



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.

► To cite this version:

Mickael Hedde, Olivier Blight, Maria J.I. Briones, Jonathan Bonfanti, Alain A. Brauman, et al.. A common framework for developing robust soil fauna classifications. *Geoderma*, 2022, 426, pp.116073. 10.1016/j.geoderma.2022.116073 . hal-03749556

HAL Id: hal-03749556

<https://hal.inrae.fr/hal-03749556>

Submitted on 11 Aug 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Title: A common framework for developing robust soil fauna classifications

List of authors: Mickael Hedde¹, Olivier Blight², Maria J.I. Briones³, Jonathan Bonfanti⁴, Alain Brauman¹, Margot Brondani¹, Irene Calderón Sanou⁵, Julia Clause⁶, Erminia Conti⁷, Jérôme Cortet⁴, Thibaud Decaëns⁴, Amandine Erktan¹, Sylvain Gérard¹, Arnaud Goulpeau⁴, Maeva Iannelli¹, Sophie Joimel-Boulanger⁸, Pascal Jouquet⁹, Nicolas Le Guillarme⁵, Claire Marsden¹, Camille Martinez Almoyna⁵, Christian Mulder⁷, William Perrin⁴, Julien Pétillon^{10,11}, Benjamin Pey¹², Anton M. Potapov^{13,14}, Sara Si-moussi⁵, Wilfried Thuiller⁵, Jean Trap¹, Alan Vergnes⁴, Andrey Zaitsev¹⁵, Yvan Capowiez¹⁶

Affiliations:

1. Eco&Sols, INRAE – IRD – CIRAD – Institut Agro, Montpellier, France.
2. IMBE, Univ. Avignon – Univ. Aix Marseille – CNRS – IRD, Avignon, France.
3. Dept. Ecología y Biología Animal, Univ. Vigo, Vigo, Spain.
4. CEFÉ, Univ Montpellier, CNRS, EPHE, IRD, Univ Paul-Valéry, Montpellier, France.
5. LECA, Univ. Grenoble Alpes – Univ. Savoie Mont Blanc – CNRS, Grenoble, France.
6. EBI, Univ. Poitiers – CNRS, Poitiers, France.
7. Dept. Biological, Geological and Environmental Sciences, Univ. Catania, Catania, Italy.
8. EcoSys, Univ. Paris-Saclay – INRAE – AgroParisTech, Thiverval-Grignon, France.
9. iEES Paris, IRD – Sorbonne Univ. – UPEC – CNRS – INRAe, Bondy, France.
10. ECOBIO, CNRS – Univ. Rennes 1, Rennes, France
11. Institute for Coastal and Marine Research, Nelson Mandela University, Port Elizabeth, South Africa
12. LEFE, Univ. Toulouse – CNRS, Toulouse, France.
13. J. F. Blumenbach Instit. Zoology and Anthropology, Univ. Göttingen, Göttingen, Germany.
14. A.N. Severtsov Instit. Ecology and Evolution, Russian Acad. of Sciences, Moscow, Russia
15. Insitute of Animal Ecology, Justus-Liebig-University, Giessen, Germany

27 16. EMMAH, INRAE – Univ. Avignon, Avignon, France.

28 **Corresponding author:** Mickael HEDDE; mickael.hedde@inrae.fr

Abstract

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

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

1. Introduction

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

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

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

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

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

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

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

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

2. Existing classifications were not built on the same grounds

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

2.1. Criteria used to cluster species

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

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

2.2. Number of groups in classifications

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

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

2.3. Classifications do not describe all individuals of the species

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

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

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

3. Misuses limit the meaningfulness of classifications

3.1. May local classification be universal in scope?

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

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

3.4. Phenotypic plasticity precludes assigning species to one single group

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

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

3.5. Misuses of concepts behind classifications

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

Box1/ Proposed definitions

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

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

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

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

4. Creating meaningful classifications

4.1. Criteria for a meaningful classification

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

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

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

4.2. Clearly stating the objective of the classification

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

4.3. Trait-based approaches as a playground

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

5. Conclusions

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

Acknowledgements

MH, OB, JB, JC, JC, SJB, PJ, WP, BP, JT and YC are grateful for stimulating exchanges at the TEBIS VII annual meeting (1-3 October, 2019 in Lille, France) that have generated some of the ideas we have explored here. Ideas also matured during 'Traits' working group meetings

480 of the EUdaphobase COST Action (CA18237) (MH, MJIB, EC, SJB, CM, AMP, SS, AZ), and
481 of the GlobNets project (ANR 16-CE02-0009) (MH, ICS, NLG, CMA, WT). ICS's PhD thesis is
482 funded by GlobNets project, MB's PhD thesis is funded by O-Nemato-P project (ANR 21-CE32-
483 0004), MI's PhD thesis is funded by a grant from the *Fondation de France* (00117720), SG's
484 PhD thesis is funded by a grant from the French Minister of Higher Education, Research and
485 Innovation (MESRI), AG's PhD is funded by GAIA Doctoral School (Univ. Montpellier).

References

- Altiero, T., Bertolani, R., Rebecchi, L., 2009. Hatching phenology and resting eggs in tardigrades. *J. Zool.* 280, 290–296.
- Andersen, A.N., 1995. A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. *J. Biogeogr.* 22, 15–29.
- Asshoff, R., Scheu, S., Eisenhauer, N., 2010. Different earthworm ecological groups interactively impact seedling establishment. *Eur. J. Soil Biol.* 46, 330–334.
- Bastardie, F., Capowiez, Y., Renault, P., Cluzeau, D., 2005. A radio-labelled study of earthworm behaviour in artificial soil cores in term of ecological types. *Biol. Fertil. Soils* 41, 320–327.
- Behan, V.M., Hill, S.B., 1978. Feeding habits and spore dispersal of Oribatid mites in the North American arctic. *Rev. Ecol. Biol. Sol* 15, 497–516.
- Berg, M.P., Stoffer, M., van den Heuvel, H.H., 2004. Feeding guilds in Collembola based on digestive enzymes. *Pedobiol.* 48, 589–601.
- Bertolani, R., 2001. Evolution of the reproductive mechanisms in Tardigrades – A review. *Zoologischer Anzeiger* 240, 247–252.
- Bertolani, R., Rebecchi, L., Claxton, S. K., 1996. Phylogenetic significance of egg shell variation in tardigrades. *Zool. J. Linn. Soc.* 116, 139–148.
- Blanchart, E., Albrecht, A., Alegre, J., Duboisset, A., Gilot, C., Pashanasi, B., Lavelle, P., Brussaard, L., 1999. Effects of earthworms on soil structure and physical properties, in: Lavelle, P., Brussaard, L., Hendrix, P. (Eds.), *Earthworm management in tropical agroecosystems*. Wallingford: CABI, 149–172.
- Blondel, J., 2003. Guilds or functional groups: does it matter? *Oikos* 100, 223–231.

510 Blicharska, M., Smithers, R.J., Mikusiński, G., Rönnbäck, P., Harrison, P.A., Nilsson, M.,
511 Sutherland, W.J., 2019. Biodiversity's contributions to sustainable development. *Nat Sustain*
512 2, 1083–1093.

513 Bloor, J.M.G, Si-Moussi, S., Taberlet, P., Carrère, P., Hedde, M., 2021. Analysis of complex
514 trophic networks reveals the signature of land-use intensification on soil communities in
515 agroecosystems. *Sci. Rep.* 11, 18260

516 Bohac, J., 1999. Staphylinid beetles as bioindicators. *Agr. Ecosyst. Environ.* 74, 357-372.

517 Bongers, T., 1990. The maturity index: an ecological measure of environmental disturbance
518 based on nematode species composition. *Oecol.* 83, 14–19

519 Bongers, T., 1999. The Maturity Index, the evolution of nematode life history traits, adaptive
520 radiation and cp-scaling. *Plant Soil* 212, 13–22

521 Bongers, T., Bongers, M., 1998. Functional diversity of nematodes. *Appl. Soil Ecol.* 10, 239-
522 251. Botta-Dukát, Z., 2005. Rao's quadratic entropy as a measure of functional diversity
523 based on multiple traits. *J. Veg. Sci.* 16, 533–540.

524 Bottinelli, N., Kaupenjohann, M., Märten, M., Jouquet, P., Soucémariadin, L., Baudin, F.,
525 Tran, T.M., Rumpel, C., 2020. Age matters: Fate of soil organic matter during ageing of
526 earthworm casts produced by the anecic earthworm *Amyntas khami*. *Soil Biol. Biochem.*,
527 148, 107906.

528 Bottinelli, N., Capowiez, Y, 2021. Earthworm ecological categories are not functional groups.
529 *Biol. Fert. Soils* 57, 329-331.

530 Boulangeat, I., Philippe, P., Abdulhak, S., Douzet, R., Garraud, L., Lavergne, S., Lavorel, S.,
531 Van Es, J., Vittoz, P., Thuiller, W., 2012. Improving plant functional groups for dynamic
532 models of biodiversity: at the crossroads between functional and community ecology. *Glob.*
533 *Change Biol.* 18, 10.1111/j.1365-2486.2012.02783.x.

534 Bouma, J., 2019. How to communicate soil expertise more effectively in the information age
535 when aiming at the UN Sustainable Development Goals. *Soil Use Manag.* 35, 32-38.

536 Bornemissza, G.F., 1969. A new type of brood care observed in the dung beetle *Oniticellus*
537 *cinctus* (Scarabaeidae). Pedobiol. 9, 223-225.

538 Bornemissza, G.F., 1976. The Australian dung beetle project 1965-1975. Australian Meat
539 Research Committee Review 30, 1–30.

540 Bouché, M.B., 1972. Lombriciens de France. Écologie et systématique. INRA. 671 p.

541 Bouché, M.B., 1977. Stratégies lombriciennes, in: Lohm, U., Persson, T. (Eds.), soil
542 organisms as components of ecosystems. Ecol. Bull., Stockholm. 122–132pp.

543 Briones, M.J.I., 2010. Soil biology and warming play a key role in the release of 'old C' from
544 organic soils. Soil Biol. Biochem. 42, 960-967.

545 Briones, M.J.I., 2014. Soil fauna and soil functions: a jigsaw puzzle. Front. Envir. Sci.
546 <https://doi.org/10.3389/fenvs.2014.00007>

547 Brousseau, P.-M., Gravel, D., Handa, I.T., 2018. On the development of a predictive
548 functional trait approach for studying terrestrial arthropods. J. Animal Ecol. 87, 1209-1220

549 Brussaard, L., 2012. Ecosystem services provided by the soil biota, in: Soil ecology and
550 ecosystem services, Wall (Ed.) Oxford University Press, pp45-58.

551 Buckingham, S., Murphy, N., Gibbb, H., 2019. Effects of fire severity on the composition and
552 functional traits of litter-dwelling macroinvertebrates in a temperate forest. Forest Ecol.
553 Manag. 434, 279-288.

554 Bulanova-Zakhvatkina, E.M., 1952. Ecological types of oribatid mites and their distribution in
555 soil. Zoolog. Zhurn. 31,549-555 (in Russian)

556 Cammeraat, E.L.H., Rish, A.C., 2008. The impact of ants on mineral soil properties and
557 processes at different spatial scales. J. Appl. Entomol. 132, 285–294.

558 Chahartaghi, M., Langel, R., Scheu, S., Ruess, L., 2005. Feeding guilds in Collembola
559 based on nitrogen stable isotope ratios. Soil Biol. Biochem. 37, 1718-1725.

560 Chapin, F.S. III, Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L.,
561 Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., Díaz, S., 2000.
562 Consequences of changing biodiversity. *Nature* 405, 234–242.

563 Christiansen, K., 1964. Bionomics of Collembola. *Ann. Rev. Entomol.* 9, 147-178.

564 Cohen, J. E., Mulder, C., 2014. Soil invertebrates, chemistry, weather, human management,
565 and edaphic food webs at 135 sites in the Netherlands: SIZEWEB. *Ecology* 95, 578.

566 Conti, E., Mulder, C., Pappalardo, A.M., Ferrito, V., Costa, G., 2019. How soil granulometry,
567 temperature, and water predict genetic differentiation in Namibian spiders (*Ariadna*:
568 *Segestriidae*) and explain their behaviour. *Ecol. Evol.* 9, 4382–4391

569 Conti, E., Costa, G., Liberatori, G., Vannuccini, M.L., Protano, G., Nannoni, F., Corsi, I.,
570 2018. *Ariadna* spiders as bioindicator of heavy elements contamination in the Central Namib
571 Desert. *Ecol. Indic.* 95, 663–672.

572 Conti, E., Dattilo, S., Scamporrino, A., Costa, G., Samperi, F., 2020. Novel amino acid
573 assembly in the silk tubes of arid-adapted *Segestriid* spiders. *J. Chem. Ecol.* 46, 48–62.

574 Currie, C., Spence, J., Niemelä, J., 1996. Competition, cannibalism and intraguild predation
575 among ground beetles (Coleoptera: Carabidae): a laboratory study. *The Coleopter. Bull.* 50,
576 135-148

577 de Bello, F., Carmona, C.P., Mason, N.W.H., Sebastià, M.-T., Lepš, J., 2013. Which trait
578 dissimilarity for functional diversity: trait means or trait overlap? *J. Veg. Sci.* 24, 807-819.

579 de Bello, F., Botta-Dukát, Z., Lepš J., Fibich, P. 2021. Towards a more balanced combination
580 of multiple traits when computing functional differences between species. *Method. Ecol. Evol.*
581 12, 443–448.

582 de Ruiter, P.C., Neutel, A.M., Moore, J.C., 1996. Energetics and stability in below ground
583 food webs, in Polis, G., Winemiller, K.O (Eds.), *Food webs: integration of patterns and*
584 *dynamics*, Chapman and Hall.

585 Decaëns, T., Jimenez, J.J., Gioia, C., Measey, G.J., Lavelle, P., 2006. The values of soil
586 animals for conservation biology. *Eur. J. Soil Biol.* 42, 23–38.

587 Decaëns, T., 2010. Macroecological patterns in soil communities. *Glob. Ecol. Biogeogr.* 19,
588 287–302.

589 Depkat-Jakob, P.S., Hilgarth, M., Horn, M.A., Drake, H.L., 2010. Effect of earthworm feeding
590 guilds on ingested dissimilatory nitrate reducers and denitrifiers in the alimentary canal of the
591 earthworm. *Appl. Environ. Microbiol.* 76, 6205-6214.

592 Díaz, S., Cabido, M., 2001. Vive la différence: plant functional diversity matters to ecosystem
593 processes. *Trends Ecol. Evol.* 16, 646-655.

594 Didden, W.A.M., 1993. Ecology of terrestrial Enchytraeidae. *Pedobiol.* 37, 2–29.

595 Dignac, M.F., Derrien, D., Barre, P., Barot, S., Cécillon, L., Chenu, C., Chevallier, T.,
596 Freschet, G.T., Garnier, P., Guenet, B., Hedde, M., Klumpp, K., Lashermes, G., Maron, P.-A.,
597 Nunan, N., Roumet, C., Basile-Doelsch, I., 2017. Increasing soil carbon storage:
598 mechanisms, effects of agricultural practices and proxies. *Agr. Sust. Dev.*, 37, 14.

599 Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation
600 in the Anthropocene. *Science* 345, 401–406

601 Donovan, S.E., Eggleton, P., Bignell, D.E., 2001. Gut content analysis and a new feeding
602 group classification of termites. *Ecol. Entom.*, 26, 356-366.

603 Dostal, P., Breznova, M., Kozlickova, V., Herben, T., Kovar, P., 2005. Ant-induced soil
604 modification and its effect on plant below-ground biomass. *Pedobiol.* 49, 127-137.

605 Doube, B.M., 1990. A functional classification for analysis of the structure of dung beetle
606 assemblages. *Ecol. Entom.* 15, 371-383.

607 Dray, S., Legendre, P., 2008. Testing the species traits environment relationships: The
608 fourth-corner problem revisited. *Ecol.* 89, 3400-3412.

609 Edney, E., 1977. *Water Balance in Land Arthropods*. Springer, Germany.

610 Eisenhauer, N., Bonn, A., Guerra, C.A., 2019. Recognizing the quiet extinction of
611 invertebrates. *Nature Comm.* 10, 1-3.

612 Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W., Paulißen, D., 1992. Zeigerwerte
613 von Pflanzen in Mitteleuropa. Indicator values of plants in Central Europe. Verlag Erich
614 Goltze, Göttingen. 258 pp

615 Ellers, J., Berg, M.P., Dias, A.T.C., Fontana, S., Ooms, A., Moretti, M., 2018. Diversity in form
616 and function: vertical distribution of soil fauna mediates multidimensional trait variation. *J*
617 *Anim. Ecol.* 87, 933–944.

618 Elton, C., 1927. *Animal Ecology*. Sidgwick and Jackson, London.

619 Ernst, G., Felten, D., Vohland, M., Emmerling, C., 2009. Impact of ecologically different
620 earthworm species on soil water characteristics. *Eur. J. Soil Biol.* 45, 207-213.

621 FAO, ITPS, GSBI, SCBD, and EC. *State of Knowledge of Soil Biodiversity Status,*
622 *Challenges and Potentialities, Report 2020*. Rome: FAO, 2020.

623 Ferris, H., Bongers, T., de Goede, R.G.M., 2001. A framework for soil food web diagnostics:
624 extension of the nematode faunal analysis concept. *Appl. Soil Ecol.* 18, 13-29.

625 Finn, J.A., Gittings, T., 2003. A review of competition in north temperate dung beetle
626 communities. *Ecol. Entom.* 28, 1-13.

627 Fragoso, C., 1999. A survey of tropical earthworms: taxonomy, biogeography and
628 environmental plasticity, in: Lavelle, P., Brussaard, L., Hendrix, P. (Eds.), *Earthworm*
629 *management in tropical agroecosystems*. CAB International.

630 Gallagher, R.V., Falster, D.S., Maitner, B.S. *et al.*, 2020. Open Science principles for
631 accelerating trait-based science across the Tree of Life. *Nat. Ecol. Evol.* 4, 294–303.

632 Gisin, H.R., 1943. Ökologie und lebensgemeinschaften der collembohlen im schweizerischen
633 exkursionsgebiet Basels. *Rev. Suisse Zool.* 50, 131–224.

634 Gitay, H.T., Noble, I.R., 1997. What are functional types and how should we seek them?, in:
635 Smith, T., Shugart, H., Woodward, F. (Eds), Plant functional types: their relevance to
636 ecosystem properties and global change. Cambridge University Press; New York: 1997. pp.
637 3–19.

638 Gittings, T., Giller, P.S., 1997. Life history traits and resource utilisation in an assemblage of
639 North temperate *Aphodius* Dung Beetles (Coleoptera: Scarabaeidae). Ecograph. 20, 55–66.

640 Gobat, J.-M., Aragno, M., Matthey, W., 1998. Le sol vivant. Bases de pédologie, biologie des
641 sols. Presses Universitaires et Polytechniques romandes, Lausanne.

642 Gongalsky, K.B., Zaitsev, A.S., Korobushkin, D.I., Saifutdinov, R.A., Butenko, K.O., de Vries,
643 F.T., Ekschmitt, K., Degtyarev, M.I., Gorbunova, A.Y., Kostina, N.V., Rakhleeva, A.A.,
644 Shakhab, S.V., Yazrikova, T.E., Wolters, V., Bardgett, R.D., 2021. Forest fire induces short-
645 term shifts in soil food webs with consequences for carbon cycling. Ecol. Lett. 24, 438–450.

646 Gongalsky, K.B., 2021. Soil macrofauna: Study problems and perspectives. Soil Biol.
647 Biochem. 159, 108281.

648 Gower, J.C., 1971. General coefficient of similarity and some of its properties. Biometr. 27,
649 857–871.

650 Graefe, U., Schmelz, R.M., 1999. Indicator values, strategy types and life forms of terrestrial
651 Enchytraeidae and other microannelids. Newsl. Enchytraeidae 6, 59–67.

652 Grassé, P.P., 1984. Termitologia. Masson, Paris.

653 Gravel, D., Albouy, C., Thuiller, W., 2016. The meaning of functional trait composition of food
654 webs for ecosystem functioning. Phil. Trans. Roy. Soc. B: Biol. Sci., 371, 20150268.

655 Greenslade, P.J.M., 1978. Ants, in Low, W.A. (Ed.), The physical and biological features of
656 Kunoth paddock in central Australia. CSIRO Division of Land Resources Tech. Paper No. 4.
657 Canberra, Australia: CSIRO. pp. 109–13.

658 Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its
659 relevance for ecological and evolutionary theory. Am. Nat. 111, 1169–1194.

660 Grinnell, J., 1917. The niche-relationships of the California Thrasher. *The Auk*, 34, 427-433.

661 Guidetti, R., Bertolani, R., Rebecchi, L., 2013. Comparative analysis of the tardigrade feeding
662 apparatus: adaptive convergence and evolutionary pattern of the piercing stylet system. *J.*
663 *Limnol.* 72, 24-35.

664 Guerra, C. A., Bardgett, R. D., Caon, L., Crowther, T. W., Delgado-Baquerizo, M.,
665 Montanarella, L., ..., Eisenhauer, N., 2021. Tracking, targeting, and conserving soil
666 biodiversity. *Science*, 371(6526), 239-241

667 Guidetti, R., Altiero, T., Bertolani, R., Grazioso, P., Rebecchi, L., 2011. Survival of freezing by
668 hydrated tardigrades inhabiting terrestrial and freshwater habitats. *Zool.* 114, 123–128.

669 Guidetti, R., Altiero, T., Marchioro, T., Sarzi Amadè, L., Avdonina, A.M., Bertolani, R.,
670 Rebecchi, L., 2012. Form and function of the feeding apparatus in Eutardigrada (Tardigrada).
671 *Zoomorph.* 131, 127–148.

672 Halffter, G., 1977. Evolution of nidification in the Scarabaeinae (Coleoptera, Scarabaeidae).
673 *Quaest. Entom.* 13, 231-253.

674 Halffter, G., Edmonds, W.D., 1982. The nesting behaviour of dung beetles (Scarabaeinae):
675 an ecological and evolutive approach. Instituto de Ecología, Mexico, 176p.

676 Halffter, G., Matthews, E.G., 1966. The natural history of dung beetles of the subfamily
677 Scarabaeinae (Coleoptera: Scarabaeidae). *Folia Entom. Mex.* 12-14, 1-312.

678 Hammond, P.M., 2000. Coastal Staphylinidae (rove beetles) in the British Isles, with special
679 reference to saltmarshes, in: Sherwood, B.R., Gardiner, B.G., Harris, T. (Eds.) *British Salt-*
680 *marshes: Joint symposium on British Saltmarshes organized between the Linnean Society*
681 *of London, the Royal Society for the Protection of Birds, and English Nature.* Cardigan,
682 London, 247-302.

683 Hanski, I., Cambefort, Y., 1991. *Dung Beetle Ecology.* Princeton University Press, Princeton,
684 New Jersey.

685 Hedde, M., Lavelle, P., Joffre, R., Jiménez, J.J., Decaëns, T., 2005. Specific functional
686 signature in soil macro-invertebrate biostructures. *Funct. Ecol.* 19, 785-793.

687 Henneron, L., Bernard, L., Hedde, M., Pelosi, C., Villenave, C., Chenu, C., Bertrand, M.,
688 Girardin, C., Blanchart, E., 2015. Fourteen years of evidence for positive effects of
689 conservation agriculture and organic farming on soil life. *Agr. Sust. Dev.* 35, 169-181.

690 Higashi, M., Abe, T., and Burns, T.P., 1992. Carbon—nitrogen balance and termite ecology.
691 *Proc. Roy. Soc. London. Series B: Biolog. Sci.* 249, 303-308.

692 Hoese, B., 1981. Morphologie und Funktion des Wasserleitungssystems der terrestrischen
693 Isopoden (Crustacea, Isopoda, Oniscoidea). *Zoomorphol.* 98, 135–167.

694 Hoese, B., 1984. The marsupium of terrestrial isopods. *Symp. Zool. Soc. Lond.* 53, 1-6.

695 Holt, J.A., Lepage, M., 2000. Termites and soil properties, in Holt, J.A., Lepage, M. (Eds.)
696 *Termites: evolution, sociality, symbioses, ecology*, pp389-407.

697 Hopkin, S.P., 1997. *Biology of the Springtails (Insecta: Collembola)*. Oxford University Press
698 p. 330.

699 Horgan, F.G., 2008. Dung beetle assemblages in forests and pastures of El Salvador: a
700 functional comparison. *Biodiv. Conserv.* 17, 2961-2978.

701 Huang, C.-Y., Hendrix, P.F., Fahey, T.J., Bohlen, P.J., Groffman, P.M., 2010. A simulation
702 model to evaluate the impacts of invasive earthworms on soil carbon dynamics. *Ecol. Model.*
703 221, 2447-2457.

704 Hutchinson, G., 1957. Concluding remarks. – *Cold Spring Harb. Symp. Quant. Biol.* 22, 415–
705 427.

706 Jaillard, B., Richon, C., Deleporte, P., Loreau, M., Violle, C., 2018. An a posteriori species
707 clustering for quantifying the effects of species interactions on ecosystem functioning.
708 *Method. Ecol. Evol.* 9, 704–715.

709 Jay-Robert, P., Errouissi, F. Lumaret, J.P., 2008. Temporal coexistence of dung-dweller and
 710 soil-digger dung beetles (Coleoptera, Scarabaeoidea) in contrasting Mediterranean habitats.
 711 Bull. Entom. Res. 98, 303–316.

712 Jégou, D., Cluzeau, D., Balesdent, J., Tréhen, P., 1998. Effects of four ecological categories
 713 of earthworms on carbon transfer in soil. Appl. Soil Ecol. 9, 249-255.

714 Joimel, S., Schwartz, C., Hedde, M., Kiyota, S., Krogh, P.H., Nahmani, J., Pérès, G.,
 715 Vergnes, A., Cortet, J., 2017. Urban and industrial land uses have a higher soil biological
 716 quality than expected from physicochemical quality. Sci. Total Environ. 15, 614-621.

717 Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as
 718 physical ecosystem engineers. Ecol. 78, 1946–1957.

719 Jouquet, P., Traoré, S., Choosai, C., Hartmann, C., and Bignell, D., 2011. Influence of
 720 termites on ecosystem functioning. Ecosystem services provided by termites. Eur. J. Soil
 721 Biol. 47, 215-222.

722 Keller, L., 1995. Social life: the paradox of multiple-queen colonies. Trends Ecol. Evol. 10,
 723 355-360.

724 Kibblewhite, M.G., Ritz, K., Swift, M.J., 2008. Soil health in agricultural systems. Philos.
 725 Trans. R. Soc. B-Biol. Sci. 363, 685–701.

726 Knulle, W., 1957. Die Verteilung der Acari: Oribatei im Boden. Ztschr. Morph. Okol. Tiere. 46,
 727 397-432.

728 Koch, K., 1989-1993. Die Käfer Mitteleuropas. Ökologie, 1-4. Goecke and Evers, Krefeld,
 729 1595 pp.

730 Krause, A., Sandmann, D., Bluhm, S.L., Ermilov, S., Widyastuti, R., Farikhah Haneda, N.,
 731 Scheu, S., Maraun, M., 2019. Shift in trophic niches of soil microarthropods with conversion of
 732 tropical rainforest into plantations as indicated by stable isotopes (^{15}N , ^{13}C). PLOS ONE 14,
 733 10 (2019): e0224520.

734 Krivolutsky, D.A., 1995. Oribatid mites. Moscow: Nauka publishers. 224 pp. (in Russian with
735 English summary)

736 Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional
737 diversity from multiple traits. *Ecol.* 91, 299-305.

738 Lavelle, P. (1997) Faunal activities and soil processes: adaptive strategies that determine
739 ecosystem function. *Adv. Ecol. Res.* 27, 93-132.

740 Lavelle, P., Bignell, D., Lepage, M., Walters, V., Roger, P., Lavelle, P., 1997. Soil function in
741 a changing world: the role of invertebrate ecosystem engineers. *Eur. J. Soil Biol.* 33, 159–
742 193.

743 Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P.,
744 Rossi, J.P., 2006. Soil invertebrates and ecosystem services. *Eur. J. Soil Biol.* 42, 3–15.

745 Lavelle, P., Barot, S., Blouin, M., Decaëns, T., Jimenez, J. J., Jouquet, P., 2007. Earthworms
746 as key actors in self-organised soil systems, in Cuddington, K., Byers, J. E., Wilson, W. G.,
747 Hastings, A. (Eds.), *Ecosystem Engineers: From Protists to Plants*. Academic Press,
748 *Theoretical Ecology Series*, pp. 77–106.

749 Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem
750 functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.* 16, 545-556.

751 Lee, K.E., 1959. The earthworm fauna of New Zealand. *Res. Bull. New Zealand Dept. Sci.*
752 *Industr. Res.* 130. 486 pp.

753 Luxton, M., 1972. Studies on the oribatid mites of a Danish beech wood soil. I. Nutritional
754 biology. *Pedobiol.* 12, 434–463.

755 MacArthur, R., Levins, R., 1964. Competition, habitat selection, and character displacement in
756 a patchy environment. *Proc. Nat. Acad. Sci. U.S.A.* 51, 1207-1210.

757 Majka, C.G., Klimaszewski, J., Lauff, R.F., 2008. The coastal rove beetles (Coleoptera,
758 Staphylinidae) of Atlantic Canada: a survey and new records, in: Majka, C.G., Klimaszewski,

759 J. (Eds.), Biodiversity, Biosystematics, and Ecology of Canadian Coleoptera. ZooKeys 2: 115-
760 150.

761 Malcicka, M., Ruther, J., Ellers, J., 2017. *De novo* synthesis of linoleic acid in multiple
762 Collembola Species. J. Chem. Ecol., 43, 911– 919.

763 Mariet, A.L., Gauthier-Manuel, H., Lagiewski, T., Bégeot, C., Walter-Simonnet, A.V., Gimbert,
764 F., 2020. Impact assessment of legacy wastes from ancient mining activities on current
765 earthworm community. J. Hazard. Mater. 393, 122369.

766 Maraun, M., Erdmann G., Fischer, B.M., Pollierer, M.M., Norton, R.A., Schneider, K., Scheu,
767 S., 2011. Stable isotopes revisited: Their use and limits for oribatid mite trophic ecology. Soil
768 Biol. Biochem. 43, 877-882.

769 Martin-Perea, D., Fesharaki, O., Domingo, M. S., Gamboa, S., and Fernández, M.H., 2019.
770 *Messor barbarus* ants as soil bioturbators: Implications for granulometry, mineralogical
771 composition and fossil remains extraction in Somosaguas site (Madrid basin, Spain). Catena
772 172, 664-677.

773 Martinez-Almoyna, C., Thuiller, W., Chalmandrier, L., Ohlmann, M., Foulquier, A., Clément, J.-
774 C., Zinger, L., Münkemüller, T., 2019. Multi-trophic β -diversity mediates the effect of
775 environmental gradients on the turnover of multiple ecosystem functions. Funct. Ecol. 33,
776 2053-2064.

777 McLean, M., Stuart-Smith, R.D., Villéger, S., Auber, E.G.J., MacNeil, M.A., Loiseau, N.,
778 Leprieur, F., Mouillot, D., 2021. Trait similarity in reef fish faunas across the world's oceans.
779 Proc. Nat. Acad. Sci. U.S.A. 118, e2012318118.

780 Milcu, A., Partsch, S., Langel, R., Scheu, S., 2006. The response of decomposers
781 (earthworms, springtails and microorganisms) to variations in species and functional group
782 diversity of plants. OIKOS 112, 513-524.

783 Milotić, T., Baltzinger, C., Eichberg, C., Eycott, A.E., Heurich, M., Müller, J., Noriega, J.A.,

784 Menendez, R., Stadler, J., Ádám, R., Bargmann, T., Bilger, I., Buse, J., Calatayud, J.,
 785 Ciubuc, C., Boros, G., Jay- Robert, P., Kruus, M., Merivee, E., Miessen, G., Must, A., Ardali,
 786 E., Preda, E., Rahimi, I., Rohwedder, D., Rose, R., Slade, E. M., Somay, L., Tahmasebi, P.,
 787 Ziani, S., Hoffmann, M., 2019. Functionally richer communities improve ecosystem
 788 functioning: dung removal and secondary seed dispersal by dung beetles in the Western
 789 Palaearctic. *J. Biogeogr.* 46, 70–82.

790 Moranz, R. A., Debinski, D.M., Winkler, L., Trager, J., McGranahan, D.A., Engle, D.M., Miller,
 791 J.R., 2013. Effects of grassland management practices on ant functional groups in central
 792 North America. *J. Insect Conserv.* 17, 699-713.

793 Mouillot, D., Villegier, S., Parravicini, V., Kulbicki, M., Arias-Gonzalez, J.E., Bender, M.,
 794 Chabanet, P., Floeter, S.R., Friedlander, A., Vigliola, L., Bellwood, D.R., 2014. Functional
 795 over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proc.*
 796 *Nat. Acad. Sci. U.S.A.* 111, 13757–13762.

797 Mulder, C., Vonk, J.A., 2011. Nematode traits and environmental constraints in 200 soil
 798 systems: Scaling within the 60–6,000 μm body size range. *Ecology* 92, 2004.

799 Mulder, C., Conti, E., Costa, G., 2019. Belowground thermoregulation in Namibian desert
 800 spiders that burrow their own chemostats. *Acta Oecol.* 96, 18–23.

801 O'Connor, L.M., Pollock, L.J., Braga, J., Ficetola, G.F., Maiorano, L., Martinez- Almoyna, C.,
 802 Montemaggiori, A., Ohlmann, M., Thuiller, W., 2020. Unveiling the food webs of tetrapods
 803 across Europe through the prism of the Eltonian niche. *J. Biogeogr.* 47, 181-192.

804 Ohlmann M., Mazel F., Chalmandrier L., Bec S., Coissac E., Gielly, L., Pansu, J., Schilling,
 805 V., Taberlet, P., Zinger, L., Chave, J., Wilfried T., 2018. Mapping the imprint of biotic
 806 interactions on β -diversity. *Ecol. Lett.* 21, 1660-1669.

807 Orgiazzi, A., Bardgett, R.D., Barrios, E., Behan-Pelletier, V., Briones, M.J.I., Chotte, J-L., De
 808 Deyn, G.B., Eggleton, P., Fierer, N., Fraser, T., Hedlund, K., Jeffery, S., Johnson, N.C.,

809 Jones, A., Kandeler, E., Kaneko, N., Lavelle, P., Lemanceau, P., Miko, L., Montanarella, L.,
 810 Moreira, F.M.S., Ramirez, K.S., Scheu, S., Singh, B.K., Six, J., van der Putten, W.H., Wall,
 811 D.H., 2016. Global Soil Biodiversity Atlas. European Commission, Publications Office of the
 812 European Union, Luxembourg.

813 Parr, C.L., Dunn, R.R., Sanders, N.J., Weiser, M.D., Photakis, M., Bishop, T.R., Fitzpatrick,
 814 M.C., Arnan, X., Baccaro, F., Brandão, C.R.F., Chick, L., Donoso, D., Fayle, T.M., Gómez,
 815 C., Grossman, B., Gibb, H., 2017. GlobalAnts: a new database on the geography of ant traits
 816 (Hymenoptera: Formicidae). *Insect Conserv. Diver.* 10, 5-20.

817 Perrin, W., Moretti, M., Vergnes, A., Borcard, D., Jay-Robert, P., 2020. Response of dung
 818 beetle assemblages to grazing intensity in two distinct bioclimatic contexts. *Agr. Ecosyst.*
 819 *Env.* 289, 106740.

820 Perrin, W., Fontana, S., Coq, S., Berlioz, L., Jay-Robert, P., Moretti, M., 2021. The influence
 821 of fine-scale grazing heterogeneity on dung beetle assemblages: what trait analysis teaches
 822 us. *Environ. Entomol.* 17, 1332-1343.

823 Pessôa, M.B., Izzo, T.J., Vaz-de-Mello, F.Z., 2017. Assemblage and functional categorization
 824 of dung beetles (Coleoptera: Scarabaeinae) from the Pantanal. *PeerJ* 5, e3978. doi:
 825 10.7717/peerj.3978

826 Pey, B., Nahmani, J., Auclerc, A., Capowiez, Y., Cluzeau, D., Cortet, J., Decaëns, T.,
 827 Deharveng, L., Dubs, F., Joimel, S., Guernion, M., Grumiaux, F., Laporte, M.-A., Pasquet, A.,
 828 Pelosi, C., Pernin, C., Ponge, J.-F., Salmon, S., Santorufo, L., Hedde, M., 2014. A thesaurus
 829 for soil invertebrate trait-based approaches. *PLOS One* 9, e108985.

830 Perel, T.S., 1975. Life forms of earthworms (Lumbricidae). *Zhurnal Obshchei Biologii* 36,
 831 189-202 (in Russian).

832 Pey, B., Cortet, J., Watteau, F., Cheynier, K., Schwartz, C., 2013. Structure of earthworm
 833 burrows related to organic matter of a constructed Technosol. *Geoderma* 202–203, 103-111.

834 Pigot, A.L., Sheard, C., Miller, E.T., Bregman, T.P., Freeman, B.G., Roll, U., Seddon, N.,
835 Trisos, C.H., Weeks, B.C., Tobias, J.A., 2020. Macroevolutionary convergence connects
836 morphological form to ecological function in birds. *Nature Ecol. Evol.* 4, 230–239.

837 Ponge, J.-F., 1993. Biocenoses of Collembola in atlantic temperate grass-woodland
838 ecosystems. *Pedobiol.* 37, 223-244.

839 Potapov, A.M., Semenina, E.E., Korotkevich, A.Y., Kuznetsova, N.A., Tiunov A.V., 2016.
840 Connecting taxonomy and ecology: Trophic niches of collembolans as related to taxonomic
841 identity and life forms. *Soil Biol. Biochem.* 101, 20-31.

842 Potapov, A.M., Tiunov, A.V., Scheu, S., 2019. Uncovering trophic positions and food
843 resources of soil animals using bulk natural stable isotope composition. *Biol. Rev.* 94, 37–59.

844 Potapov, A.M., Rozanova, O.L., Semenina, E.E., Leonov, V.D., Belyakova, O.I., Bogatyreva,
845 V.Y., Degtyarev, M.I., Esaulov, A.S., Korotkevich, A.Y., Kudrin, A.A., Malysheva, E.A., Mazei,
846 Y.A., Tsurikov, S.M., Zuev, A.G., Tiunov, A.V., 2021. Size compartmentalization of energy
847 channeling in terrestrial belowground food webs. *Ecol.* 102, e03421.

848 Potapov, A.M., Pollierer, M.M., Salmon, S., Šustr, V., Chen, T.-W., 2021. Multidimensional
849 trophic niche revealed by complementary approaches: gut content, digestive enzymes, fatty
850 acids and stable isotopes in Collembola. *J. Animal Ecol.* 90, 1919-1933.

851 Potapov, A.M., 2022. Multifunctionality of belowground food webs: resource, size and spatial
852 energy channels. *Biological Reviews*, 2022. <https://doi.org/10.1111/brv.12857>.

853 Potapov, A.M., Beaulieu, F., Birkhofer, K., Bluhm, S.L., Degtyarev, M.I., Devetter, M.,
854 Goncharov, A.A., Gongalsky, K.B., Klärner, B., Korobushkin, D.I., Liebke, D.F., Maraun, M.,
855 Mc Donnell, R.J., Pollierer, M.M., Schaefer, I., Shrubovych, J., Semenyuk, I.I., Sendra, A.,
856 Tuma, J., Tůmová, M., Vassilieva, A.B., Chen, T.-W., Geisen, S., Schmidt, O., Tiunov, A.V.
857 and Scheu, S., 2022. Feeding habits and multifunctional classification of soil-associated
858 consumers from protists to vertebrates. *Biol. Reviews* 97, 1057–1117.

859 Potapov, A. M., Sun, X., Barnes, A. D., Briones, M. J., Brown, G. G., Cameron, E. K., Chang,
860 C.-H., Cortet, J., Eisenhauer, N., Franco, A. L., Fujii, S., Geisen, S., Guerra, C., Gongalsky,
861 K., Haimi, J., Handa, I. T., Janion-Sheepers, C., Karaban, K., Lindo, Z., Matthieu, J., Moreno,
862 M. L., Murvanidze, M., Nielsen, U., Scheu, S., Schmidt, O., Schneider, C., Seeber, J.,
863 Tsiafouli, M., Tuma, J., Tiunov, A., Zaytsev, A. S., Ashwood, F., Callaham, M., Wall, D.,
864 2022. Global monitoring of soil animal communities using a common methodology. *SOIL*
865 *ORGANISMS*, 94(1), 55–68.

866 Rainford, J.L., Mayhew, P.J., 2015. Diet evolution and clade richness in Hexapoda: a
867 phylogenetic study of higher taxa. *Am. Nat.* 186, 777-791.

868 Richardson, J.B., Görres, J.H., Sizmur, T., 2020. Synthesis of earthworm trace metal uptake
869 and bioaccumulation data: Role of soil concentration, earthworm ecophysiology, and
870 experimental design. *Environ. Pollut.* 262, 114126.

871 Root, R.B., 1967. The niche exploitation pattern of the Bluegray Gnatcatcher. *Ecol. Monogr.*
872 37, 317–350.

873 Rusek, J., 1989. Ecology of Collembola, in Dallai, R. (Ed.), 3rd International Seminar on
874 Apterygota, Siena: Univ. Siena Press. pp271–281.

875 Rusek, J., 2007. A new classification of Collembola and Protura life forms. *Contributions to*
876 *soil zoology in Central Europe II* 5: 109–115.

877 Sandmann, D., Scheu, S., Potapov, A., 2019. Ecotaxonomy: Linking taxa with traits and
878 integrating taxonomical and ecological research. *Biodiver. Inform. Sci. Stand.* 3, e37146.

879 Satchell, J.E., 1980. r worms and K worms: a basis for classifying lumbricid earthworm
880 strategies, in Dindal D.L. (Ed.), *Soil biology as related to land use practices. Proc. VIIth Int.*
881 *Soil Zool. Coll.*, EPA, Washington DC, pp. 848–864.

882 Savolainen, R., Vepsäläinen, K., 1988. A competition hierarchy among boreal ants: impact on
883 resource partitioning and community structure. *Oikos* 51, 135-155.

884 Schmalzfuss, H., 1984. Eco-morphological strategies in terrestrial isopods. Symp. Zool. Soc.
885 London. 53, 49 – 63.

886 Schneider, K., Migge, S., Norton, R.A., Scheu, S., Langel, R., Reineking, A., Maraun, M.,
887 2004. Trophic niche differentiation in soil microarthropods (Oribatida, Acari): evidence from
888 stable isotope ratios ($^{15}\text{N}/^{14}\text{N}$). Soil Biol. Biochem. 36, 1769-1774.

889 Schuster, R., 1956. Der Anteil der Oribatiden an den Zersetzungsvorgängen im Boden. Z.
890 Morphol. Ökol. Tiere 45, 1–33.

891 Sechi, V., Brussaard, L., de Goede, R.G.M., Rutgers, M., Mulder, C., 2015. Choice of
892 resolution by functional trait or taxonomy affects allometric scaling in soil food webs. Am. Nat.
893 185, 142–149.

894 Sharova, I.K., 1981. Life Forms of Carabids (Coleoptera, Carabidae). Nauka, Moscow, 359
895 pp.

896 Siepel, H., 1994. Life-history tactics of soil microarthropods. Biol. Fert. Soils 18, 263–278.

897 Siepel, H., de Ruiter-Dijkman, E.M., 1993. Feeding guilds of oribatid mites based on their
898 carbohydrase activities. Soil Biol. Biochem. 25, 1491-1497.

899 Simberloff, D., Dayan, T., 1991. The guild concept and the structure of ecological
900 communities. Annu. Rev. Ecol. Syst., 22, 115–143.

901 Sosiak, C. E., Barden, P., 2021. Multidimensional trait morphology predicts ecology across
902 ant lineages. Funct. Ecol. 35, 139-152.

903 Stebaeva, S.K., 1970. Life forms of springtails (Collembola). Zool. Zh. 49, 1437-1455.

904 Susanti, W.I., Widyastuti, R., Scheu, S., Potapov, A.A., 2021. Trophic niche differentiation
905 and utilisation of food resources in Collembola is altered by rainforest conversion to
906 plantation systems'. PeerJ 9: e10971.

907 Sutton, S.L., Hassall, M., Willows, R., Davis, R.C., Grundy, A., Sunderland, K.D., 1984. Life
908 histories of terrestrial isopods: A study of intra- and interspecific variation. Symp. Zool.
909 Soc. London 53, 269-294.

910 Suter, R. B., Benson, K., 2014. Nocturnal, diurnal, crepuscular: activity assessments of
 911 Pisauridae and Lycosidae. *J. Arachnol.* 42, 178-191.
 912 Swift, M.J., Heal, O.W., Anderson, J.M., Anderson, J.M., 1979. Decomposition in terrestrial
 913 ecosystems. Univ of California Press.
 914 Tayasu, I., Abe, T., Eggleton, P., and Bignell, D.E., 1997. Nitrogen and carbon isotope ratios
 915 in termites: an indicator of trophic habit along the gradient from wood-feeding to soil-feeding.
 916 *Ecol. Entom.* 22, 343-351.
 917 Thibaud, J.-M., D'Haese, C.A., 2010. Le Petit Collembolle Illustré. *Arvernsis*, 51–52: 1–56.
 918 Tonelli, M., 2021. Some considerations on the terminology applied to dung beetle functional
 919 groups. *Ecol. Entomol.* 46: 772-776.
 920 Vandel, A., 1960. Isopodes terrestres. *Faune de France* 64.
 921 Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let
 922 the concept of trait be functional! *Oikos* 116, 882-892.
 923 Violle, C., Jiang L., 2009. Towards a trait-based quantification of species niche. *J. Plant Ecol.*
 924 2, 87–93.
 925 Violle, C., Thuiller, W., Mouquet, N., Munoz, F., Kraft, N.J.B., Cadotte, M.W., Livingstone,
 926 S.W., Mouillot, D., 2017. Functional rarity: the ecology of outliers. *Trends Ecol. Evol.* 32, 356-
 927 367
 928 Wall, D.H., Ritz, K., Six, J., Strong, D.R., van der Putten, W.H., 2012. Soil ecology and
 929 ecosystem services. Oxford University Press. 406p
 930 Wardle, D.A., 2002. *Communities and Ecosystems: Linking the Aboveground and*
 931 *Belowground Components*. Princeton and Oxford: Princeton University Press.
 932 Wilson, E.O., 1987. The little things that run the world (the importance and conservation of
 933 invertebrates). *Conserv. Biol.* 1, 344–346.
 934 Wilson, J.B., 1999. Guilds, functional types, and ecological groups. *Oikos* 86, 507–522.

935 Winemiller, K.O., Fitzgerald, D.B., Bower, L.M., Pianka, E.R., 2015. Functional traits,
936 convergent evolution, and periodic tables of niches. *Ecol. Lett.* 18:737–51.

937 Wurst, S., De Deyn, G.B., Owen, K., 2012. Soil biodiversity and functions, in: Wall, D. (Ed.)
938 Soil ecology and ecosystem services. Oxford University Press, Oxford, UK. pp. 28–44.

939 Yeates, G.W., Bongers, T., De Goede, R.G., Freckman, D.W., Georgieva, S.S., 1993.
940 Feeding habits in soil nematode families and genera-an outline for soil ecologists. *J.*
941 *Nematol.* 25, 315–331.

942 Zhang, L., He, N., Chang, D., Liu, X., Zhang, X., Xu, Y., Zhao, C., Sun, J., Li, W., Li, H., Hua,
943 F., Xu, L., 2018. Does ecotype matter? The influence of ecophysiology on benzo[a]pyrene
944 and cadmium accumulation and distribution in earthworms. *Soil Biol. Biochem.* 121: 24-34.

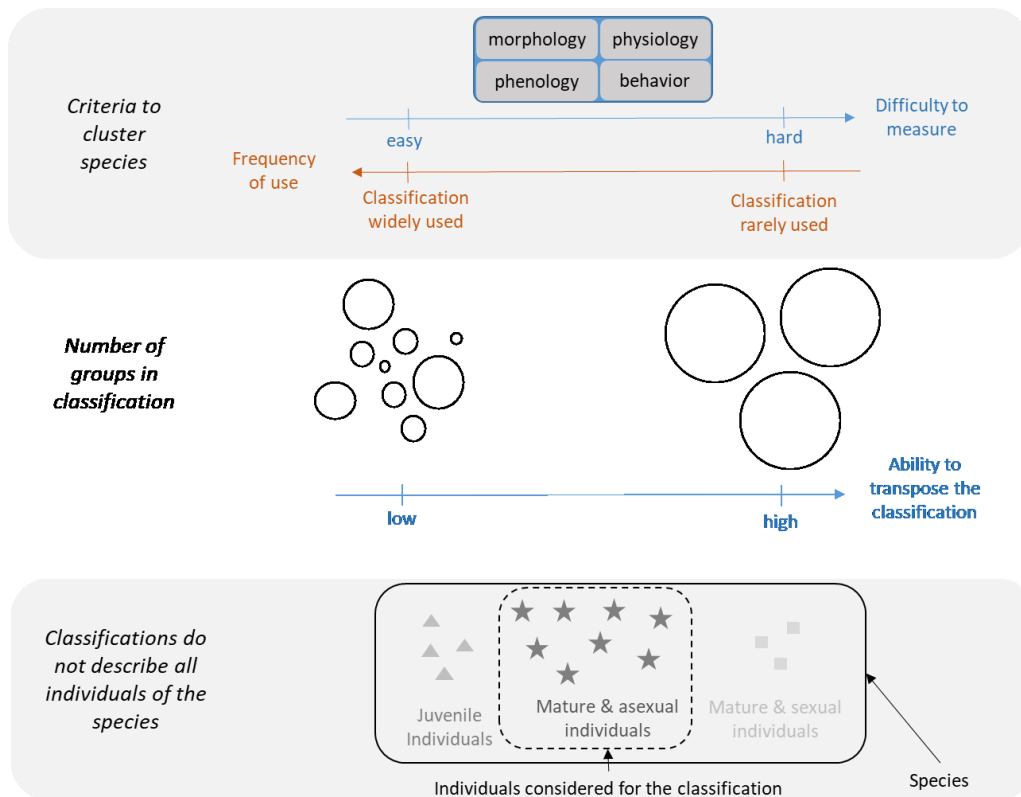
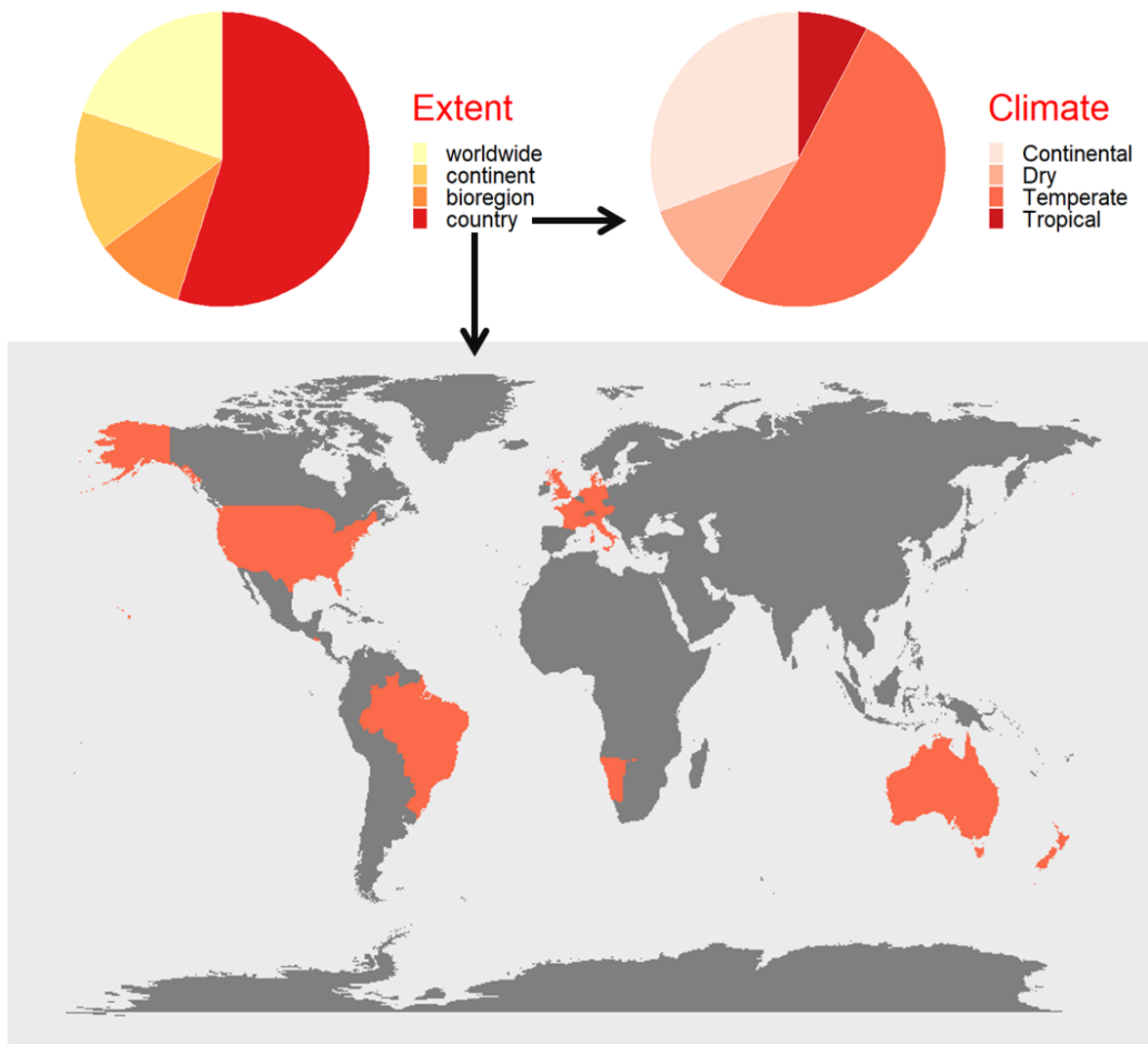


Figure 1: Existing classifications were not built on the same grounds. Upper panel illustrates that different species traits were used to cluster species into groups. Middle panel shows that classification systems may lead to different number of groups and that it may influence the transposability of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



956

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).

960

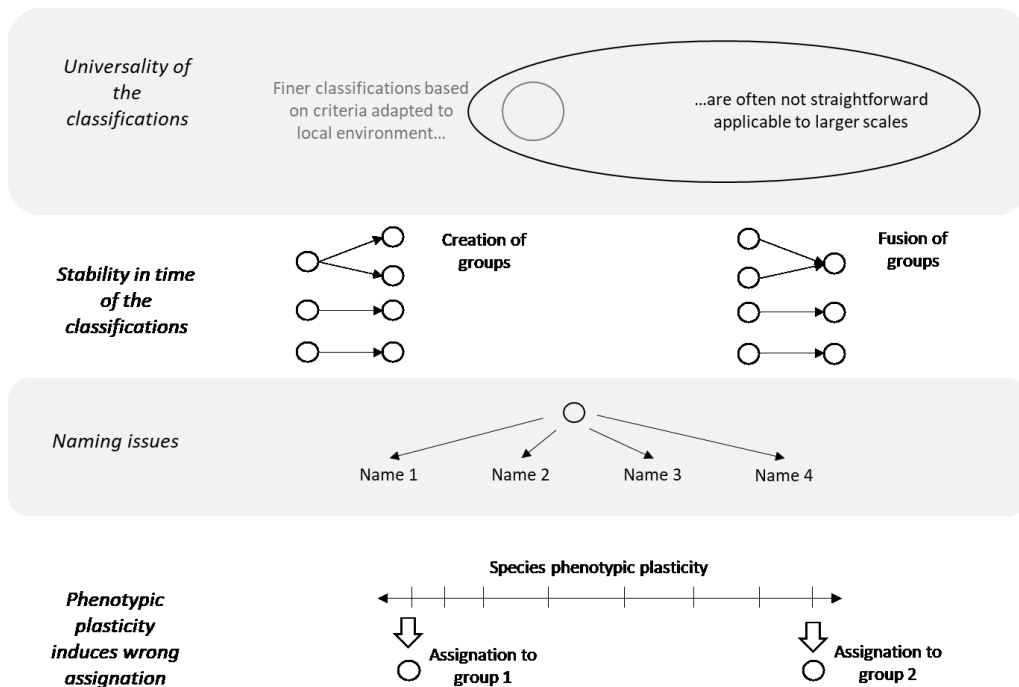
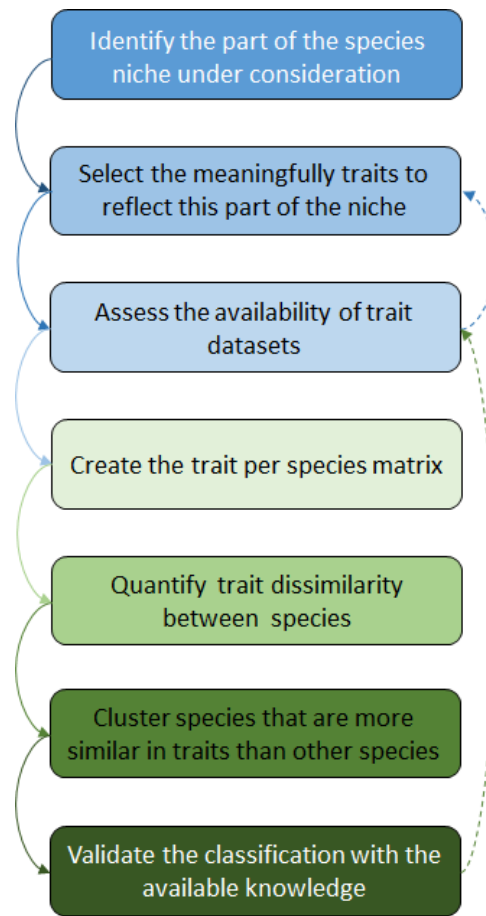


Figure 3: Misuses limit the meaningfulness of classifications: universality in scope (upper panel), stability of groups and of name over time (2nd and 3rd panels), and difficulty of assignment due to species phenotypic plasticity.

968



969

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 Ruiter-Dijkman (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)					
	Halfpeter 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
	Halfpeter (1977) Halfpeter 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