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Trait concepts, categories, and databases in soil invertebrates ecology – ordering the mess

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Abstract

The trait-based approach is increasingly used for soil invertebrates. Complementary to the taxonomy based approach, the trait-based approach can provide a more mechanistic understanding of the responses of organisms to environmental disturbances and of their effects on soil functioning. However, the application of the trait-based approach across studies is limited by the lack of conceptual consensus among researchers due to the historical development of the idea. There is a large ambiguity and variability in using the term 'functional traits' by zoologists and ecologists working on soil invertebrates. In this study, we used a questionnaire and literature scanning to review the practical use of functional traits concept in soil ecology over the last decade. We clarified and expanded the functional trait definition as 'A functional trait is a measurable characteristic of an individual organism or its colony that has a link to the organism's fitness and/or its effect on other organisms and/or the environment'. We also reviewed existing

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trait databases showing a high amount, but also high heterogeneity and low accessibility of data on the functional traits of soil invertebrates. We suggest synthesising existing trait data and databases, using the functional trait-based approach consistently and reproducibly, and disseminating it to facilitate research in soil ecology.

Keywords Functional traits | soil invertebrates | functional ecology | community ecology | terminology

1. Introduction

Soil organisms regulate nutrient cycling, dynamics of soil organic matter, greenhouse gas emissions, soil physical structure and water regimes, contributing thus to numerous ecosystem services (Kibblewhite et al. 2008, Wardle et al. 2004). To understand how soil communities assemble, protect them from threats, and manage their interactions to provide ecosystem services, we need better knowledge of soil biology and ecology, as well as a mechanistic understanding of the links between the diversity of soil communities and soil processes. Soil invertebrates present a vast diversity of sizes, shapes, life history strategies, and diets, each differently impacting soil functioning from the matrix scale (composition of mineral and organic matter) to the structural scale (arrangement of organic and mineral matter) and the soil profile scale (organisation of aggregates, pores and horizons) (Lavelle et al. 2006). While rapidly developing molecular tools fuel the progress in soil functional and community ecology, quantifying the role of invertebrates in soil functioning or understanding community assembly requires a description of their functional diversity.

Soil invertebrates have been grouped by ecologists according to several criteria to a number of ecological groups, such as guilds or functional groups, to embrace their tremendous biological diversity (Briones 2014, Hedde et al. 2022). Such an approach postulates that a group is represented by species sharing similar roles in a given ecological function and/or responding similarly to environmental gradients. While being generally satisfactory, the approach has several methodological and conceptual drawbacks. For example, such groups do not consider within-group variation and often consider adults and not juveniles (Hedde et al. 2022). Many misuses of concepts behind classifications are also noticed (Hedde et al. 2022).

The concept of functional traits was expanded from plants (Violle et al. 2007) to soil invertebrates to overcome these problems (Pey et al. 2014b). According to the conventional definition, functional traits are any morphological, physiological, phenological or behavioural features that can be measured in individuals and affect their fitness (Pey et al. 2014b). Over the last decade, a growing body of literature on traits appeared in soil invertebrate ecology. Many studies focused on providing additional insights into understanding the responses of soil biodiversity to environmental pressures (the ‘response’ aspect of functional traits, Lavorel and Garnier, 2002). It was shown that traits may better explain soil biodiversity patterns in response to environmental changes including soil contamination (Hedde et al. 2013a, 2013b, Santorufo et al. 2014), land-use (Joimel et al. 2021, Marliac et al. 2016, Pelosi et al. 2016, 2014, Santorufo et al. 2014, Susanti et al. 2021), or climate change (Bonfanti et al. 2022). Other studies attempted to mechanistically link soil organisms with soil processes or functions (Hedde et al. 2022): the ‘effect’ aspect of functional traits. For example, the long-standing consensus on the relationship between functional groups and processes in termites (Jouquet et al. 2022) or earthworms (Capowiez et al. 2024) was revised. The trait approach could also be used in evolutionary ecology to predict biodiversity responses to environmental changes of various organisms (Kearney et al. 2021) or in the feeding ecology of springtails (Chen et al. 2017). However, eco-evolutionary approaches are still rarely used in soil invertebrate research (Dalos et al. 2022).

Due to the growing interest in functional traits, which is by far not limited to soil organisms, several papers discussing the concept of traits have appeared in recent years (e.g. Dawson et al. 2021, Kearney et al. 2021, Streit & Bellwood 2023, Weiss & Ray 2019). However, trait-based ecology is sometimes considered to be biased because research tends to focus on the same ecosystems, sometimes poor in species, on the same taxonomic groups, mainly plants (e.g. Díaz et al. 2013), with approaches that are rarely multi-group (Schleuning et al. 2023). As a result, trait-based ecology needs to integrate more animal taxa and a diversity of ecosystems in their approach. Reviews that focus on terrestrial arthropods (Brousseau et al. 2018, Wong et al. 2019) do not include other important groups of soil invertebrates, such as earthworms, springtails or potworms. Currently, the term ‘functional traits’ is used by zoologists and ecologists working on soil invertebrates ambiguously and with different meanings. The confusion in the understanding the trait concept seems particularly pronounced in arthropod studies (Wong et al. 2019) but is also present in other groups (Dawson et al. 2021). Adopting common definitions within the trait concept is the basis for semantic integration in trait ecology. By defining the terms and logical relationships between them and linking them to data, we can avoid confusion in science and improve the management of trait data to allow studies and cross-taxa comparisons, as advocated by Weiss et Ray (2019). Strong theoretical concepts, rarely mentioned in trait data collection, could help interpret and prioritise trait acquisition (Kearney et al. 2021). Thus, a unification of functional trait semantics is urgently needed to synthesise trait-based research on soil invertebrate taxa and facilitate the methodology of this research field with, for example, future AI-based semantic solutions.

Increasing trait data availability also requires semantic homogenisation. Over the last years, the development of trait-based approaches has resulted in the creation of several databases of soil invertebrates traits. As for the centralised TRY database on plant traits (Kattge et al. 2011), most of the trait data on soil invertebrates are dispersed among taxon-specific databases (e.g. Formicidae or Carabidae) (Homburg et al. 2014, Carabids, Parr et al. 2017, GlobalAnts). Recently, several database initiatives emerged (e.g. BETSI, Ecotaxonomy), gathering traits of soil invertebrates in general rather than for specific taxa (Pey et al. 2014a, Potapov et al. 2019). However, until today, there has been no single initiative that aims to link the existing databases on soil invertebrate traits into a single accessible and interoperable platform for cross-taxa ecological and eco-evolutionary research. The large amount of missing data is still a limit to their current use (Auclerc et al. 2022).

As the first crucial step, there is an urgent need to review the existing trait databases, traits used, trait data available, and the understanding of the trait concept among soil ecologists. Very few papers have been published on soil invertebrate trait databases (but see Homburg et al. 2014, Parr et al. 2017, Potapov et al. 2019) and many uncertainties about available data and animal groups they cover remain. To fill these knowledge gaps, here we (i) refine the existing functional trait concepts used by soil ecologists to avoid scientific misunderstandings and improve trait data interoperability and use and (ii) list trait data sources, traits and their use in soil invertebrate research to improve the accessibility of this information and facilitate the development of integrative cross-taxa and cross-database tools and projects based on trait-based approaches**.**

2. Materials and methods

We used a questionnaire addressed to zoologists and ecologists working on soil invertebrates, who were familiar with the functional trait approach to identify the existing concepts and the cognitive representations about functional traits, the use of functional traits and trait databases.

The questionnaire included 14 questions (online S1). The questions included information about (i) participants (career stage, experience in trait approaches and specific taxa), (ii) their definition and classification of the 'functional traits', (iii) examples of traits used, as well as information about available trait datasets and databases. The questionnaire was distributed electronically on the 10th January 2021 among participants of the EUdaphobase COST Action (https://www.eudaphobase.eu) and Global Soil Biodiversity Initiative (GSBI; https://www.globalsoilbiodiversity.org). We encouraged colleagues to distribute the questionnaire among their colleagues. Although these networks are biased towards the European and North American research communities, we believe they are informative and represent current trends in soil ecology.

Overall, answers from 78 respondents were collected by the 30th of June 2021. Most respondents already used a functional trait approach for soil invertebrates in their research (79 %), while others planned to do this approach and were familiar with the concept. Mid- to late-career researchers were better represented (73 % were professors or associate professors) compared to early-career researchers (23 % were PhD students or postdocs). Other respondents were students or non-academic people (4 %). Respondents had experience mostly with earthworms (55 %) and springtails (52 %). Other studied taxa were mites (35 %), beetles (27 %), nematodes (27 %) and myriapods (23 %).

The results of the questionnaire were complemented with a literature search on the Web of Science and Google Scholar platforms with the keywords: 'traits' AND 'database*' AND 'soil invertebrates' or 'soil fauna' and personal literature libraries of the paper authors.

3. Concepts and applications of functional traits in soil ecology

3.1 What is a functional trait?

Pey et al. (2014a) proposed the following definition of functional traits for soil invertebrates: *'Functional traits are any morphological, physiological, phenological or behavioural feature that can be measured at individual level and that affect its fitness'.* This definition seems to be well accepted by the respondents. In the survey, 96 % agreed with this definition, considering that it fits a broader functional ecology set of concepts and is nicely balanced. This common definition is based on the widely accepted concept of functional traits developed for plants by Violle et al. (2007), who made many efforts to unify and standardise the terminology of 'morphology, performance and fitness' traits from Arnold (1983). This general definition is globaly used with flexibility by scientists across taxa as, for example, for the notion of invidual level, which can be extended to several individuals in the case of bacteria or corals (Dawson et al. 2021). Pey et al. (2014) added also the category of 'behaviour' to the definition of traits for soil invertebrates. As mentioned by Wong et al. (2019), if technical applications of trait-based approaches vary among fields, researchers specialising in plants and animals agree on the general properties of traits, defining them as phenotypic features that are strictly measurable in individual organisms. However, several suggestions for the modification of this definition were submitted by the respondents. Some respondents (38 %) suggested modifying the definition by including: (i) reference to ecological functions or (ii) new trait categories. The next sections will detail the discussion around the functional trait definition.

3.2 'Trait' or 'functional trait'?

The main disagreement pointed out by respondents was that this definition does not take the trait 'functionality' into account. These researchers argue that the functional trait definition should clearly identify the link between the function of a trait and associated ecosystem functions or services for human well-being. Although many researchers agree that traits need to be 'functional' (Wong et al. 2019), there is no consensus in the current literature and the survey on understanding of what the 'functional' term in the trait definition means. Frequent inconsistencies in the literature led to recent suggestions to abandon the adjective 'functional' completely, as it became redundant to the 'trait' itself (Streit & Bellwood 2023). The semantic complexity of the term 'functional trait' could lead to misunderstandings in ecological research (Mlambo 2014). Indeed, a function presents multiple semantic facets in ecology (Glenk et al. 2012). The term 'function' is used as a synonym for processes, referring to object state changes in time (e.g. organic matter decomposition), as a term describing a sum of processes of the entire system (e.g. nutrient cycling), to describe the roles of objects (e.g. the function of earthworms), or as a synonym to ecosystem services. In ecotoxicology, functional traits are used to infer soil functions being affected by chemicals (Beaumelle et al. 2014). In the definition of functional trait by Violle et al. (2007), the term 'functional' refers to the link of this trait to the growth, reproduction and survival of an individual (Arnold 1983, Violle et al. 2007) and not to the impact of this trait on a specific ecosystem function. This eco-evolutionary perspective of function refers to Darwinian fitness, i.e. the organismal reproductive success. Dispersal could also be listed here (Bonte & Dahirel 2017) but is not directly or systematically related to the fitness.

To take these different definitions into account, several overlapping or complementary concepts have emerged around the concept of functional traits. For example, Pey et al. (2014) specifically distinguished performance traits (i.e., growth, reproduction and survival, following Violle et al. 2007) and ecological preferences (e.g. microhabitat or moisture preference) for soil invertebrates. Lavorel & Garnier (2002) separated two types of traits: 'response traits', which reflect the influence of the environment on organisms (similar to the eco-evolutionary understanding of trait functions), and 'effect traits', which give information about the role of organisms in ecosystem functioning (similar to the 'ecosystem effect' understanding of trait functions). 1 % of the respondents suggested integrating response traits as 'traits', and effect traits as the 'functional traits'. However, for most respondents (85 %), the definition of functional trait does not exclude the response trait aspect, as the majority accept the vision of the definition by Violle et al. (2007) around organism fitness.

The widespread ecosystem-focused point of view contrasts the original 'fitness-centred' functional trait definition and may be explained by the general focus on the ecosystem functioning research in soil ecology. Notably, the same trait is often linked to both environmental response and ecosystem affect aspects of organism's ecology (e.g. body mass, mandible shape, reproduction rate). Wong et al. (2019) highlighted the ability of response traits to influence the resilience of an ecosystem (Lavorel & Garnier 2002, Violle et al. 2007, Wright et al. 2016), and there are numerous other examples of linkages between response and effect traits in plants and animals, making it difficult to strictly assign traits to these categories. That is why, although the distinction between traits and functional traits, or effect and response traits, seems to be clearly defined, it is seldom used in the literature. Parr et al. (2017) mentioned this difficulty and did not include trait categories (e.g. effect traits or response traits) in their database on ants because often this distinction depends on the scientific question asked (Petchey & Gaston 2006). There is also little empirical evidence on the links between ecosystem functioning and effect traits, and there are traits that are considered functional by definition (e.g. ‘trophic’ traits, see 5.4) due to their links with ecosystem functioning. The traits used in research are almost always directly or indirectly related to fitness, and there are hardly any traits that do not affect fitness at all. Therefore, virtually any trait has the potential to influence at least one ecosystem function and related service, as well as to react to some environmental changes.

To avoid divergence with general trait-based research, we call for consistent use of the eco-evolutionary view on ‘functional traits’ as proposed by Violle et al. (2007) for plants or by Wong et al. (2018) and Pey et al. (2013) for animals. It means that traits are functional because they influence the fitness of organisms but not because they influence soil processes, functions or services. It is important to admit that functional traits remain a fuzzy concept, as all traits could be functional to some degree (Dawson et al. 2021). Nevertheless, we recommend further use of the term functional traits (contrary to Dawson et al. 2021) due to the very generic meaning of the word ‘trait’ in English.

The main task for soil ecologists working on trait approaches is to propose and validate links among specific environmental factors, functional traits and soil processes. These processes can further be connected to ecosystem services and soil functions using measurable indicators (Morgado et al. 2018). This task seems more complex for soil invertebrates than plants because of the many indirect links between soil invertebrates and ecosystem functioning (Weiss & Ray 2019). However, the operability of such a scheme should not be underestimated. Plant ecology has established core lists of traits that are routinely measured (e.g. leaf area, leaf dry matter content, height, seed mass) and used to explain biodiversity-ecosystem functioning relationships. Studies proposing mechanistic environment-trait-process links, and experiments validating them, are the key to developing a more functional trait-based approach for soil invertebrates. Until now, very few studies or databases link traits and associated ecosystems functions, but first attempts have been made (Brousseau et al. 2018, CRITTER; Parr et al. 2017, GlobalAnt). Trait-based trophic ecology (fluxes of carbon and energy) is a way to connect community ecology (responses) to functional ecology (Gravel et al. 2016, Schleuning et al. 2023, 2015).

3.3 Morphological, physiological, phenological and behavioural traits

As described above, the definition of a functional trait is evolving. From the definition of Violle et al. (2007), several adjustments were made to adapt this definition to different taxonomic groups. We can thus note the addition of categories, such as behaviour, proposed by Pey et al. (2014b). Also, some respondents propose to add new categories, such as chemical, physical or by emphasing life history. These proposed additions are also found in Dawson et al. (2021) with behavioural and cultural traits. In this line, Moretti et al. (2016) used five categories of traits for terrestrial invertebrates: morphology (e.g. body size, number of eyes), feeding (e.g. ingestion rate, biting force), life history (e.g. ontogeny, clutch size), physiology (e.g. resting metabolic rate, relative growth rate), and behaviour (e.g. activity time, sociality). According to Pey et al. (2014b), life history is rather a population parameter that can serve as responses/indicators of the underlying trait-based processes and reflect the success of an organism in a specific environment. Finding a universally accepted categorisation is probably impossible for all biota (Dawson et al. 2021) and it seems complex even for soil invertebrates only. Categories proposed by Pey et al. (2014), i.e. morphological, physiological, phenological or behavioural, are often used in publications and seem generic enough to fit most needs. However, different categorisations are not exclusive and depend on the context of how traits are applied. The response-effect categorisation can be used to link specific environmental factors and ecosystem functions to traits. According to their associated function, traits can also be categorised into, e.g., feeding, mobility or engineering traits. While emphasising the flexibility of such categorisations, we also call for using standard categories whenever possible and clearly justifying the use of alternative categorisations and stating the differences.

3.4 Level of organisation of traits

Another frequent debate is the measurement at the ‘individual’ level ‘without reference to any other level of organisation’. This disagreement predominantly stems from the superorganism or colony-level traits in social insects, for which several individuals act as a single unit (e.g. ant colony, Hölldobler & Wilson 2009) or for microorganisms, where individuals are difficult to define (fungi, Dawson et al. 2021). Parr et al. (2017) argue that natural selection can operate at the individual and colony levels for ants (Keller 1995), so ant functional traits may be quantified at both levels: an individual worker and the colony. Examples of such traits are the nesting or foraging type of a colony (Kreider et al. 2021). Such traits can help predict the occurrence of a species in the environment (e.g. due to the presence of suitable microhabitats) and the effect of this species on the ecosystem functions (e.g. resource acquisition). Thus, a broad trait definition should include colony-level traits if a common approach is extended to social insects (e.g. ants) or other soil organisms beyond invertebrates such as microorganisms (De almeida et al. 2024, Elizalde et al. 2020).

3.5 Suggestion for a clear definition of functional traits

Due to these misunderstandings in the trait concept, some authors do not restrict themselves to any specific definition of traits and integrate all possible species characteristics, letting users select traits according to their study needs (Jeliazkov et al. 2020). Since the trait concept is unclear, many researchers do not use it. Several authors have, thus, called for simplifying and clarifying the definition of traits to facilitate their use and comparability among different groups of organisms (Dawson et al. 2021). We can only agree and propose to clarify the definition by Pey et al. (2014b) as follows: *'A functional trait is a measurable characteristic of an individual organism or its colony that has a link to the organism's fitness and/or its effect on other organisms and/or the environment'.* This definition *sensu lato* is sufficiently broad to include all groups of soil invertebrates (Figure 1).

Measurable in this definition should be considered as the expression of traits on different mathematical measurement scales (e.g. ordinal or nominal). In the case of a colour, for example, colour measurement is the quantitative expression of colour and there are a number of methods to quantify color (i.e. colorimetry and spectrophotometry). Also, nominal (or categorial) variables such as body shape or coloration are simplifications of more complex measurements involving ratios (body shape) or characterization tools that are not yet used in soil ecology (color).

4. List of traits

A total of 202 'traits' were listed by respondents in our questionnaire, illustrating the large current application of the functional trait concept and diversity in its interpretations. Some terms were quoted several times while some have only appeared once. After screening through the list, we merged records with a similar meaning (e.g. body size and body length) and classified all traits into ecological niches traits, morphological, physiological, and phenological traits. An additional category of elemental and molecular composition traits was suggested to categorise e.g. isotopic and biochemical composition of organisms (Table 1). The full unedited list of responses is given in the online S2.

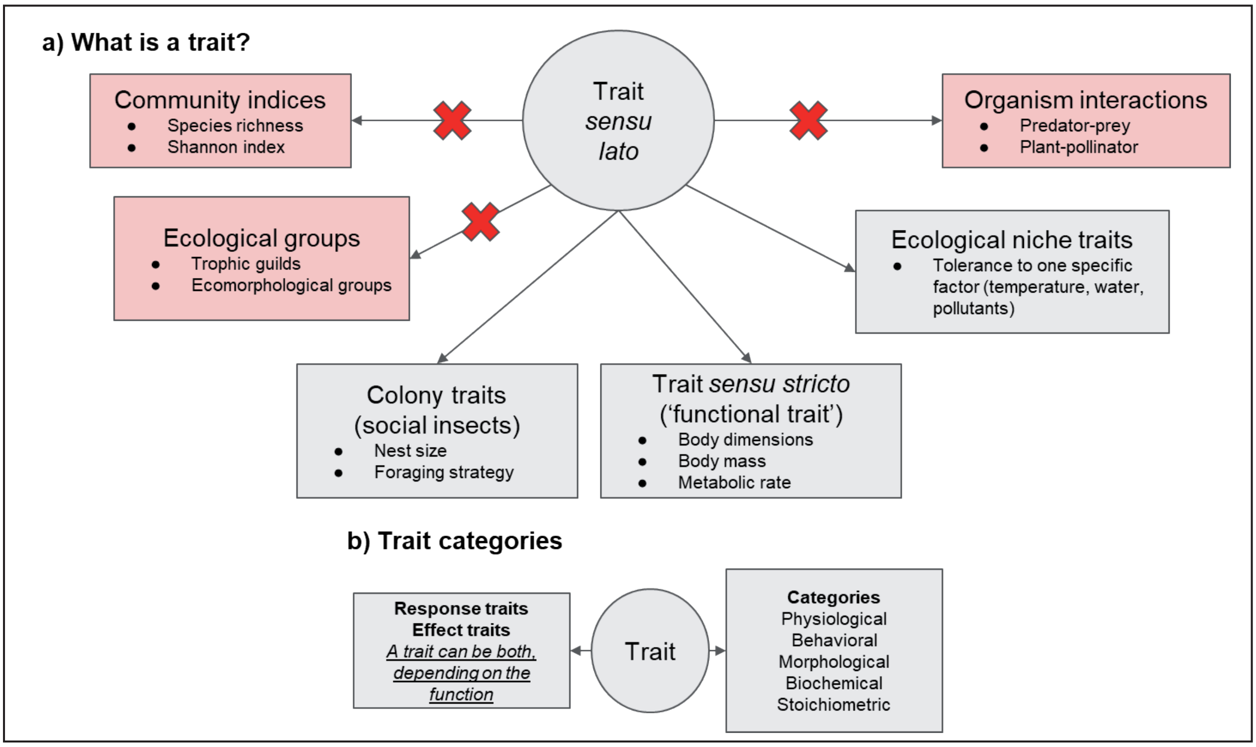

Figure 1. Clarification of functional trait definition; The figure shows the different terminologies used to define a 'functional trait'. Part a) shows the primary terminology used, emphasising what is included in our *sensu lato* definition and what terms are excluded from it (in red). Part b) specifies trait categories that may be used in this definition.

4.1 Morphological, physiological, phenological and behavioural traits

In line with the data available in databases, the vast majority of the traits cited belong to the category of morphological traits. Among the most frequent, the 'body size' trait were mentioned 59 times, mostly expressing the 'body size' or 'size' (n=30) and 'body length' or 'length' (n=21) (Table 1). In the databases, it is found almost every time and there is even a database focused solely on this trait (Egrowth). In the same vein, the size of the different parts of the body (e.g. legs, antennae), body shape, colouration, body mass and mouthpart morphology are also frequent. We also noted the citation of many dichotomous traits linked to the presence or absence of organs (e.g. furca, wings, glands). Among traits related to life history, reproduction mode (i.e. sexual versus parthenogenetic) was frequently named. However, other traits, such as reproductive output, were rarely mentioned despite being fundamental intrinsic components of organism fitness. Physiological traits were mentioned even less frequently despite their potential importance for digestion and environmental responses. Among behavioural traits, mobility and feeding behaviour were the most common.

4.2 Ecological preferences and tolerances: ecological niche traits

Many respondents listed traits beginning with 'preference for' humus, carbon content, habitat type (n=14) or with 'tolerance to', for example, temperature (n=14). Here, tolerance refers to the niche width (limits), whereas preference refers to the niche optimum. As highlighted by some authors (Middleton-Welling et al. 2020, Pey et al. 2014b, Wong et al. 2019), these characteristics, present in several publications, are not always considered as 'traits' and might be termed as 'ecological preferences' (Pey et al. 2014b). To fit better with the niche theory (Chase & Leibold 2003), we propose to rename this group of traits as 'ecological niche' that includes the parameters of the distribution of individuals on an ecological gradient: the position (max, min, mode, etc) and the dispersion (range, variance, etc). Position and dispersion parameters reflect eco-evolutionary adaptations through different, often undetermined, trait syndromes. Among those, respondents often mentioned temperature, (micro)habitat preferences and desiccation/water regime preferences. These characteristics are present in several databases such as GlobTherm, which is dedicated to cold or heat tolerance, and are crucial to predict species responses to environmental changes. For instance, tolerance may be defined as the quantile of the distribution in which the species is still present while its fitness is not optimal.

Ecotoxicological responses can be considered among traits related to the tolerance of organisms to environmental factors or physiological traits related to biomarkers of exposition (e.g. the expression of stress-related proteins). Individual tolerance to toxic chemicals, such as, pesticides, define the fitness of an organism and, in consequence, the probability of a population to persist in a polluted environment (e.g. Geiger et al. 2010, Sánchez-Bayo & Wyckhuys 2019). Presently, tolerance is described separately for each pollutant that organisms may encounter and finding general patterns/traits should be addressed in the future.

4.3 Elemental and molecular traits

In a few cases (n=5), the respondents mentioned stable isotope, elemental, or molecular composition of organism as traits. These characteristics can be measured at an individual level, are often taxon-specific (Potapov et al. 2019a), and are informative to predict both responses and impacts of soil invertebrates (Potapov et al. 2019b). Some example studies include stable isotope and fatty acid compositions in trait-type analyses to understand the evolution and ecological responses of soil invertebrates (Chen et al. 2017, Zhou et al. 2022). These traits such as stable isotope composition is relation to fitness of soil invertebrates because they clarified clarified basal food resources and allow a more comprehensive understanding of the structure and functioning of soil food webs (Potapov et al. 2019b). We thus propose to include these characteristics in the commonly used functional traits.

4.4 Functional groups and trait syndrome

Trophic guilds, feeding groups, or other ecological or morphology-based categories were mentioned 20 times by the respondents. Can they be considered functional traits? Brousseau et al. (2018) argue that they cannot because they typically describe a combination of traits rather than a functional attribute per se. It is therefore more of a trait syndrome than a trait as such. Rarely defined (but see Meyer et al. 2022), this notion appears several times in the literature (e.g. Chin et al. 2023) to illustrate a simultaneous response of functional traits to a disturbance. A trait syndrome is also a combination of species traits in a community. The widespread 'functional group' approach (Wong et al. 2019) assigns species to different functional groups a priori, based on observed or assumed characteristics or functions

Table 1. Traits *sensu lato* listed by the questionnaire respondents. The responses out of the definition (e.g. ecological groups and community parameters) are removed and listed in the text (raw traits contains 202 terms of "traits", some terms were quoted several times) .

Category	Traits	Number of citations
Behaviour		
	mobility (vertical or horizontal)	6
	feeding behaviour	5
	hunting strategy/type	3
	nesting behaviour	2
	burrowing behaviour	1
	avoidance behaviour	1
	orientation behaviour	1
	feeding habits/preferences	8
Ecological niche traits		
	habitat, microhabitat, soil layer preference	14
	water regime preference (hygrophily, tolerance to water logging or flooding)	6
	drought/desiccation resistance/tolerance	5
	vertical distribution	5
	temperature tolerance/preference	4
	sensitivity (e.g. to chemicals)	3
	acidity tolerance/preference	2
	halotolerancy	1
	preference for given C/N ratios	1
	frost tolerance	1
	light sensitivity	1
Morphology		
	body length/size/width	59
	body colour/pigmentation/patten	19
	body weight/mass	18
	body shape/form/modification	11
	leg/appendages length	10
	mouthpart morphology/type/strength	10
	eye type/size/development/number	7
	wing presence/morphology	4
	postantennal organ	4
	scales	3
	presence of defensive structures/chemical defence	3
	dispersal ability/mode	3
	furca length	2
	pseudocelli	2
	leg morphology	2
	other	9
Phenology		
	time to maturity	1
	reproduction type/mode	9
	reproduction speed	1
	longevity	1
	reproductive season	1
	life time	1
	fecundity	1
Physiology		
	respiration type	2
	metabolic rate	2
	assimilation efficiency	2
	metal detoxication	1
	Mt-gene expression	1
Elemental and molecular traits		
	stable isotope composition	2
	fatty acid composition	2
	stoichiometry	1

of interest. However, in reality, many assumptions behind such groupings have no real measurements in the background (Hedde et al. 2022). For example, for earthworms or springtails, classifications can be based on morphological criteria (e.g. ecomorphological groups, figure 1) to determine spatial distribution in the soil, without the values limits or links between these values and their vertical distribution being clearly established. If functional groups could be seen as trait syndromes, they need to be better defined first. Traits can help define these groups, as has been demonstrated for the revised system of the ecological groups of earthworms defined by using several traits (Bottinelli & Capowiez 2021). In the meantime, functional group and trait approaches should be considered in parallel, being conceptually different.

4.5 Taxonomic composition and structure

More surprising was the presence in the list of traits of community indicators such as the Shannon index, biodiversity, or composition (mentioned 5 times). Indices of taxonomic diversity are *not* functional traits since they refer to the distribution of individuals across taxonomic groups. Therefore, we recommend that taxa-based indices should not be included in the functional trait approach, as this can cause serious confusion between taxonomic-based and trait-based approaches. Taxonomic-based approaches need to complement trait-based approaches, but conceptually they are different.

5. List of databases

The second aim of this study was to list trait data sources, traits and their use by soil ecologists. Currently, most trait data are distributed among private datasets/spreadsheets and online data portals with different access levels. Here we refer to ‘database’ as an overarching term, referred to any management of ecological data (Jones et al. 2006). This includes: (i) single-user databases such as spreadsheets (e.g. in Open Office, Microsoft Excel) or desktop relational database systems (e.g. in Microsoft Access, Filemaker Pro). Ecologists frequently use these formats (e.g. SoilBioStore) because they are relatively easy to set up. However, they do not allow for easy data sharing for several reasons: they are often built for a specific project which limits data standardisation, and sometimes they are built with software tools that become obsolete with time. Multiuser databases also have different levels of data standardisation. (ii) Databases published in data repositories, such as Figshare or Dryad, that integrate multiple project-specific databases. Despite being open for use, they have similar data integration drawbacks like spreadsheets or desktop databases because they do not force data standardisation and often have too generic metadata to search for specific traits or taxa. (iii) Structured databases where detailed information about the data of interest is present (metadata) (Michener 2006, Michener et al. 2007) and data are structured according to a certain format. They improve scientific data understanding and management (e.g. information on context, protocols, semantics, data structure) and can facilitate data use beyond the original goals of their collection. Metadata can be used for a specific-project database or to connect them favouring data integration and interoperability. In ecology, sets of metadata have been adopted by the community of ecologists (e.g. EML, Ecological Metadata Language) but there are many other metadata standards, which are not automatically compatible and that trait data standardisation requires additional efforts by data providers.

In total 12 databases were mentioned in the questionnaire and many are single-user databases. The most used databases cited in the questionnaire were: BETSI (20 times), Ecotaxonomy and Nempaplex (5 times each). Through literature search and expert consultations, we identified 15 other databases, resulting in 27 databases that include data on soil invertebrates traits (Table 2). Note that some databases are not displayed as trait databases but are used as such (e.g. Tardigrada Register).

The availability of databases varies greatly. Access to single-user databases (e.g. Microsoft Excel spreadsheets or Microsoft Access databases) is often at the author’s discretion. However, some authors provide data openly via a website or in R (e.g. Egrowth, SoilBioStore), or as an article supplement (e.g. Ellers et al. 2018, Hishi et al. 2019, Makkonen et al. 2011). Notably, however, most of trait databases used in publications are not provided in any format. This is of concern because of poor data standardisation across studies as each author formats data and defines traits in his/her own way. Moreover, this hampers reproducibility of the study, violating foundations of scientific research publication. We thus call for open sharing of trait data (Gallagher et al. 2020) via, e.g., a data paper format, which is now offered by many journals and provides benefits for the data author regarding of publication and citations.

Most multi-user databases have open data but require registration before these data can be accessed. Only a few databases provide the definitions associated with the traits, although some are based on an editable thesaurus (e.g. Myriatrix, MilliBase and Ecotaxonomy). There were also difficulties with access due to offline

Table 2. Information on the 27 databases (including single-user spreadsheets, spreadsheets published in data repositories, and structured databases) hosting data on functional traits of soil invertebrates. References list includes database papers if existing or examples of database use.

Database name	Taxonomic groups	References	Open data	Number of traits/taxa if known	Example of traits
Multitaxa databases					
BETSI - Biological and Ecological Traits for Soil Invertebrates	multiple soil invertebrate taxa	Pey et al. 2014a 2014b	Open data	Up to 300 traits (up to 1300 taxa)	body length, adult activity, reproduction type
CESTES - metaCommunity Ecology: Species, Traits, Environment and Space	multiple soil invertebrate taxa	Jeliazkov et al. 2020	Access upon special request	14 traits (72 taxa)	ability to burrow, body mass, body length
CRITTER - Canadian Repository of Invertebrate Traits and Trait-like Ecological Records	multiple soil invertebrate taxa	Brousseau et al. 2018, Handa et al. 2017	Open data after registration	50 traits (400 taxa)	mouthpart type, Body shape, Diet Activity
Ecotaxonomy	multiple soil invertebrate taxa	Potapov et al. 2019, Sandmann et al. 2019	Open data	Over 500	D13C bulk, feeding mechanism, furca shape
ECOTOX Knowledgebase	multiple soil invertebrate taxa	Olker et al. 2022	Access upon special request	-	single chemical environmental toxicity data
Edaphobase	multiple soil invertebrate taxa	Burkhardt et al. 2014	Open data after registration	-	morphometric data
GlobTherm - a global database on thermal tolerances for aquatic and terrestrial organisms	multiple soil invertebrate taxa	Bennett et al. 2018	Access upon special request	Up to 2000 taxa	heat tolerance, cold tolerance, acclimatisation
M.P. Berg (VU University Amsterdam, unpublished data)	Isopoda & Collembola	Bokhorst et al. 2012, Ellers et al. 2018, Makkonen et al. 2011, Widenfalk et al. 2016	Closed, except a few datasets published with papers	10-20 traits	body length, drought resistance, macro-habitat width
NEON - National Ecological Observatory Network	multiple soil invertebrate taxa	Stachewicz et al. 2021	Access upon special request	Up to 2700 taxa	body length, head width, antennae length
Single-taxon databases					
Dataset Oribatida	Acari (mites)	Minor et al. 2017	Closed	3 traits	maximum body length, feeding guilds, and reproduction modes
Spiders Functional Trait Dataset	Araneae (spiders)	Macías-Hernández et al. 2020	Open data	12 traits (506 taxa)	body length, vertical stratification, foraging strategy
Carabids.org - a dynamic online database of ground beetle species traits (Coleoptera, Carabidae).	Carabidae (ground beetle)	Homburg et al. 2014	Open data after registration (but unavailable for several years)	6 traits (up to 1000 taxa)	body size, hind wing development, hibernation, reproduction time
COLTRAIT	Collembola (springtails)	Salmon et al. 2014	Closed	25 traits	body size, reproduction type, body shape
SoilBioStore	Collembola (springtails)	D'Annibale et al. 2017	Open data	18 traits (132 taxa)	colouration, mouthpart, moisture preference
Taxonomy, Distribution, and Trait Data Sets of Japanese Collembola	Collembola (springtails)	Hishi et al. 2019	Open data	13 traits	body length, furca length, anal spine
Ant Profiler - A database of ecological characteristics of ants	Formicidae	Bertelsmeier et al. 2013	Open data after registration (but unavailable in 11/2021)	24 traits	habitat, diet, body size, colony

Table 2 continued.

Database name	Taxonomic groups	References	Open data	Number of traits/taxa if known	Example of traits
GlobalAnts - a new database on the geography of ant traits	Formicidae	Parr et al. 2017	Open data after registration	26 traits (up to 1913 species)	colony type, worker number, pilosity, mandible length
Shelled Gastropods of Western Europe	Gastropoda (snails)	Falkner et al. 2001, Astor et al. 2017	Paying CD/ book except datasets published with papers	At least 9 traits (up to 270 taxa)	shell shape, age at maturity, humidity preference
Egrowth -A global database on intraspecific body growth variability in earthworm	Lumbricina (earthworms)	Mathieu 2018	Open data	1 trait (51 species)	body mass
Dataset Chilopoda	Myriapoda	Bonato et al. 2018	Open data	6 traits	maximum body length, number of ocelli
APHIA et MilliBase	Myriapoda		Open data	-	stage, body size, functional group
NINJA	Nematoda	Sieriebriennikov et al. 2014	Open data	-	feeding types
Mulder & Vonk (2011)	Nematoda	Mulder and Vonk 2011	Closed	5 traits (up to 30000 individuals)	body length, width, and estimated mass of nematodes
NEMAguilds	Nematoda	-	Open data	-	trophic functional traits
NEMAPLEX	Nematoda	-	Open data	4 traits (up to 8500 taxa)	body mass, feeding type
Dataset protists	Protists	Fiore Donno et al. 2019	Open data	3 traits	feeding mode, morphology, and locomotion mode
Tardigrada Register	Tardigrada	-	Open data	-	cuticle, buccal, legs &claws

time of consultation (e.g. carabids.org, Nov. 2021) or even disappearing access interfaces from the web (Ant Profiler, Nov. 2021). Existing multi-user databases are not always interoperable with e.g. DarwinCore or other informatic language standards (Wieczorek et al. 2012). Although we should note the efforts made in the user interface Ecotaxonomy or the assistance programmes for the coding of functional traits in BETSI, we have to admit that the general interoperability and other open science principles (Wilkinson et al. 2016) are still in their infancy in trait-based research on soil invertebrates.

Many databases focus on a single taxonomic group. Although several databases aimed at covering multiple taxonomic groups (e.g. BETSI), they usually still focus on a few groups or even a single group. Among the groups covered the best in the existing multi-taxa databases we find springtails, earthworms and carabid beetles, which are also well represented in the single-group databases. On the other hand, four databases are available for nematodes but this group is not included in multi-taxa databases. The number of traits defined in the databases varies from just one (e.g. Egrowth) to over 300 (e.g. BETSI, Ecotaxonomy). However only a few most common traits are well informed in the latter.

Very few databases have addressed the issue of intra-specific or even intra-individual variability (but see Egrowth for body length). The reason is undoubtedly very prosaic: taking individual measurements takes time. To compensate for this, some databases, such as BETSI, integrate data from different literature sources, making it possible to concatenate trait data from different countries, at least on the European continental scale. It has been shown that this intra-specific variability, particularly in body length, can play a role in diversity/function links, both from measurements taken from the literature (Bonfanti et al. 2018) and experimental measurements (Chassain et al. 2023). However, there is still a long way going to analyse trait data on continental or global scales, and even more so with an intraspecific analytical approach.

While we consider databases on microorganisms (see Cébron et al. 2022) which is out of our scope here, an integrative approach across microorganisms and invertebrates can be proposed in the future (Romillac & Santorufo 2021). Overall, we conclude that trait data on soil invertebrates are currently very heterogeneous and dispersed over a multitude of sources, varying in the level of purpose, standardisation, and access level. This situation is unfortunate and we call for integration of the databases in the future to aid cross-taxon and cross-continental studies on functional traits in soil animal ecology.

6. Conclusions

This review reflects on the development of trait approaches in soil ecology over the last decade. A wide diversity in the understanding of the concept has led to a diversification in the research field, but also to poor integration and standardisation across studies. We advocate that additional effort should be made by researchers to clearly define the traits that they use and the concepts that they apply. Based on recent publications, the questionnaire among specialists and our own experience, we propose a broad definition of functional traits for soil invertebrates and outline what should not or must not be considered a trait (e.g. ecological groups or community parameters). We suggested including colony-level traits for social insects to make the functional trait approach more universal across taxa. We also identified a new category of 'elemental and molecular' traits derived from the body composition but measured at the organismic level and informing on the processes at the organismic level. The ecotoxicological characteristics of species are currently neglected in ecological trait databases even if they are crucial for understanding and predicting the responses of populations and communities in an ever more contaminated world. Plenty of data on the functional traits of soil invertebrates exist. However, most data are not easily accessible and distributed across multiple databases with different interoperability and access levels. Better integration across databases and acceptance of open science principles among researchers will promote standardisation, dissemination and development of trait-based approaches in soil ecology.

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