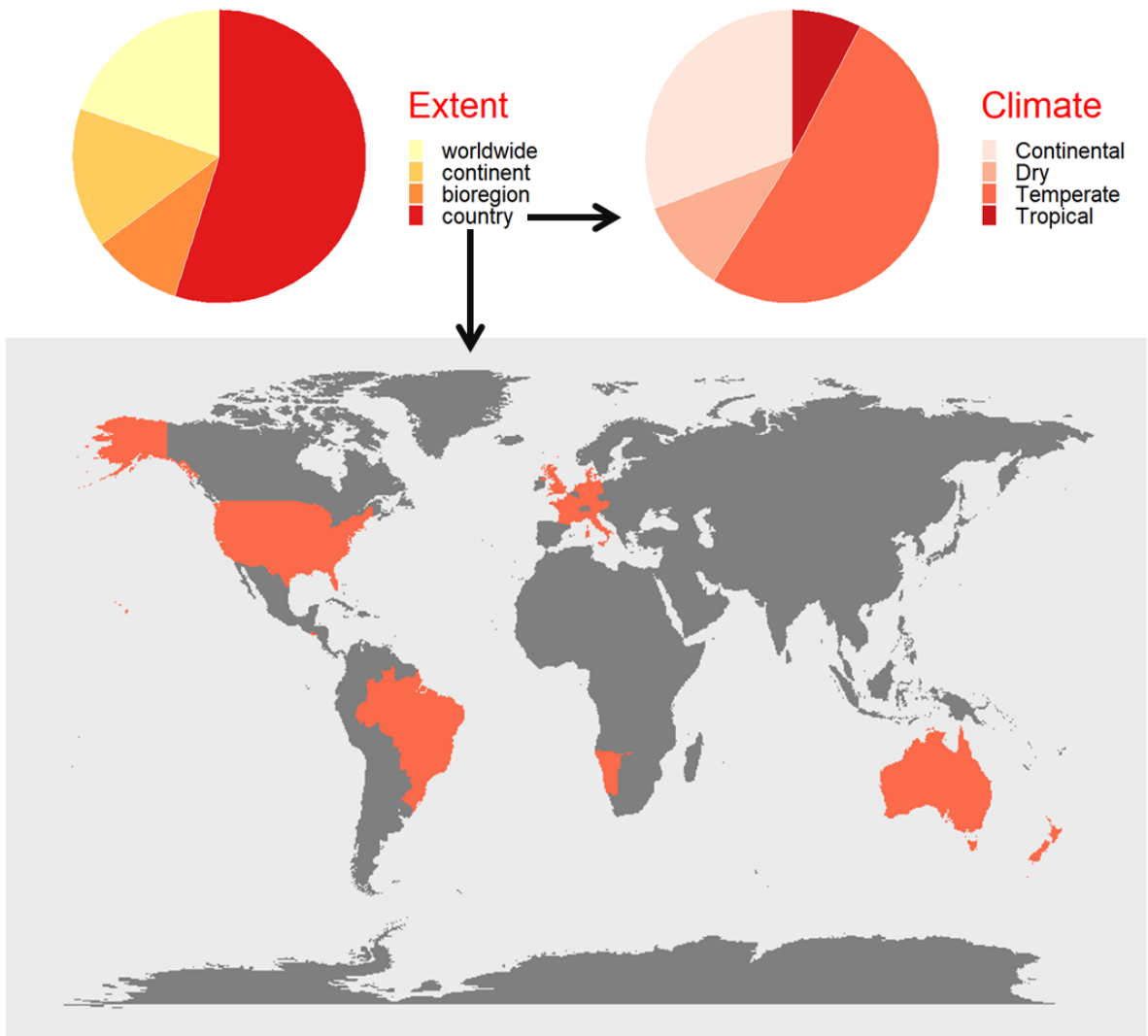
946

947 Figure 1: Existing classifications were not built on the same grounds. Upper panel illustrates  
 948 that different species traits were used to cluster species into groups. Middle panel shows that  
 949 classification systems may lead to different number of groups and that it may influence the  
 950 transposability of the classification system to other ecological or biogeographical contexts.  
 951 The lower panel exemplify whether assignment to a group was based on all or a part of  
 952 individuals of species.

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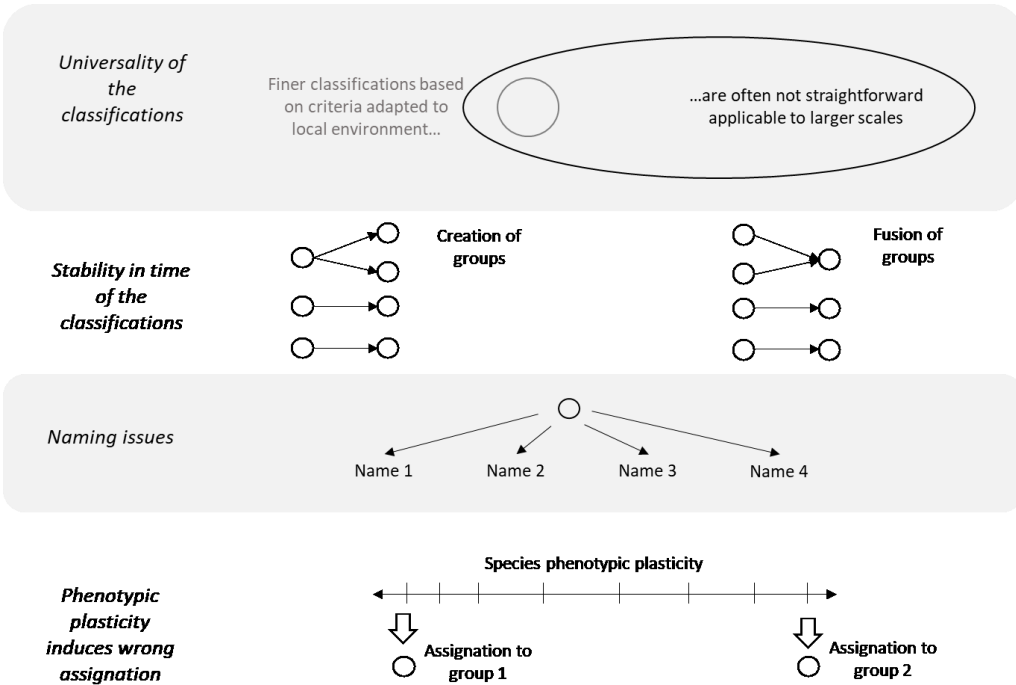
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957 Figure 2. Geographical scope of the classifications (upper left pie chart). For country-wide  
 958 classifications (>50% of studied classifications): the country for which the classification was  
 959 created (map) and its climate (upper right pie chart).

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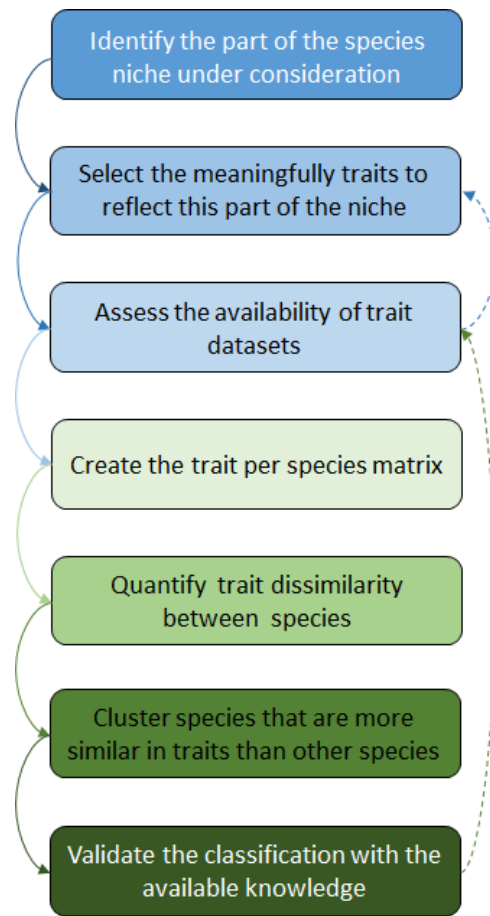
963 Figure 3: Misuses limit the meaningfulness of classifications: universality in scope (upper

964 panel), stability of groups and of name over time (2<sup>nd</sup> and 3<sup>rd</sup> panels), and difficulty of

965 assignment due to species phenotypic plasticity.

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970 Figure 4. Proposed seven-step hierarchical procedure to define guilds, functional groups and

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trophic groups within soil fauna

Table 1. Overview of classifications of various soil invertebrates (Nematoda, Annelida, Tardigrada, Crustacea, Collembola, Arachnida, Insecta)

|  | Papers                          | Criteria  | Clustering method   | # groups   | Initial biogeographic range |
|--|---------------------------------|---|---|--|-----------------------------|
| <b>Nematodes</b> (Phylum : Nematoda)                                       |                                 |   |   |  |                             |
|  | Bongers (1990)<br>Ferris (2001) | <b>Life history groups</b> (life-history traits, reproduction rate, egg size, egg number, ability to survive, cuticle permeability, presence in polluted sites, etc.)   | <b>Expertise:</b> synthesis of works (published or not) based on anatomy, laboratory rearing and field observations   | <b>5</b> (free-living nematodes)<br><b>4</b> (plant-feeders) | Netherlands                 |
|  | Yeates et al. (1993)            | <b>Trophic groups</b> (mouth shape armature and pharynx, but also feeding behavior and gut composition analyses)  | <b>Expertise:</b> synthesis of works (published or not) based on anatomy, laboratory rearing and field observations   | <b>8</b>   | Worldwide                   |
|  | Bongers and Bongers (1998)      | <b>Functional guilds</b> (trophic and demographic groups)   | <b>Combination of life history and trophic groups</b>   | <b>16</b>  | Netherlands                 |
| <b>Earthworms</b> (Phylum: Annelida, Order: Haplotaxida)                   |                                 |   |   |  |                             |
|  | Lee (1959)                      | <b>Effect on soil</b> (cast, burrow), <b>Morphology</b> (size of matured individuals, body pigmentation, structure of the gut, muscular development), <b>Behaviour</b> (reaction to touch), <b>other</b> (predatory pressure, geographic distribution of individual species, reaction to change in land-use patterns)                             | Not described   | <b>3</b>   | New-Zealand                 |
|  | Bouché (1972)                   | <b>Morpho-anatomy</b> (Skin coloration, Muscle of the dissepiment, Muscle structure of the body wall, Tail, Size, Body wall thickness), <b>Physiology</b> (Respiratory intensity, Regeneration ability, Nephridia pores, Resting stage), <b>Behaviour</b> (Mobility / Contractibility)  | <b>Statistical</b> (not described)  | <b>3 to 7</b>  | France                      |
|  | Bouché (1977)                   | <b>Morpho-anatomy</b> (Skin coloration, Adult size, Muscle of the dissepiment, Setae), <b>Physiology</b> (External humidity, Regeneration ability, Resistance to bad conditions, Reproduction, Maturation, Respiration, Resistance to irritant, Speed of the gut transit), <b>Behaviour</b> (Diet, Light avoidance, Longitudinal contractibility) | <b>Statistical</b> (not described)  | <b>3 to 7</b>  | France                      |
|  | Perel (1975)                    | <b>Morphology</b> (intestine shape, typhlosolis shape, pigmentation, tail shape, prostomium shape), <b>Behaviour</b> (mobility, response time to physical stimuli)  | Not described   | <b>2</b>   | Eastern Europe              |
|  | Satchell (1980)                 | <b>Effect on soil</b> (burrows type, recognizable cast), <b>Behaviour</b> (aestivation), <b>Morphology</b> (color), <b>Life-history traits</b> (fertility, sexual maturity, number of generation per year)  | Not described   | <b>2</b>   | United Kingdom              |
|  | Blanchart et al. (1999)         | <b>Soil aggregation</b>   | <b>Expertise</b> Expert judgement based on empirical records and literature survey  | <b>2</b>   | Tropical soils              |
| <b>Pot worms</b> (Phylum: Annelida, Order: Enchytraeida)                   |                                 |   |   |  |                             |
|  | Didden (1993)                   | <b>Life history</b> (acceleration or deceleration of the embryogenesis)   | <b>Expertise</b> Empirical observations   | <b>2</b>   | The Netherlands             |
|  | Graefe and Schmelz (1999)       | <b>Physiology</b> (pH, moisture and salinity)   | <b>Expertise</b> Expert judgement based on empirical records and literature survey, inspired by Ellenberg's indicator values for plants (Ellenberg et al. 1992) | <b>4</b> (moisture)<br><b>5</b> (pH)<br><b>8</b> (salinity)  | Germany                     |
|  | Graefe and Schmelz (1999)       | <b>Life history</b> (r-, K- and A-continuum)  | <b>Expertise</b> Expert judgement based on empirical records and literature survey  | <b>5</b>   | Germany                     |
|  | Graefe and Schmelz (1999)       | <b>Life forms</b> (vertical distribution in the humus profile and their occurrence in the gradient of humus forms),   | <b>Expertise</b> Expert judgement based on empirical records and literature survey  | <b>14</b>  | Germany                     |
| <b>Tardigrades</b> (Phylum: Tardigrada)                                    |                                 |   |   |  |                             |
|  | Bertolani (2001)                | <b>Life history groups</b> (Reproductive mode)  | <b>Expertise</b> Expert judgement based on empirical records and literature survey  | <b>4</b>   | Worldwide                   |
|  | Altiero et al. (2009)           | <b>Life-history</b> (hatching phenology)  | <b>Expertise</b> Expert judgement   |  | Italy                       |
|  | Guidetti et al. (2011)          | <b>Ecological traits</b>  | <b>Expertise</b> Expert judgement   | <b>5</b>   | Italy                       |
|  | Guidetti et al. (2012, 2013)    | <b>Ecological traits</b> (Buccal morphology; Piercing stylets; Branching of furca)  | <b>Expertise</b> Expert judgement   | <b>8</b>   | Italy                       |
| <b>Woodlice</b> (Phylum: Arthropoda; Class: Malacostracea; Order: Isopoda) |                                 |   |   |  |                             |

|   |  |   |   |             |                                 |
|---|--|---|---|-------------|---------------------------------|
|   | Vandel (1960)                                    | <b>Habitat</b>  | <b>Expertise:</b> synthesis of works (published or not) based on field observations   | <b>17</b>   | France                          |
|   | Edney (1977)                                     | <b>Physiology</b> (Tolerance to water loss)   | <b>Expertise</b>  | <b>3</b>    | Worldwide                       |
|   | Hoese (1981)                                     | <b>Physiology</b> (Salt homeostasis)  | <b>Expertise</b>  | <b>2</b>    | Europe                          |
|   | Schmalfuss (1984)                                | <b>Morphology and life strategies</b>   | <b>Expertise</b>  | <b>6</b>    | Europe                          |
|   | Hoese (1984)                                     | <b>Biology</b> (Type of marsupium linked with offspring protection)   | <b>Expertise</b>  | <b>2</b>    |                                 |
|   | Sutton et al. (1984)                             | <b>Life history traits</b>  | <b>Expertise</b>  | <b>2</b>    |                                 |
| <b>Springtails</b> (Phylum: Arthropoda; Class: Collembola)  |  |   |   |             |                                 |
|   | Gisin (1943)                                     | <b>Life-forms</b> (morphology, vertical position, moisture preference)  | <b>Expertise</b> Expert judgement based on empirical records and literature survey  | <b>3</b>    |                                 |
|   | Christiansen (1964)                              | <b>Life-forms</b> (morphology, vertical position, moisture preference)  | <b>Expertise</b>  | <b>5</b>    |                                 |
|   | Berg et al. (2004)                               | <b>Feeding guilds</b> (enzyme activity evaluating the ability of springtails to digest cellulose, chitin and threalose) | Dominance of specific digestive enzymes or their combinations   | <b>4</b>    | Dutch grasslands                |
|   | Chahartaghi et al. (2005)                        | <b>Feeding guilds</b> (Nitrogen stable isotope ratios)  | Assuming a <sup>15</sup> N enrichment of about 3‰ per trophic level   | <b>3</b>    | German forests                  |
|   | Thibaud and D'Haese (2010)                       | <b>Life-forms</b> (morphology, vertical position, moisture preference)  |   | <b>9</b>    |                                 |
|   | Potapov et al. (2016)                            | <b>Functional guilds</b> (stable isotopic composition, taxonomic identity and life forms)                               | Significant differences in C and N stable isotope composition among life form - order combinations  | <b>4</b>    | Global temperate forests        |
|   | Rusek (1989)                                     | <b>Life forms</b> (morphology, abiotic preferences: microhabitat, moisture preference)                                  | Expert opinion, knowledge on the species biology, specific morphological adaptations  | <b>5</b>    | Central Europe                  |
| <b>Springtails</b> (Phylum: Arthropoda; Class: Collembola) and <b>mites</b> (Phylum: Arthropoda; Class : Arachnida; Order: Oribatida) |  |   |   |             |                                 |
|   | Siepel (1994)                                    | <b>Life-history tactics</b> (Reproduction; Development; Synchronization; Migration)                                     | Iterative method by taking sufficiently described species and placing them one by one in every possible combination. All possible combination are not found in nature, the list presents the ones that may be observed. | <b>13</b>   |                                 |
| <b>Oribatid mites</b> (Phylum: Arthropoda; Class : Arachnida; Order: Oribatida)   |  |   |   |             |                                 |
|   | Schuster (1956)                                  | <b>Feeding guilds</b>   | <b>Expertise:</b> synthesis of works (published or not) based on gut content and food choice experiments  | <b>3</b>    | Austrian forest                 |
|   | Knulle (1957)                                    | <b>Isovalent groups</b> (habitat)   | <b>Expertise</b>  | <b>17+1</b> | Germany                         |
|   | Bulanova-Zakhvatkina (1952)                      | <b>Ecological types</b> (cuticle thickness, legs length, resistance to drought)   | <b>Expertise</b>  | <b>3</b>    | Moscow region, Russia           |
|   | Luxton (1972)                                    | <b>Feeding guilds</b>   | <b>Expertise:</b> synthesis of works (published or not) based on gut content and food choice experiments  | <b>6</b>    | Denmark                         |
|   | Behan and Hill (1978)                            | <b>Feeding guilds</b>   | <b>Expertise:</b> synthesis of works (published or not) based on gut content  | <b>6</b>    | North America (artic, subartic) |
|   | Siepel and Ruiterdijkman (1993)                  | <b>Feeding guilds</b> (enzyme activity evaluating the ability of mites to digest cellulose, chitin and threalose)       | <b>Expertise:</b> Dominance of specific digestive enzymes or their combinations   | <b>7</b>    | The Netherlands                 |
|   | Krivolutsky (1995)                               | <b>Morpho-ecological types</b> (morphological features and life history tactics)  | <b>Expertise</b>  | <b>16</b>   | Eurasia                         |
|   | Schneider et al. (2004) and Maraun et al. (2011) | <b>Feeding guilds</b> (Nitrogen stable isotope ratios)  | Assuming a <sup>15</sup> N enrichment of about 3‰ per trophic level   | <b>4</b>    | German forests                  |
| <b>Spiders</b> (Phylum : Arthropoda; Class : Arachnida; Order: Araneae)   |  |   |   |             |                                 |
|   | Enders (1976)                                    | <b>Hunting guilds</b>   | <b>Expertise:</b> Bibliographic survey  | <b>5</b>    | Worldwide                       |
|   | Schaefer (1976)                                  | <b>Life cycle / Overwintering</b>   | <b>Expertise:</b> synthesis of works (published or not) based on field observations   | <b>5</b>    | Germany                         |
|   | Post and Riechert (1977)                         | <b>Hunting guilds</b>   | <b>Expertise</b>  | <b>11</b>   | USA                             |
|   | Bell et al. (2005)                               | <b>Long-distance dispersal</b>  | <b>Expertise:</b> Bibliographic survey  | <b>2</b>    | Worldwide                       |
|   | Pétillon et al. (2011)                           | <b>Tolerance to coastal environments</b>  | Lab' experiments  | <b>3</b>    | France                          |
|   | Pekár and Toft (2015)                            | <b>Food specialization</b>  | <b>Expertise:</b> Bibliographic survey  | <b>4</b>    | Worldwide                       |

|  |   |  |   |                                    |   |
|--|---|--|---|------------------------------------|---|
|  | Conti et al. (2018, 2019)                       | <b>Life history groups</b> (Thermal regulation and ability to survive, presence in polluted sites, etc.)   | <b>Measures</b> : Field and molecular measurements  | <b>5</b>                           | Namibia   |
|  | Conti et al. (2020)                             | <b>Functional traits</b><br><b>Biochemistry of silks</b>   | Mass spectrometry measurements  | <b>5</b>                           | Namibia   |
|  | Mulder et al. (2019)                            | <b>Behavioural traits</b><br><b>Burrow depth</b>   | Empirical observations  | <b>5</b>                           | Namibia   |
| <b>Dung beetles</b> (Phylum : Arthropoda; Class : Insecta; Order: Coleoptera, Family: Scarabaeidae)  |   |  |   |                                    |   |
|  | Halffter and Matthews (1966)                    | <b>Nesting behavior</b> (sequence of behavioral steps leading to the completed nest)   | <b>Expertise</b> : synthesis of works (published or not) based on laboratory rearing and field observations | <b>4</b>                           | Worldwide   |
|  | Halffter (1977)<br>Halffter and Edmonds (1982)  | <b>Nesting behaviour</b> (Form of larval provision; Nest location; Nest complexity; Disposition of brood masses/balls in compound and subterranean nests; Manipulation of larval provision; Provisioning of subterranean nests; Outer surface of brood ball; Location of egg chamber; Male-female cooperation; Brood care) | <b>Expertise</b> : synthesis of works (published or not) based on laboratory rearing and field observations | <b>7</b>                           | Worldwide   |
|  | Doube (1990)                                    | <b>Nesting behaviour</b> (way to use and remove dung),<br><b>Dry body mass</b>   | <b>Expertise</b> : synthesis of works (published or not) based on laboratory rearing and field observations | <b>7</b>                           | Austral Africa  |
|  | Pessôa et al. (2017)                            | <b>'Physical' traits</b> (Size, Prothorax height, Area of the anterior tibia, Wing load, Mesotibia ratio); <b>Behavioral traits</b> (Generalism in food preferences, Horizontal displacement, Nest building, Ball or pear-shaped nest); <b>Phenological traits</b> (Daily activity)  | <b>Statistical</b> : dissimilarity matrix (Gower) + non-hierarchical K-Means clustering method              | <b>8</b>                           | South-America   |
|  | Bornemissza (1969)<br>Bornemissza (1976)        | <b>Nesting behaviour</b> (nest position relative to the food source)   | <b>Expertise</b> : synthesis of works (published or not) based on laboratory rearing and field observations | <b>3</b>                           | Worldwide   |
|  | Hanski and Cambefort (1991)                     | <b>Nesting behaviour</b>   | <b>Expertise</b> : synthesis of works (published or not) based on laboratory rearing and field observations | <b>4</b>                           | Worldwide   |
|  | Finn and Gittings (2003)                        | <b>Larval food</b> (dung, facultative coprophages/saprophages, saprophages);<br><b>Oviposition site</b> (dung, soil); <b>Site of larval development</b> (dung, soil (small dung masses), soil);<br><b>Body size</b> (small vs large)   | <b>Expertise</b> : synthesis of works (published or not) based on laboratory rearing and field observations | <b>7</b>                           | North temperate countries                                       |
|  | Tonelli (2021)                                  | <b>Feeding behaviour</b><br><b>Nesting behaviour</b>   | Propose an unified approach relying on published studies  | <b>5</b><br><b>4</b>               | Worldwide   |
|  | Horgan (2008)                                   | <b>Reproductive output</b> (life-time fecundity); <b>Food nutritional requirements</b> ; <b>Requirements for terrain suitability</b> ; <b>Size of food source</b> ;<br><b>Relocation and utilization times</b> ;<br><b>Successional mean occurrence</b> ; <b>Function</b>  | <b>Expertise</b> : synthesis of works (published or not) based on laboratory rearing and field observations | <b>10</b>                          | Central-America (El Salvador)                                   |
| <b>Rove Beetles</b> (Phylum : Arthropoda; Class : Insecta; Order: Coleoptera, Family: Staphylinidae) |   |  |   |                                    |   |
|  | Bohac (1999)                                    | <b>Life forms</b> (Size ; Trophic specialization; Habitat)   | <b>Expertise</b> : Based on Sharova (1981)  | <b>23</b>                          | Holarctic region  |
|  | Majka et al. (2008)                             | <b>Tolerance to coastal environment</b>  | <b>Expertise</b> : Adapted from Koch (1989-1993) and Hammond (2000)   | <b>4</b>                           | North America   |
| <b>Termites</b> (Phylum : Arthropoda; Class : Insecta; Order: Isoptera)                              |   |  |   |                                    |   |
|  | Grassé (1984)                                   | <b>Function within the colony</b> (Castes)   | <b>Expertise</b>  | <b>2</b><br>that can be subdivided | Mainly tropics but a few sp. can be found in temperate ecosyst. |
|  | Grassé (1984)                                   | <b>Interaction with microbes</b>   | <b>Expertise</b>  | <b>2</b>                           | Mainly tropics but a few sp. can be found in temperate ecosyst. |
|  | Higashi et al. (1992)                           | <b>Nesting strategy</b>  | <b>Expertise</b>  | <b>3</b>                           |   |
|  | Tayasu et al. (1997)                            | <b>Trophic groups</b>  | <b>Expertise</b>  | <b>5</b>                           | Mainly tropics but a few sp. can be found in temperate ecosyst. |
|  | Holt and Lepage (2000)<br>Jouquet et al. (2011) | <b>Trophic groups and building strategies</b>  | <b>Expertise</b>  | <b>3</b>                           | Mainly tropics but a few sp. can be found in temperate ecosyst. |
|  | Donovan et al. (2001)                           | <b>Trophic groups</b> (Gut content analysis)   | <b>Expertise</b>  | <b>4</b>                           | Mainly tropics but a few sp. can be found in temperate ecosyst. |
| <b>Ants</b> (Phylum : Arthropoda; Class : Insecta; Order: Hymenoptera; Family: Formicidae)           |   |  |   |                                    |   |



|  |                                      |  |                  |           |                 |
|--|--------------------------------------|--|------------------|-----------|-----------------|
|  | Greenslade (1978)<br>Andersen (1995) | <b>Competitive interactions and habitat requirements</b><br>Foraging behavior (solitary, group or mass recruitment); Competitive behavior (aggressive species vs non aggressive); Morphological traits (individual and colony size) ; Physiological traits (thermal tolerance) | <b>Expertise</b> | <b>7</b>  | Australia       |
|  | Savolainen and Vepsäläinen (1988)    | <b>Competition hierarchy</b><br>Behavioural traits measured at the colony level or the individual level (colony size, radius of foraging areas, size of workers, recruitment of food, defence of food, nest, and foraging area)  | <b>Expertise</b> | <b>3</b>  | Northern Europe |
|  | Sosiak and Barden (2020)             | <b>Ecomorph syndromes</b><br>Classification initially based on nesting, foraging and functional role niche data but then defined using 17 morphological traits   | <b>Expertise</b> | <b>10</b> | Worldwide       |