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# Fostering the use of soil invertebrate traits to restore ecosystem functioning

Apolline Auclerc[a,*], Léa Beaumelle[b], Sandra Barantal[c], Matthieu Chauvat[d], Jérôme Cortet[c], Tania De Almeida[e,f,h], Anne-Maïmiti Dulaurent[g], Thierry Dutoit[e], Sophie Joimel[h], Geoffroy Séré[a], Olivier Blight[e]

[a] Université de Lorraine, INRAE, LSE, F-54000 Nancy, France
[b] INRAE, Bordeaux Sciences Agro, ISVV, SAVE, Villenave d'Ornon, France
[c] UMR 5175 CEFE. Univ Paul Valery Montpellier 3, Univ. Montpellier, EPHE, CNRS, IRD, F34000 Montpellier, France
[d] ECODIV EA 1293 / USC INRAE, Normandie Université, UNIROUEN, Rouen, France
[e] Avignon Université, Aix Marseille Univ, CNRS, IRD, IMBE, Avignon, France
[f] Institut de Recherche de la Tour du Valat, Tour du Valat Le Sambuc, 13200 Arles, France
[g] UniLaSalle, AGHYLE (SFR Condorcet FR CNRS 3417), 19 rue Pierre Waguet, 60026 Beauvais, France
[h] UMR ECOSYS, INRAE, AgroParisTech, Université Paris-Saclay, 78850 Thiverval-Grignon, France

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A B S T R A C T

Ecological engineering of degraded ecosystems often manipulates plants, with positive outcomes for their restoration or ecosystem services production. The importance of soil biota for successional plant communities has prompted consideration of direct inoculation (active) or attraction (passive) of soil organisms as a relevant restoration strategy. However, few attempts have manipulated soil invertebrates as part of nature based solutions for ecosystem restoration, despite their major role in many soil ecological processes and in plant-soil feedback processes. In addition, while ecological restoration and ecological engineering approaches successfully incorporate plant traits, soil invertebrate traits remain underused. Exploiting the functional diversity of soil communities by adopting a trait-based approach could enhance restoration of soil chemical, biological and physical properties. Here, we conduct a narrative review and identify a set of soil invertebrate functional traits with great potential in ecosystem restoration. We focus on traits related to four main ecological functions that are often at the core of restoration plans: nutrient cycling and carbon cycling, pollutant detoxification, soil structure arrangement, and biological control agent by prey/pest regulation. This paper further proposes guidelines for stakeholders that need to be addressed to successfully integrate soil organism traits into ecological engineering. Finally, we highlight main knowledge gaps and limitations currently impeding the use of soil invertebrate traits in ecological engineering, and identify avenues for future research. We especially bring out (i) that few studies still use soil invertebrates in restoration, so even fewer are based on traits, (ii) a lack of data about soil invertebrate species role in ecosystems, (iii) a lack of data about attributes from specific traits and groups in existing soil functional trait databases, (iv) the complex relationships between functions and traits and (v) that future studies are needed to demonstrate the benefits of such trait-based approaches compared to approaches relying on emblematic species.

## 1. Introduction

Human activities are degrading the land surface (Gibbs and Salmon, 2015), going so far as to alter the ecosystem services we depend on. Indeed, human activities have affected about 70 % of the terrestrial land surfaces, and land degradation undermines the well-being of circa 3.2 billion people according to recent estimates (IPBES, 2018). Large areas are from now on being abandoned because of low soil physico-chemical fertility and/or high soil pollutant concentrations (Rodríguez-Eugenio et al., 2018), but land (and soil) is a limited resource. Therefore, sustainable land and soil management is crucial to limit global warming and to obviate for an increase of social instability, poverty, conflict and migration. Managing soil quality, defined as its ability to fulfill ecosystem functions and provide a wide range of ecosystem services

* Corresponding author at: Laboratoire Sols et Environnement LSE, UMR 1120 INRAE – Université de Lorraine, 2 Avenue De La Foret De Haye, BP 20163 54505 Vandoeuvre Cedex, France.
*E-mail address:* apolline.auclerc@univ-lorraine.fr (A. Auclerc).

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(Morel et al., 2015), is particularly urgent given its importance for ecosystem multifunctionality and human well-being (Lal, 2015; IPBES, 2018; Nolan et al., 2021).

In this context, ecological restoration, "*the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed*" (SERI, 2004), is needed to revert soil degradation. Ecological restoration is sometimes considered as a branch of ecological engineering (Mitsch and Jørgensen, 2003), an assumption which has been strongly criticized (*e.g.* Aronson et al., 2016). Here, the term ecological engineering is employed in the sense of Clewell and Aronson (2013), "*the manipulation and use of living organisms or other materials of biological origin to solve problems that affect people*". Ecological engineering thus contrasts from civil engineering that still rarely considers the sustainability of the processes used to achieve restoration goals. Ecological engineering approaches can rely on spontaneous species recolonization by habitat restoration following passive restoration (*e.g.* Frainer et al., 2018; Ostertag et al., 2020). Other approaches use active restoration that consists in introducing target organisms into the ecosystem based on their specific role (*e.g.* predator of a target species, biological control agent) such as with aquatic invertebrates (Jourdan et al., 2019), following direct organism translocation (Bellis et al., 2019) or by soil transplantation (Kardol et al., 2009; Moradi et al., 2018).

Partly due to the wide diversity of soil habitats, soil invertebrates are extremely diverse, building highly complex interaction networks involving trophic (*e.g.* predator–prey) and non-trophic relationships (*e.g.* competition or facilitation) with each other or with other soil organisms (*e.g.* microbes, plant roots) and with aboveground components of ecosystems (*e.g.* plant-soil interactions; Kardol and Wardle, 2010). Soil biodiversity is a key to the regulation of many processes occurring in ecosystems (Briones, 2018; FAO et al., 2020). Soil invertebrates are active in soil formation and physical structure maintenance, prey/pest regulation, nutrient cycling through decomposition processes, consequently assisting primary production (Lavelle et al., 2006). Therefore, they can profoundly shape ecosystem functioning and services, and are thus vital to human well-being (Wall et al., 2015; Geisen et al., 2019). Incorporating soil invertebrates in ecological engineering has thus the potential to promote multiple ecosystem functions simultaneously in impaired ecosystems. While soil organisms are often used as indicators of restoration success, they could also be major assets in ecological restoration (Callaham and Stanturf, 2021). Because of their well-known key role in soil, earthworms are frequently used in ecological engineering studies (Jouquet et al., 2014). The introduction of selected earthworms into degraded or newly restored land promotes soil quality (Butt, 2008; Forey et al., 2018). Earthworms have been used to restore soils which had been previously eroded (Sparovek, 1998), compacted (Ampoorter et al., 2011; Ducasse et al., 2021) or degraded after mining activities (Boyer and Wratten, 2010). In tropical biomes, several studies indicate that termites can restore soil functioning (Khan et al., 2018; Jouquet et al., 2020). Termite mounds significantly increased soil restoration, plant richness and plant diversity on hardened ferruginous soils (Padonou et al., 2020). Moreover, ants are considered good candidates not only for soil but also for above ground herbaceous vegetation (De Almeida et al., 2020a).

A key challenge in ecological engineering is to identify target organisms. Ecosystem engineers are good candidates because they *directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials* (Jones et al., 1994). Many taxa have representatives that are able to perform key ecosystem engineering functions in a wide variety of terrestrial ecosystems. The challenge lies in determining which species will provide the most desirable outcomes in terms of community and ecosystem processes. Moreover, the selection of species is often site- and context-dependent, thereby limiting generalizations across communities and ecosystems. To overcome these limitations, functional trait-based approaches have recently emerged in the field of ecological restoration, and is mostly implemented for plants (Van Mechelen et al., 2015; Carlucci et al., 2020).

Pey et al. (2014) defined soil invertebrate traits as "*morphological, physiological, phenological or behavioral features, measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization*". Traits are classified as either (i) response traits, properties of individuals which govern their responses to their environment, or (ii) effect traits, an individual property which affects an upper level of organization (*e.g.* ecosystem processes). Ecology increasingly uses trait-based approaches to shed light on ecosystem functioning, especially through the description of effect traits (de Bello et al., 2010; Laughlin, 2014).

A quick review of the ISI Web of Science database lists 2526 results by searching for "restoration plant traits", while 20 results for " restoration soil fauna traits " and 53 for "restoration soil animal traits" were retrieved. Moreover, these last reviews listed especially papers on characterization of soil fauna communities after ecosystem restoration.

Specific functional groups of soil invertebrates can be used in ecosystem management as tools to restore soil structure and/or processes (Snyder and Hendrix, 2008; Bender et al., 2016; Bach et al., 2020; Contos et al., 2021), but the question is then: how to find the best candidate(s)?

In this paper, we conduct a narrative review to identify relevant soil invertebrate traits for ecological engineering, and highlight potential fruitful areas for future research to foster the use of functional trait-based approaches in ecosystem restoration process. We identify a set of traits associated with four major biodiversity-based ecological functions that are crucial in ecological engineering, based on Kibblewhite et al. (2008), on the FAO global report on soil biodiversity (2020), and that incorporate the role of soil fauna in restoration of polluted soils, which is a major threat (Rodriguez-Eugenio et al., 2018): (i) nutrient cycling and carbon storage and turnover, ii) transformation of potentially harmful elements and compounds; iii) soil structure arrangement, and iv) biological control agent by prey/pest regulation. Table 1 lists functional traits of soil invertebrates related to these four main ecological functions that meet restoration objectives.

We further highlight the main knowledge gaps and guidelines for stakeholders that need to be addressed if soil invertebrate traits are to be successfully integrated into ecological engineering in the longer term.

## 2. Nutrient cycling and carbon storage and turnover

Restoring or improving soil chemical fertility is a key goal in ecological engineering. Soil fauna affects organic matter (OM) transformation directly by fragmenting and digesting the OM and indirectly by altering the structure and functions of microbial communities (Coulibaly et al., 2019; Joly et al., 2020; Wolters, 2000). Their interactions with microbial communities include grazing on the microbial biomass as well as modifying the accessibility and chemistry of OM for microbial decomposers. Overall, they can promote litter mass loss and its incorporation into underlying soil (García-Palacios et al., 2013), may enhance carbon (C) sequestration (Wolters, 2000) and contribute to increased nutrient availability (Bardgett and Chan, 1999; David, 2014).

The extent of soil fauna contribution to C and nutrient recycling depends primarily on the diet trait. The detritivorous invertebrates (i.e. saprophagous, saproxylophagous, necrophagous, coprophagous) have a direct impact on OM transformation, while the microbivores indirectly impact OM transformation through their influence on microbial communities. Indeed, several studies have used detritivores (earthworms, millipedes, and isopods) to accomplish restoration goals (reviewed by Snyder and Hendrix (2008)). Furthermore, body size is a key functional trait in OM decomposition. Although a high density of small bodied invertebrates can have a significant impact on OM decomposition (Schrader et al., 1997), larger animals generally have the strongest effects on decomposition (McCary and Schmitz, 2021).

OM ingestion rate and assimilation efficiency are traits revealing the direct effects of soil fauna on litter mass loss, as well as C and nutrient

**Table 1**
List of key traits of soil invertebrates in ecological engineering.

| Functions | Impacted processes | Effect traits[1] | Ecological preferences[1] | Examples of involved organisms |
|---|---|---|---|---|
| Nutrient cycling and Carbon storage and turnover | Organic Matter (OM) transformation, decomposition, mineralization and distribution via direct or indirect (microbial regulation by grazing or priming effect) effects | Traits of invertebrates: Diet trait, body size and mass, ingestion rate and assimilation efficiency of organic matter, ability to burrow, mouthpart type and morphology(Importance of invertebrate density) traits associated with mobility and dispersal ability Traits of ingested OM and faeces/casts: C:N:P stoichiometry; structure, chemistry and quantity of produced faeces | Habitat, microhabitat and soil preferences, vertical distribution | Microbivores and detritivorous invertebrates from small (nematodes, Collembola, enchytraeids, oribatid mites) to large size animals (*e.g.* earthworms, dung beetles, millipedes, woodlice) |
| Transformation of potentially harmful elements and compounds | Success of pollutant remediation and stabilization, *dissemination of pollution and biomagnification*[2] | Diet trait, body size and mass, presence of specific organs dedicated to the detoxification of contaminants, pollutant excretion efficiency traits associated with mobility and dispersal ability | Habitat, microhabitat and soil preferences, vertical distributionLethal (LC) and effect (EC) concentration of pollutants; NOEC (No observed effect concentration); LOEC (Lowest observed effect concentration); bioaccumulation potential; critical body residue (CBR) | Microbivores and detritivorous invertebrates from small (nematodes, Collembola, enchytraeids, oribatid mites) to large size animals (*e.g.* earthworms, woodlice, millipedes) |
| Soil structure arrangement | Soil structure and aggregation, clay weathering, soil bulk density, infiltration rate and water retention capacity, macro- and micro-porosity | Body size, size of worker mandibles, ability to burrow, size and age of social insect colonies, traits associated with mobility and dispersal ability (Importance of invertebrate density) Traits of faeces/casts and other biogenic structure structure, chemistry and quantity of produced faeces, burrow permanency, nest architecture, size of nest entrance | Habitat, microhabitat and soil preferences, vertical distribution | Soil engineers, bioturbators and aggregate re-organizers (*e.g.* earthworms), detritivorous species (*e.g.* Collembola), social insects (ants, termites) |
| Biological control | Prey (pest) regulation (direct and indirect) | Diet trait, body size and mass, gender, life stage, mouthpart type and morphology, predator biting force, activity period, foraging strategy, ingestion rate, digestion time, reproductive potential, breading season,traits associated with mobility, dispersal ability and attack rate (*e.g.* movement speed, motion strategy, length of legs, wing morphology, visual search organs) | Habitat, microhabitat and soil preferences, vertical distribution | Zoophagous invertebrates (*e.g.* centipedes, spiders, gamasid mites, pseudoscorpions), microbivores (*e.g.* Collembola, Nematodes) |

[1]: sensus Pey et al. (2014).
Trait: Any morphological, physiological, phenological or behavioural feature measurable at the individual level, from the cell to the whole-organism level, without reference to any other level of organization.
Ecological preference: the optimum and/or the breadth of distribution of a trait on an environmental gradient.
[2]: in italic, processes leading to disservices regarding ecological engineering.

release. A substantial amount of initially consumed litter/soil returns to the soil as faeces or casts, and egested OM differs physically and chemically from the ingested material, thereby altering the fate of OM (Jouquet et al., 2008). Litter conversion into faeces accelerates OM turnover which may stimulate soil OM formation (Joly et al., 2020). Interestingly, the OM lability in faeces and their subsequent decomposition varied among the detritivore species. Thus, species exhibiting high faeces production rates, and whose faecal characteristics (*e.g.* nutrient content, C quality, surface area: volume, degree of conglomeration and cohesiveness of particles) are correlated with highest decomposition rate, could promote C turnover.

Other traits related to the impact of soil invertebrates on the distribution of OM and its physical accessibility to microbial decomposers could be important to consider. For example, species vertical stratification, ability to burrow, and to fragment the litter are linked to traits such as mouthpart type and morphology. Invertebrate ability to burrow allows the translocation of OM through the soil profile and mixing with mineral particles, contributing to C stabilization (Frouz, 2018).

A challenge is that soil invertebrates exhibit species-specific feeding preference. Detritivore diet strongly depends on initial OM quality (OM traits). Recent studies have found spatial covariations among palatability traits of litter and feeding traits of detritivore species based on mouthpart morphology (Brousseau et al., 2019; Raymond-Léonard et al., 2019). Theses mouthpart traits could be promising to predict the interactions between detritivore diet and OM quality but more studies under different environmental context are needed. For instance, soil fauna feeding activity could be steered by specific OM amendments: using low or high OM amendments according to the restoration goal (*e.g.*, Lowe and Butt, 2002; Sauvadet et al., 2017; Singh et al., 2020). Indeed, the attractiveness of litter to many invertebrates increases with its nutrient content, and decreases with recalcitrant C such as lignin or condensed tanins (Coq et al., 2010, García-Palacios et al., 2013; Zhou et al., 2020).

## 3. Transformation of potentially harmful elements and compounds

Soil invertebrates could play important roles in the remediation of contaminated soils (i) by direct uptake into their tissues through bio-accumulation, depending on their behavior and ecology, (ii) indirectly, by impacting other soil functions that affect remediation (*e.g.* nutrient recycling, soil structure), and (iii) also indirectly, via their interactions with aboveground and belowground organisms (*e.g.* plants and microbes) that play key roles in phytostabilization and phytoextraction trace elements and biodegradation of organic pollutants (Haimi, 2000; Cortet et al., 2006; Krumins et al., 2015).

Soil invertebrates live in close contact with soil, and many ingest and sometimes accumulate bioavailable pollutants in their tissues (Lanno et al., 2004). Different species exhibit distinct bioaccumulation potential that could be predicted by specific functional traits. For example, the presence of specific organs dedicated to contaminant detoxification in the organism (*e.g.* the hepatopancreas of isopods or snails (Fritsch et al., 2011), the chloragogenous tissue of earthworms (Sizmur and Hodson, 2009) could be particularly useful in the ecological restoration of contaminated site.

The fate of contaminants in soils depends upon soil characteristics such as pH and OM level (Durães et al., 2018). Given the importance of soil fauna in soil structure formation and nutrient recycling, their presence in contaminated soils can have major indirect impacts on the success of pollution remediation. Traits associated with soil structure maintenance or improvement and nutrient cycling functions might then also help identify relevant species to use in the remediation of contaminated sites. Favoring functional groups that promote soil OM levels and C sequestration while being tolerant to soil pollution holds promise for restoration (Boyer and Wratten, 2010).

So far, most research on the role of soil invertebrate in the restoration of contaminated sites has focused on the impacts of emblematic taxonomic groups such as earthworms (*e.g.* Jusselme et al., 2012; Sizmur and Richardson, 2020). There is still limited evidence for the role of specific traits in such processes. Identifying particular soil functional groups and traits that promote contaminant stabilization in soils, their uptake by plants (phytoextraction), their degradation by microorganisms, and/or that are crucial in plant succession, are important future research avenues to promote the use of soil invertebrate traits in ecological restoration of polluted sites.

## 4. Soil structure arrangement

Soil fauna plays key role in soil structuring that justifies its importance in ecological engineering (Snyder and Hendrix, 2008; Bottinelli et al., 2015). Several invertebrate traits can identify species that may improve soil structure the most according to the site-specific restoration goals.

First, body size is a key trait affecting soil organism role on soil structure, with large species having the largest effects (Lehmann et al., 2017). For instance, large earthworms can produce large burrows that increase soil porosity and water infiltration (Lee and Foster, 1991). Many large soil invertebrate species are considered soil engineers having profound effects on soil macrostructure. Different types of engineer species affect soil structure through different mechanisms, such as burrowing activity, translocation, consumption, and modification of soil aggregates affecting mineral weathering (Bottinelli et al., 2015). Small-bodied soil invertebrates also play a role in soil structure alteration at a smaller scale through litter comminution, casting, and other disintegration mechanisms. Due to their high density, small detritivores process OM and create a large quantity of faecal pellets, thus affecting soil microporosity (Schrader et al., 1997; Maaß et al., 2015). Since microbivores impact fungi and bacteria community activity (Coulibaly et al., 2019), they indirectly contribute to soil structure dynamics through mucilage secretion and hyphal networks.

Moreover, functional groupings such as earthworm morpho-ecological groups (epigeic, endogeic, anecic) and collembola ecomorphological classification according to vertical distribution (epedaphic, hemidaphic and euedaphic, Rusek, 1998) are key traits to identify species with specific impacts on soil structure. While endogeic earthworm species build extensive, temporary burrow systems that rarely come out on the surface of the soil, anecic earthworm species live in permanent burrows that come out on the surface. Endogeic species may be particularly useful to improve soil aggregation, as demonstrated in a meta-analysis (Lehmann et al., 2017). Anecic species may be preferred to create Technosol mixing green waste compost and industrial soil as their specific burrowing activities can enhance green waste compost incorporation more than endogeic species (Pey et al., 2013).

The nature and structure of faecal pellets are also important effect traits that influence soil structure. Casts produced by earthworms modify aggregation in soils (Lee and Foster, 1991). Large species produce large and compact casts that increase the proportion of large aggregates in soil and its bulk density. Unlike these “compacting species”, small earthworms (“decompacting species”) produce smaller, more fragile casts that decrease aggregates in soil and bulk density. The introduction of compacting species in agroecosystems tends to decrease the infiltration rate and to increase water retention capacity. Conversely, the introduction of decompacting species increases the infiltration rate and decreases water retention capacity (Blanchart et al., 1999).

For termites and ants, further specific traits such as sedentarity, colony size, or nest structures are important to consider. Sedentary ant species probably have higher and longer-term impacts on soil structure than nomad species. The size of the colony also affects its capacity to modify bulk density, soil aggregation and hydrological properties (Drager et al., 2016). Traits related to the size of specific body parts, such as mandible size could be important to consider (Dostál et al., 2005). Finally, both the size of the entrance to ant nests and their architecture affect their impact on bulk density and water infiltration (Wills and Landis, 2018). For example, a sedentary ant species *Messor barbarus* that forms colonies of more than 20 000 individuals, was identified as a good candidate to restructure the soil and to increase the quantity of soil nutrients after an oil leak in south-eastern France (Bulot et al., 2014; De Almeida et al., 2020b).

## 5. Biological control agent by prey/pest regulation

Enhancing biological control (the availability of predator invertebrates to regulate prey, including pests in agricultural systems), can be an important restoration goal (Headrick and Goeden, 2001). The regulation role played by soil invertebrates depends on key functional traits that affect their ability to control the density and activity of other organisms such as plants, microorganisms, and invertebrates.

The most obvious soil invertebrate trait that ecological engineering could exploit to enhance prey/pest regulation is feeding behavior (diet trait). The most relevant diet trait will depend on the restoration goal: for example, zoophagous organisms to control arthropod pests, or microbivores to control soil-borne plant fungal diseases. Species feeding specialization (prey specialist or generalist) is also a key trait affecting species relevance for biological control (*e.g.* Pompozzi et al., 2018). For instance, fungivores can feed preferably on pathogenic rather than on antagonistic or arbuscular mycorrhizal fungal propagules (Innocenti and Sabatini, 2018). All these diets are directly linked to the mouthpart morphology of the invertebrates.

Ecological engineering can also consider body size and body mass that are important functional traits to identify species with potentially large impacts on biological control. Body size influences predator per capita consumption rates (*e.g.* Brose et al., 2006; Ball et al., 2015; Brose et al., 2019; Ostandie et al., 2021).

Behavioral traits are also key to identify species that particularly enhance biological control within ecological engineering schemes: foraging strategy (*e.g.* spiders hunting and trap strategies: space-web weaver, ground runner, foliage runner and ambusher; Rusch et al., 2015), predator attack rates, dispersal behavior, motion strategy and relative movement speed. The distance over which a predator is able to locate its prey is associated with specific morphological traits (*e.g.* legs length, wing morphology, visual search system). In addition, other phenological and physiological traits (*e.g.* digestion time, ingestion rate, reproductive potential, breeding season) can impact prey regulation, as can the life stage and gender of predators (*e.g.* Shimoda et al., 1997). Some of these traits are strongly related to body size, as highlighted by Rusch et al. (2015). Brousseau et al. (2018) showed for ground beetles and their prey that the match between two traits, predator biting force and prey cuticular toughness, can be another interesting predictor. Finally, taking account of the habitat preference of a predator and its prey can help ensure prey control success in the field through improved match in spatial predator/prey co-occurrence (Gardarin et al., 2018).

Soil invertebrates also interact with aboveground organisms. For instance, Scheu et al. (1999) showed that collembola can indirectly reduce the reproduction of plant-sucking aphids depending on the plant host. This result may be explained by an indirect effect of collembola on the growth of aphids and their plant host, through increased nutrient availability in soil. In addition, Schütz et al. (2008) suggest that aphid reproduction is reduced by collembola impact on resource allocation and plant growth. The role of earthworms on nematode abundance regulation has also been investigated (Demetrio et al., 2019). Direct grazing by earthworms, as well as the environmental modifications resulting from their activity can directly or indirectly affect many soil pests. Those processes depend on the morpho-ecological groups of earthworms.

## 6. The way forward: applications and future directions

### *6.1. From principles to applications*

The examples cited illustrate how selecting or maximizing specific functional traits within soil assemblages could participate in the restoration of four main soil functions (Fig. 1).

“Direct inoculation” and “attraction” are two interesting methods that should be tested and compared following the trait-based approach that we propose. Ecological engineering could use response traits to refine the selection of potential species or taxa group for “inoculation” approaches. The initial pool of species could be drawn from local or regional species pools (rather than exotic species, *e.g.* Drenovsky et al., 2012; McGrath et al., 2021). After identifying the ecosystem functions that meet restoration objectives, these functions could be translated into a set of relevant traits. Candidate species or taxa groups could then be selected based on the trait values that will optimize the set of relevant effect traits for each function. Finally, the effect traits could be weighted by the predicted abundance of each candidate species based on their response traits. “Attraction” approaches could identify specific management options that maximize relevant functional traits (for example increasing the proportion of semi-natural habitats in the landscape to promote the abundance and diversity of predator communities or increasing quantity of OM to attract detritivorous species).

The successful establishment of any species in a degraded ecosystem depends on its ecological preferences. As a result, other traits such as life expectancy and competitive abilities (response traits), may be important to consider when identifying species for ecological engineering. For example, remediation strategies need to implement suitable microhabitats, as well as consider species sensitivity to pollution type and level; a balance between effect traits relevant to remediation and response traits that will ensure that the species is able to survive, colonize, and play its role in the contaminated ecosystem. Databases of species sensitivity towards a variety of pollutants (maximum contaminant concentrations above which different species start to show adverse effects, *e.g.* U.S. EPA ECOTOX United States Environmental Protection Agency – Ecotoxicology Database) are publicly available. Checking targeted functional groups or traits for each specific scenario against these databases could help identify the most suitable groups for ecological remediation.

Moreover, depending on the state of ecosystem degradation, the types and objectives of ecological restoration may change. Disturbances are characterized by their type, magnitude, duration, spatial extent, frequency and timing. Ecological responses may be neutral, positive (regenerative) or negative (degrading) (Lake, 2013), and depend on their “resistance”, or ability to persist despite a disturbance or stressor

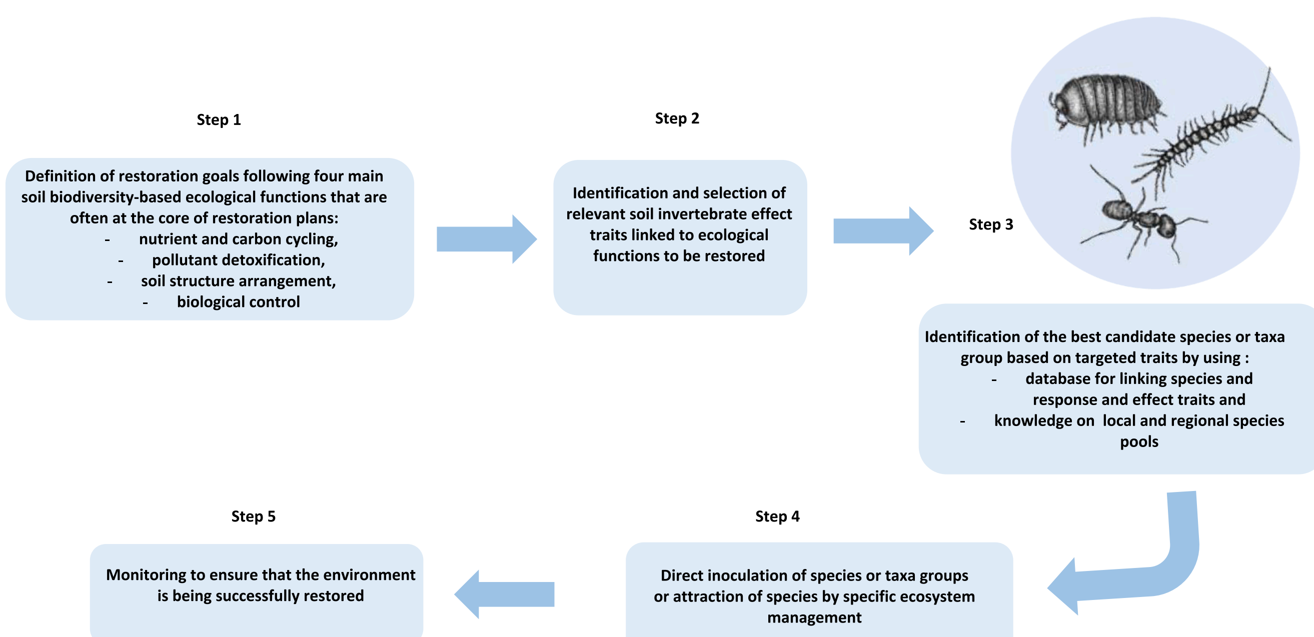


**Fig. 1.** From principles to applications: steps to incorporate soil invertebrate functional traits into ecological engineering approaches.

(Falk, 2017), and on their "resilience", or capacity to recover to a pre-disturbance state following perturbation (Hobbs & Suding, 2009; Falk, 2017; Gann et al., 2019). For slightly damaged ecosystems, actions to end the disturbance following passive restoration may be sufficient to restore the ecosystem (Gann et al., 2019). However, if the ecosystem is more disturbed, restoration of the biotic component will be necessary besides removal of the disturbance. If the disturbance has degraded both abiotic and biotic components, the priority is to restore the physical and chemical properties of the soil (Heneghan et al., 2008) by identifying the ecological functions of interest, and then the biotic component. In all cases community and population changes should be monitored to ensure that all target functions have been restored (Holl and Aide, 2011). A substantial body of evidence indicates the importance of functional diversity in the resistance and resilience of communities and ecosystems (Cadotte et al., 2011). In this regard, targeting specific functional traits in ecological restoration could potentially further enhance restoration success, by enhancing ecosystem resilience.

### 6.2. Current limitations and future research directions

Although selecting or maximizing specific functional traits within soil assemblages could participate in the restoration of soil functions, several knowledge gaps and limitations appear to prevent the use of soil invertebrate traits in ecological engineering.

From a theoretical point of view, matching the functional abilities (based on traits) of a species to re-inoculate with the processes related to specific restoration goals should improve restoration compared to an only partial match based on taxonomy. However, so far, very few studies approached that comprehensively. The use of soil invertebrates in ecosystem restoration remains scarce, and it is currently difficult to quantify the relative benefits of trait-based compared to species-based approaches. Such a framework has been successfully implemented for plants and future studies could assess the extent to which ecological engineering would benefit from trait-based selection of soil invertebrate species and taxa groups.

According to the mass ratio hypothesis (Grime, 1998), if a trait is strongly related to an ecosystem function, the abundance of this trait may well predict the function. Thus, the abundance of the species possessing the favorable trait (i.e. the functional identity of the species) could be promoted to optimize a desired function. While this seems to be straightforward and may be applied in the context of single-process restoration plans, these ones often target the enhancement of multiple functions affected by different combinations of traits (de Bello et al., 2010). Thus, it may not be possible to identify one single species possessing all the favorable trait values for all the targeted functions. Restoring multiple functions could require a combination of functionally different species with extensive trait differences between species (i.e. enhancing functional diversity) acting through complementary effects (Heemsbergen et al., 2004; Laughlin et al., 2018). But, there may be trade-offs between traits or combinations of traits having beneficial effects on one function but detrimental effects on others, following facilitative or inhibitory interactions. Indeed, the effects of fauna on soil processes depend on combinations of traits that are not necessarily correlated. Multivariate analyses can determine trait-service clusters and address the multiple relationships between traits and functions (de Bello et al., 2010). Such approaches could identify a set of key traits promoting multiple functions/services across time. Enhancing different facets of the distribution of the relevant traits (i.e. the value, range, and relative abundance of functional traits) could optimize multiple target functions. The components of functional composition (functional identity, functional complementarity) are not exclusive and can operate in concert (Gagic et al., 2015). More research is needed to assess their relative impacts on soil ecosystem processes and future research could compare the relative benefits of improving functional diversity, the abundance of specific traits, or the presence of certain keystone species in ecological engineering.

Although functional trait databases will be powerful tools in restoration, large amounts of data are currently missing from existing functional trait databases (such as BETSI database https://portail.betsi.cnrs.fr/, or Ecotaxonomy in progress https://biss.pensoft.net/article/37166/). Indeed, functional attributes of soil fauna data are globally sparse, and the majority of available data currently focus on a few soil taxa (earthworms, beetles or collembola) and traits (body size, diet) (Moretti et al., 2017). Traits, such as the behavioral composition of the candidate species population (*e.g.* dispersal ability, degree of attraction to a given resource), may be crucial to restoration of sustainable ecosystems. For instance, consistent intra-specific differences in invertebrate behavioral traits (i.e. animal personality) have important implications for key ecological interactions such as competition (Blight et al., 2016), or predation (Finke and Snyder, 2008). Studies on two species of cursorial spiders found that more active individuals (Keiser et al., 2015) or a mixture of active and inactive individuals (Royauté and Pruitt, 2015) are 50–80% more effective at suppressing pests. Despite their obvious importance, data related to behavioral traits are currently missing from trait databases and future studies need to address this gap across a wide range of taxa and effect traits.

Despite those limitations, our paper highlights that a set of key functional traits can already be a starting point for developing functional trait approaches in ecological restoration. Several traits, such as body size are key to multiple functions, and could thus help in selecting a set of relevant species among local or regional species according to the restoration goals. Furthermore, the success of trait-based approaches in plant restoration ecology encourages their use and application to soil invertebrates.

## 7. Conclusion

Soil invertebrates are major players in ecosystem functioning that are still rarely used in ecological engineering apart from a few emblematic taxa groups such as earthworms. We identified a number of effect traits for a wide range of soil organisms, that will facilitate the selection and identification of species by stakeholders interested in restoring four main ecosystem functions (nutrient cycling and carbon storage and turnover; transformation of potentially harmful elements and compounds; soil structure arrangement; biological control). The recent development of databases on soil invertebrate traits, together with a better understanding of the relationships between traits and functions will offer a unique opportunity to design comprehensive ecological engineering and restoration scenarios. Future ecological engineering programs could greatly benefit from incorporating belowground invertebrate species based on selected functional traits, but future studies are needed to demonstrate the benefits of such trait-based approaches compared to approaches relying on emblematic species. Engineering both aboveground and belowground compartments of ecosystems concomitantly could greatly benefit ecosystem restoration by maximizing internal ecological processes and positive feedbacks between the two compartments over time.

## 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.

## Data availability

No data was used for the research described in the article.

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