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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 (Boulangéat 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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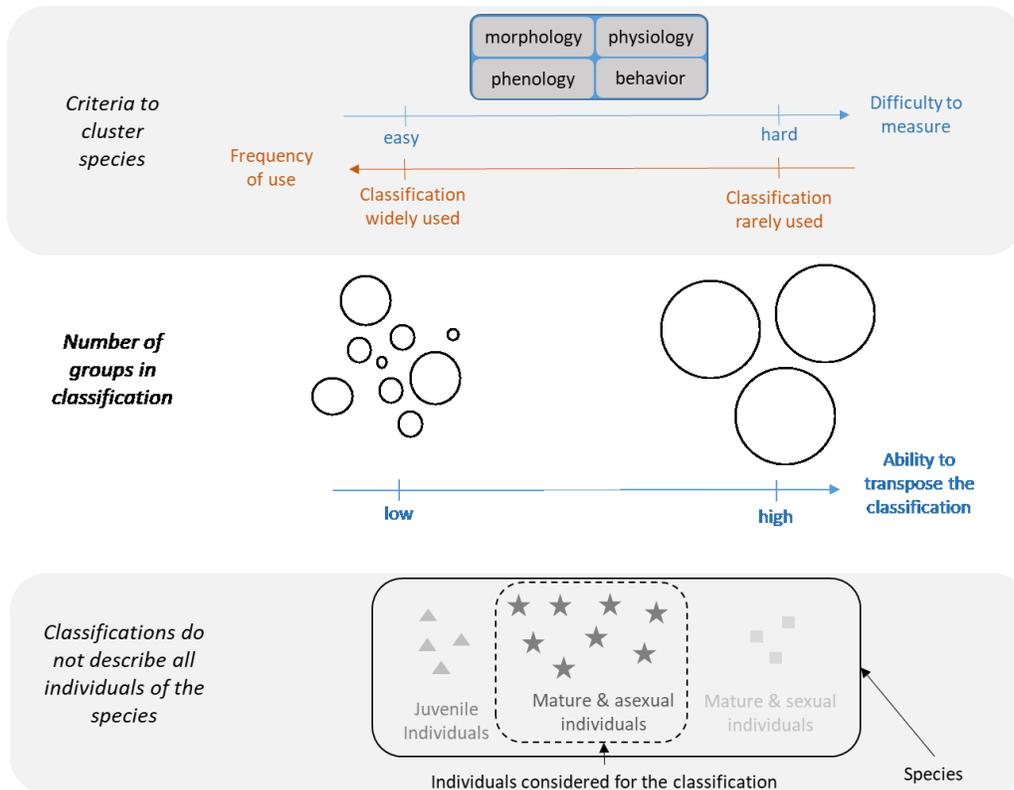
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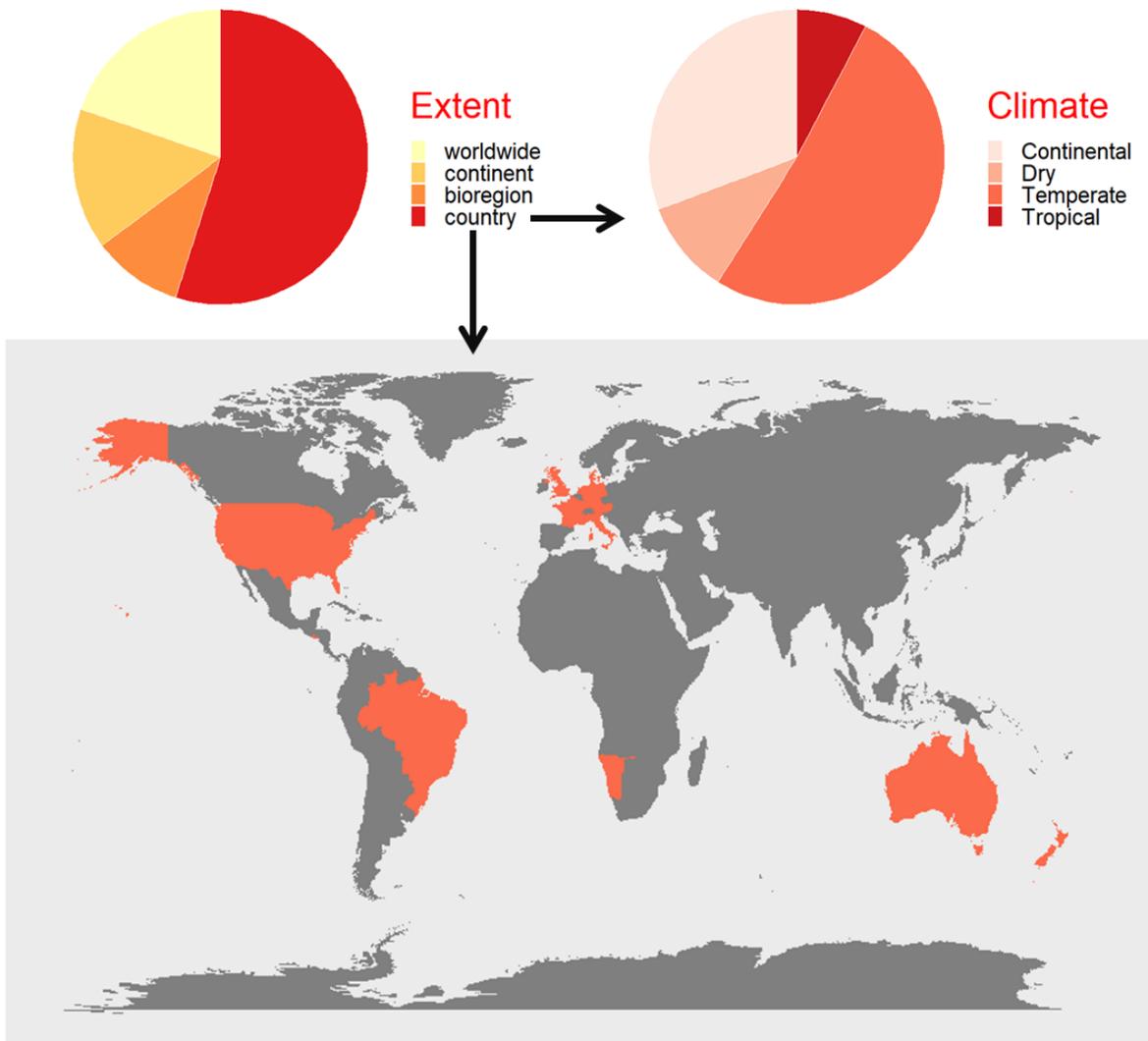
947 Figure 1: Existing classifications were not built on the same grounds. Upper panel illustrates
 948 that different species traits were used to cluster species into groups. Middle panel shows that
 949 classification systems may lead to different number of groups and that it may influence the
 950 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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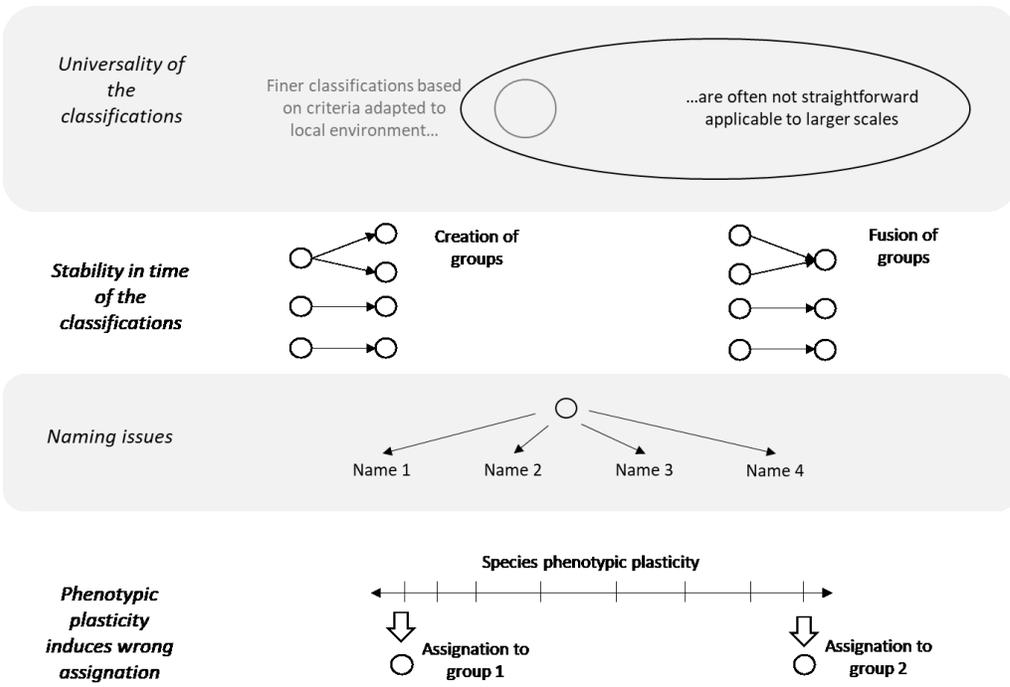
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957 Figure 2. Geographical scope of the classifications (upper left pie chart). For country-wide
 958 classifications (>50% of studied classifications): the country for which the classification was
 959 created (map) and its climate (upper right pie chart).

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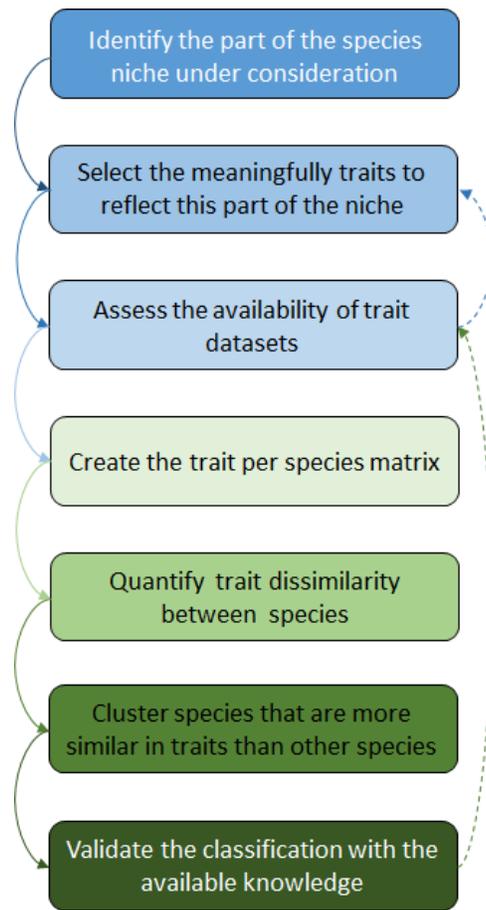
963 Figure 3: Misuses limit the meaningfulness of classifications: universality in scope (upper

964 panel), stability of groups and of name over time (2nd and 3rd 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

971

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

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

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

	Greenslade (1978) Andersen (1995)	Competitive interactions and habitat requirements Foraging behavior (solitary, group or mass recruitment); Competitive behavior (aggressive species vs non aggressive); Morphological traits (individual and colony size) ; Physiological traits (thermal tolerance)	Expertise	7	Australia
	Savolainen and Vepsäläinen (1988)	Competition hierarchy 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)	Expertise	3	Northern Europe
	Sosiak and Barden (2020)	Ecomorph syndromes Classification initially based on nesting, foraging and functional role niche data but then defined using 17 morphological traits	Expertise	10	Worldwide