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A common framework for developing robust soil fauna classifications

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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.

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

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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., 2022a). 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 different clades 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 (Fig. 1). Most classifications only consider adults and not juveniles. Certain classifications are based on non-mating individuals whereas others consider sexual ones (Fig. 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,

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 et al. (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), Guidetti et al. (2013)	**Ecological traits** (Buccal morphology; Piercing stylets; Branching of furca)	**Expertise** Expert judgement	**8**	Italy
Woodlice (Phylum: Arthopoda; 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: Arthopoda; 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**	

(*continued on next page*)

Table 1 (*continued*)

Papers	Criteria	Clustering method	# groups	Initial biogeographic range
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: Arthopoda; 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: Arthopoda; 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 de 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 / Overwinting**	**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), Conti et al. (2019)	**Life history groups** (Thermal regulation and ability to survive, presence in polluted sites, etc.)	**Measures:** Field and molecular measurements	**5**	Namibia
Conti et al. (2020)	**Functional traits** **Biochemistry of silks**	Mass spectrometry measurements	**5**	Namibia
Mulder et al. (2019)	**Behavioural traits** **Burrow depth**	Empirical observations	**5**	Namibia
Dung beetles (Phylum: Arthropoda; Class: Insecta; Order: Coleoptera, Family: Scarabaeidae)				
Halffter and Matthews (1966)	**Nesting behavior** (sequence of behavioral steps leading to the completed nest)	**Expertise**: synthesis of works (published or not) based on laboratory rearing and field observations	**4**	Worldwide
Halffter (1977) Halffter and Edmonds (1982)	**Nesting behaviour** (Form of larval provision; Nest location; Nest complexity; Disposition of brood masses/balls in compound and subterranean nests; Manipulation of larval provision; Provisioning of subterranean nests; Outer surface of brood ball; Location of egg chamber; Male-female cooperation; Brood care)	**Expertise**: synthesis of works (published or not) based on laboratory rearing and field observations	**7**	Worldwide
Doube (1990)	**Nesting behaviour** (way to use and remove dung), **Dry body mass**	**Expertise**: synthesis of works (published or not) based on laboratory rearing and field observations	**7**	Austral Africa
Pessôa et al. (2017)	**'Physical' traits** (Size, Prothorax height, Area of the anterior tibia, Wing load, Mesotibia ratio); **Behavioral traits** (Generalism in food preferences,	**Statistical**: dissimilarity matrix (Gower) + non-hierarchical K-Means clustering method	**8**	South-America

(*continued on next page*)

Table 1 (*continued*)

Papers	Criteria	Clustering method	# groups	Initial biogeographic range
	Horizontal displacement, Nest building, Ball or pear-shaped nest); **Phenological traits** (Daily activity)			
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**	Propose an unified approach relying on published studies	**5**	Worldwide
	Nesting behaviour		**4**	
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 colonoy 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 (2021)	**Ecomorph syndromes** Classification initially based on nesting, foraging and functional role niche data but then defined using 17 morphological traits	**Expertise**	**10**	Worldwide

number of ocelli, etc. (Bouché, 1977; Malcicka et al., 2017; Pessôa et al., 2017; Sosiak and Barden, 2021). 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 (Fig. 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

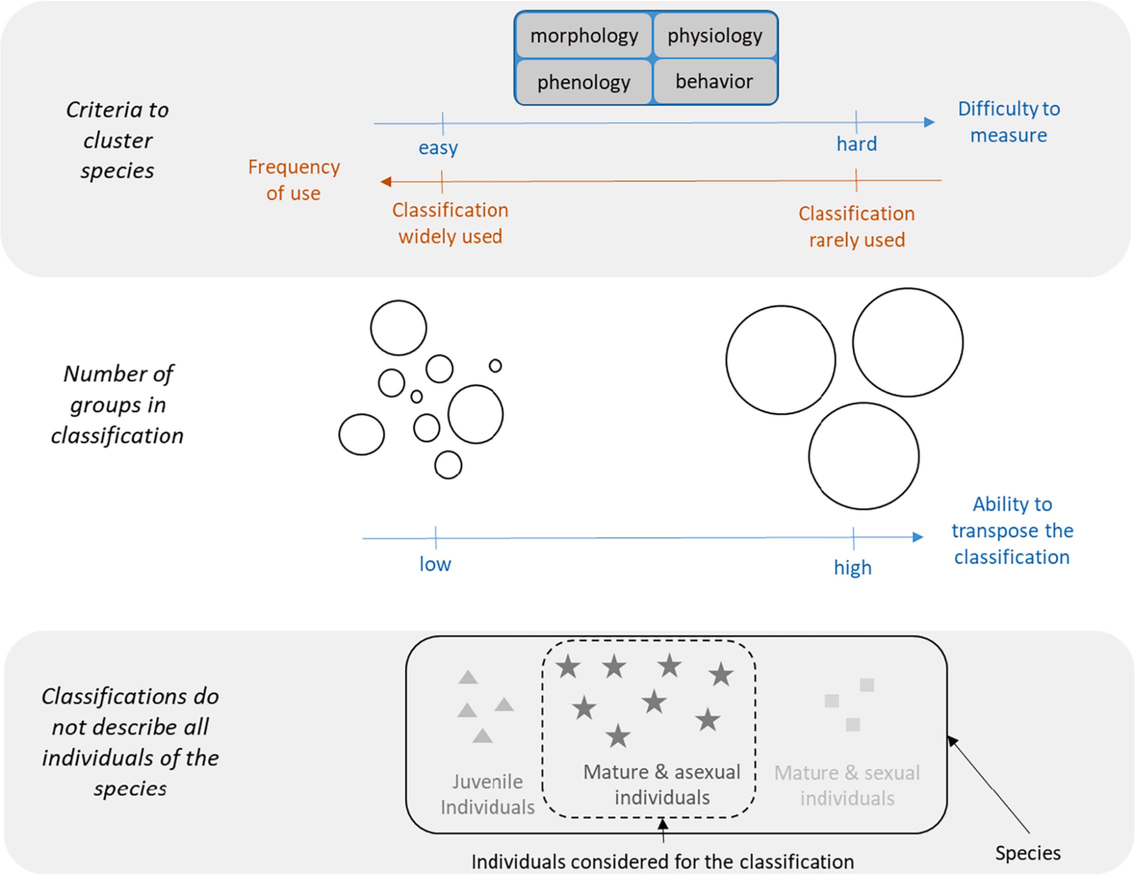

Fig. 1. Existing classifications were not built on the same grounds. Upper panel illustrates that different species traits were used to cluster species into groups. Middle panel shows that classification systems may lead to different number of groups and that it may influence the transposability of the 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.

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 (2021) 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., 2022b).

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., 2021a). 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; Cammeraat 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 (Fig. 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

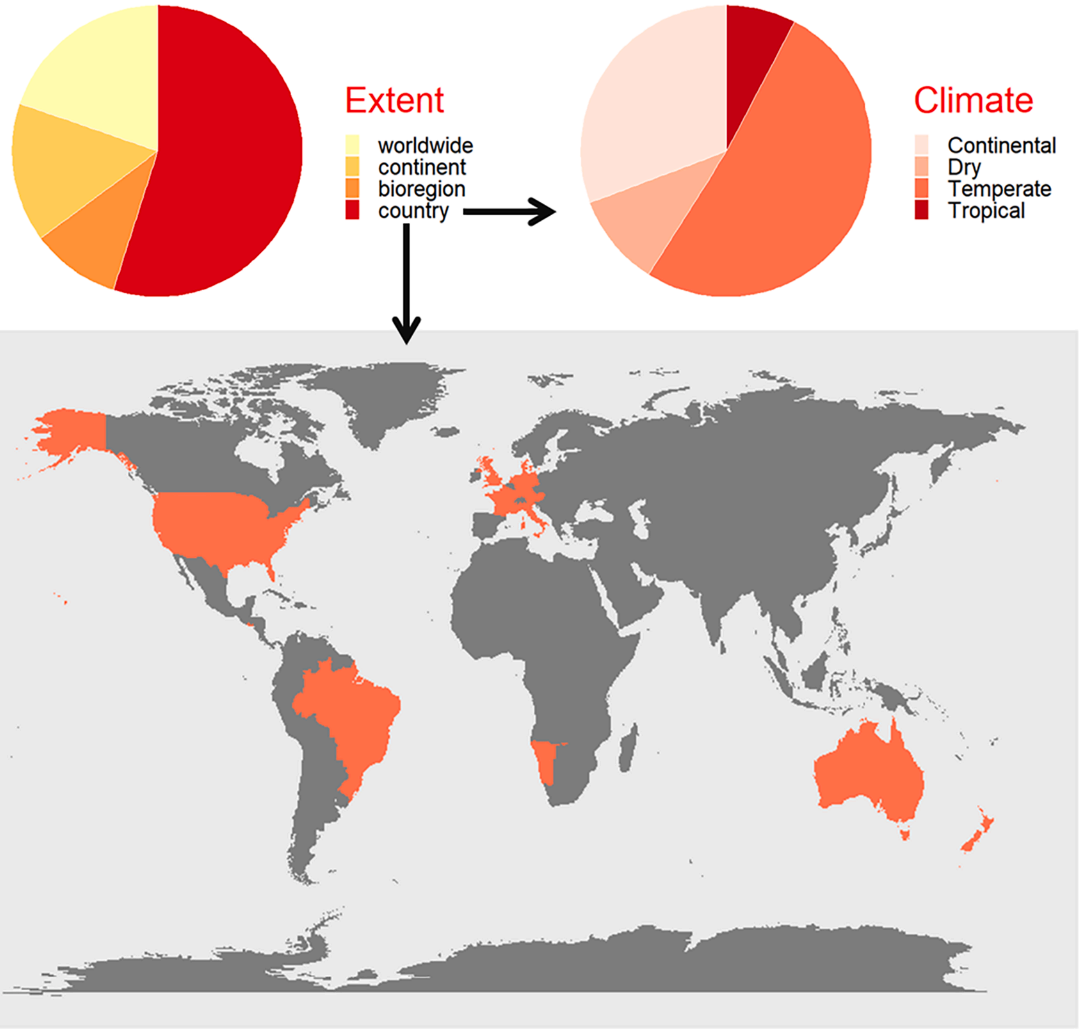

Fig. 2. Geographical scope of the classifications (upper left pie chart). For country-wide classifications (>50% of studied classifications): the country for which the classification was created (map) and its climate (upper right pie chart).

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.

3.2. Classifications are not stable in time

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

3.3. Inconsistent naming of classifications

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

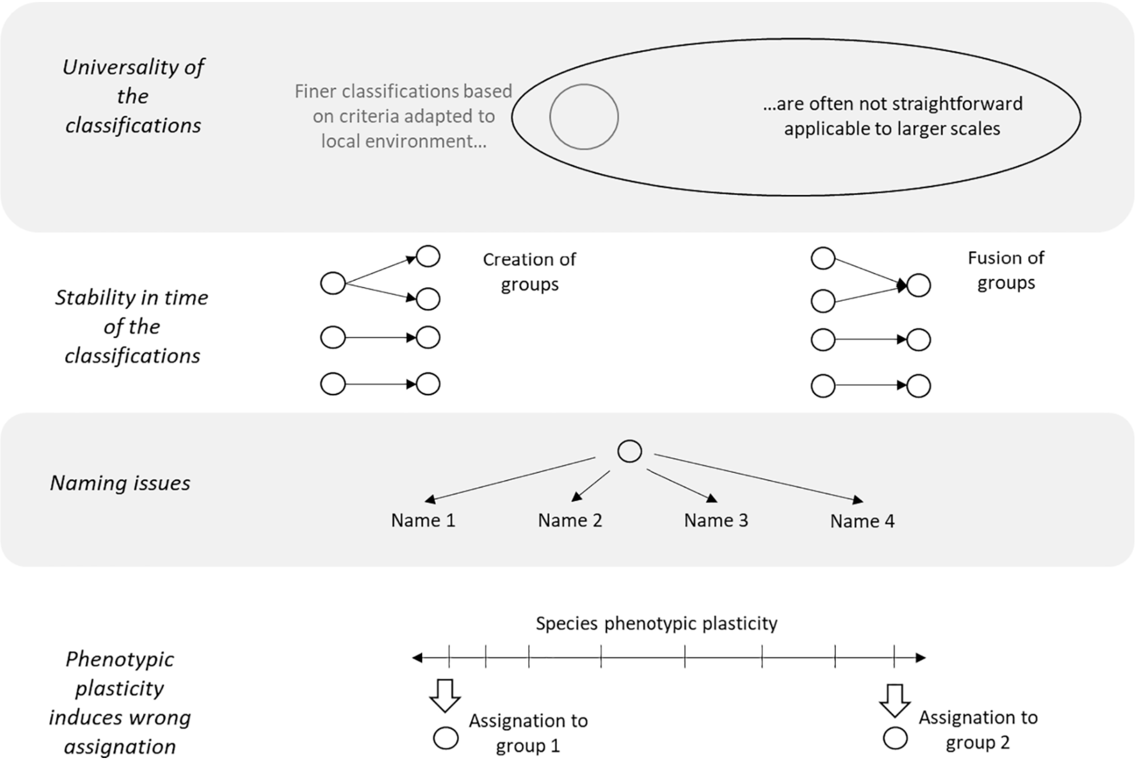

Fig. 3. Misuses limit the meaningfulness of classifications: universality in scope (upper panel), stability of groups and of name over time (2nd and 3rd panels), and difficulty of assignment due to species phenotypic plasticity.

groups (Mariet et al., 2020; 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., 2019) through 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).

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);

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).

- 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 https://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 (Fig. 4).

1. (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. (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. (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., 2018). This

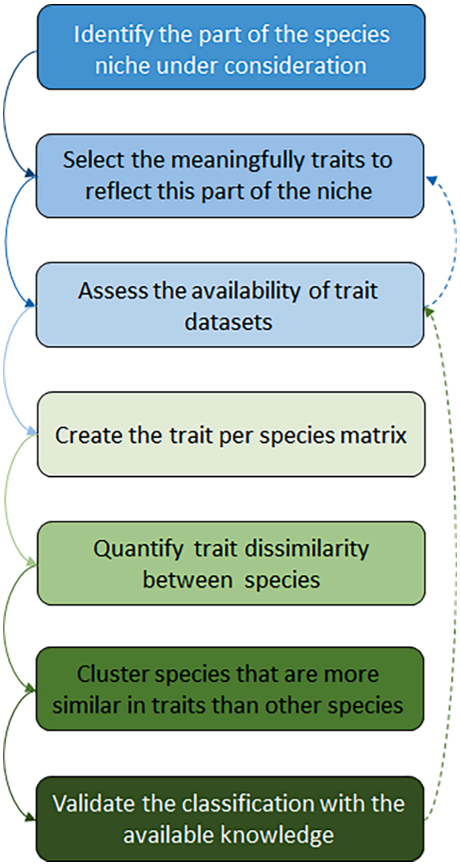

Fig. 4. Proposed seven-step hierarchical procedure to define guilds, functional groups and trophic groups within soil fauna.

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; Potapov et al., 2021b). 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, 2021). 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., 2020; Guerra et al., 2021; Potapov et al., 2022b). 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.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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