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# Knowledge on soil invertebrate macrofauna and bioturbating vertebrates: a global analysis using data science tools

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## Abstract

Soil fauna support life aboveground, are important for terrestrial ecosystems and are crucial for soil health and plant-protection. Approximately 23% of all known species are animals associated with soils, but there are many taxa with a low proportion of described species. The soil macrofauna, i.e., the invertebrates visible with the naked eye, include ca. 500 thousand species belonging to seven phyla and 47 taxonomic groups, while the soil megafauna are vertebrates that live, feed, nest in the soil or find refuge there. In the present study we evaluate knowledge and expertise on large soil fauna at country and global level, by assessing the most studied taxa, potential uses and study/sampling methods using bibliographic information and data science tools. We applied customized queries and a database in PostgreSQL connected with the R statistical program, to identify worldwide scientific output as a proxy for expertise in various subtopics covering eight macroinvertebrate taxa (ants, beetles, centipedes, earthworms, millipedes, spiders, termites) and nearly 60 megafauna taxa belonging to four Classes. Publications associated with author's country affiliations, were retrieved from Web of Science between 2011 and 2022 (macrofauna) and 2014 and 2023 (megafauna). Knowledge on soil macro and megafauna was not evenly distributed among the countries and even within the same continent. Regionally, authors affiliated to China, India, Australia, the USA, Brazil, South Africa, France, United Kingdom, Germany and Italy published the most depending on the macrofauna taxon and subtopic. Earthworms were the most studied soil macroinvertebrate worldwide and soil macrofauna were widely used as bioindicators, while bioturbating vertebrate publications were mainly from authors affiliated to USA, China, Australia and Brazil and primarily on rodents and reptiles. Especially in the African continent a major knowledge gap was identified in all aspects of the present analysis. There is a clear need for further work on soil fauna as well as a collaborative a coordinated effort to promote investment and capacity building in the countries lacking expertise, aiming to improve sustainable soil management and use and the long-term conservation of soil biodiversity.
**Keywords**: animals, soil biodiversity, macroinvertebrates, research methods, bibliographic database

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## 1. Introduction

Soil organisms are essential living beings for the functioning of terrestrial ecosystems and for foodweb interactions belowground in all landscapes in the world. They support aboveground life and are crucial for energy fluxes in soils, sometimes even more than aboveground animal food webs (Potapov et al. 2024). Furthermore, they are essential for soil health and for plant-protection as well as sources of pharmaceuticals and animal feed (Brown et al. 2018, Paoletti 2004, Wall et al. 2015, Potapov et al. 2024). However, global pressures derived from human activities such as land use change, urbanization, deforestation, and climate change, have harmed habitat conservation for soil biodiversity (FAO 2020). Considering that about one-third of the world's soils are degraded (FAO 2015) and that soils may harbor up to 59% of the world's known species (Anthony et al. 2023), soil biodiversity and the essential ecosystem services provided by soil organisms are under threat (FAO 2020, Lindo et al. this issue).

Soil animals play a key role in soil formation, and nutrient cycling, act as predators/consumers or prey in food webs, and regulate important ecosystem functions and services in soils (Lavelle et al. 2006). Their activity moves soil particles and litter, enhancing decomposition and nutrient cycling, generally improving soil aeration, water permeability, and creating habitats for smaller organisms. Some of them are plant (usually root) feeders, while many of them are predators, eating small soil insects and other arthropods as well as snails and earthworms (Table 1). Furthermore, these animals often respond quicker to changes and threats in soils than chemical or physical parameters, so are frequently used as soil quality/health bioindicators (Bünemann et al. 2018).

Among the most biodiverse and abundant animals in the world are the easily visible soil macroinvertebrates, also called soil macrofauna (Ruiz et al. 2008), encompassing up to 47 taxonomic groups belonging to seven phyla of terrestrial and aquatic invertebrates: Annelida, Arthropoda, Mollusca, Nematoda, Nematomorpha, Platyhelminthes, and Onychophora (Table 1). Most of the 35 Orders and five Classes are arthropods, and of these, more than half are insects (18 Orders). Soil macrofauna live in the soil or litter during their whole life cycle, or only partly (Ruiz et al. 2008). Soft bodied animals like earthworms and leeches, and important predators like arachnids and centipedes, as well as large chitinized arthropods like pillbugs and millipedes comprise members of the soil macrofauna community. Overall, soil animals represent approximately 23% of all known species (Anthony et al. 2023, Decaëns et al. 2006), but there are many taxa with a low proportion of described species, particularly the smaller ones (Decaëns et al. 2008). Using the updated number of species in the world, that is, approximately 2.11 million non-fossil species (IUCN 2021), this would represent around 485 thousand species.

Table 1 lists invertebrate taxa spending an important part of their life cycles in the soil or litter. Although the total reaches almost one 900 thousand species known globally, estimates for several groups are inflated due to the fact that they include numerous mainly aquatic species (e.g., Amphipoda, Decapoda, Isopoda) and/or that live aboveground or above the leaf litter, such as winged arthropods, in addition to those that inhabit epi-edaphic environments, such as epiphytic soils or "suspended" in trees (Gotsch et al. 2016), aerial parts of plants or bromeliads (e.g., Arachnida, Coleoptera, Diptera, Hemiptera, Hymenoptera, Mecoptera, Blattodea: Isoptera, Lepidoptera, Mantodea, Orthoptera, Psocoptera, Thysanoptera).

The physical limitations of living in the soil, including its compact nature, with few large pores and highly variable oxygen, water and food supply pose immense challenges to large-sized vertebrates, that must develop special adaptations to living in this dark environment. Among these, specialized sensorial organs in the head, nose or tongue, and large claws or highly-developed musculature for displacing soil and digging are quite commonplace (Orgiazzi et al. 2016). Although the term soil megafauna has been used to describe soil vertebrates (Wallwork 1970; Swift et al. 1979), this expression is not commonly used in research, and often refers to prehistoric or modern large animals (Moleón et al. 2020).

Various definitions have been proposed for soil megafauna. More restrictive definitions include only vertebrates that live in or burrow into the soil, and spend a significant amount of time within the soil, feeding in it (Orgiazzi et al. 2016). Therefore, animals burrowing within the soil but spending most of their lives on the soil surface would not be considered part of the soil megafauna, despite potential important impacts on soils and associated ecosystem services. Broader definitions include all vertebrates that move soils, interfering on soil surface and soil profile heterogeneity (FAO 2020). Hence, all soil burrowing (disturbing) vertebrates (Platt et al. 2016) would be included, regardless of whether they live in the soil or not (Table 2). Thus, carnivores like bears, badgers and meerkats; omnivores like peccaries, pigs and boars; other ungulates like elephants or bisons; birds and bird-like animals like puffins, kiwis and echidnas; rodents like mice, ground squirrels, marmots, and hedgehogs; some amphibians like salamanders, frogs and toads; as well as reptiles like tortoises, some snakes and lizards would all be part of the soil megafauna. Although more useful to identify the large number of vertebrate species that affect soils (Table 2), broader definitions still bump into the issue of including many taxa that are not truly soil-dwellers, and therefore instead of being considered soil megafauna per se, these animals should rather be called vertebrate bioturbators or soil burrowing vertebrates (Platt et al. 2016).

Independently of the definition used, vertebrates that affect soils and their properties, here considered as equivalent to the soil megafauna, include more than 8,600 species that create burrows in the soil or on the soil surface, that live permanently or temporarily within it (Table 2). They include four classes (Amphibia, Aves, Mammalia and Reptilia) and 24 orders, of which most (14) are mammals. The most species-rich are snakes (over 2,000 species), followed by rodents (sensu-lato) with over 1,600 species, and then frogs (>700 spp.) and salamanders (>600 spp.), though some of these estimates are slightly inflated by the species that are not truly terrestrial or fossorial.

Invertebrate and vertebrate animals are involved in a multitude of soil processes and include five main feeding preferences or functional groups (Table 1):

1. Soil movers or geophages that consume soil and live mostly within the soil profile (e.g., earthworms, termites, ants, and most soil-digging invertebrates and vertebrates), causing major soil bioturbation and frequently acting as soil ecosystem engineers, physically altering the soil habitat and the availability of organic resources for other organisms (Lavelle et al., 1997);
2. Detritivores, that include a wide range of consumers of organic resources of variable quality, ranging from the feces (coprophages), litter, dead animal (necrophages) and humus (humivores) feeders, ultimately affecting decomposition rates and stimulating microbial activity in the soil and gut microbiome;
3. Phytophages, which include plant shoot and/or root consumers, as well as those that eat wood (xylophages). These are often considered plant or urban pests, causing damage to agricultural or forest plantations (e.g., some beetle grubs, true bugs, lepidoptera and fly larvae), lawns and gardens (e.g., rabbits, moles), as well as houses (e.g., termites) or stored food (e.g., cockroaches);
4. Predators and parasites, which by consuming other animals totally or partially, affect their populations and/or activity rates, and sometimes act as biological control agents;
5. Microbivores, which include many animals that eat smaller non-animal eukaryotes like protists, as well as prokaryotes like fungi and bacteria, influencing nutrient cycling.

Many of the soil fauna act as predators (32 taxa of invertebrates and 53 vertebrates), while fewer of them are microbivores (13 invertebrate and 2 vertebrate taxa). A relatively similar number of taxa of invertebrates act as plant or wood feeders, detritivores or bioturbators (Table 1), while all vertebrate taxa are bioturbators (59 taxa), but fewer are plant feeders or pests (21 taxa) and even fewer are decomposers (2 taxa; Table 2).

The ultimate effects of fauna communities on soils are vast and long-lasting, and have been known since before Darwin (1881), although the overall importance for provisioning of ecosystem services is still relatively poorly known and little quantified (Decaëns et al. 2006, Brown et al. 2018, Parron et al. this issue). Digging animals can cause major soil bioturbation, affecting soil structure, water percolation and moisture in the profile, as well as nutrient cycling and food web functioning (Brown et al. 2018, Meysmann et al. 2006). In fact, the ecosystem engineers (sensu Jones et al. 1994) can significantly affect soil physical structure and the availability of resources (particularly organic) for other soil organisms. For instance, lyre-birds can move tons of soil $ha^{-1}$ in Australian forests (Ashton & Bassett 1997), while wild-pigs and boars can create many wallows in forests throughout the world, often used by other animals (Baruzzi & Krofel 2017). The burrows made by badgers, prairie-dogs, burrowing owls, rabbits, turtles and armadillos can be used by many other organisms as resting, nesting, refugia or feeding sites (Hole 1981).

By affecting ecosystem functioning and rates of delivery of several ecosystem services, soil fauna are important agents in the achievement of several of the United Nations (UN) Sustainable Developmental Goals (SDG), including SDG 2 (zero hunger), 3 (good health and well-being), 6 (clean water and sanitation), 13 (climate action) and 15 (life on land) (Bach et al. 2021). The UN SDG 15 declares the need to “protect, restore and promote sustainable use of terrestrial ecosystems, sustainably manage forests, combat desertification, and halt and reverse land degradation and halt biodiversity loss” (https://sdgs.un.org/goals/goal15). A global and organized effort is needed to achieve this, but we must first assess the current status and trends of soil biodiversity to identify and predict the land use systems and practices that help conserve and promote biodiversity, especially in soils, where a major part of the world's species live. Aiming towards this goal, the Convention on Biological Diversity called for the establishment of a Global Soil Biodiversity Observatory, and requested that the Food and Agriculture Organization of the UN (FAO) coordinate this effort. However, to establish a global observatory, one must first establish current expertise on different groups of soil organisms, and determine

**Table 1.** Soil and surface litter macrofauna (invertebrate) taxa, their common names, worldwide species richness estimates (from various sources), and their effects on soil functions (modified and expanded from Brown & Gabriac 2022 and Brown et al. 2024b). References for the number of species are provided in the footnote.

| Taxonomic classification | Common name | No. species* | Feeding preferences & Functional groups/ | | | | |
|---|---|---|---|---|---|---|---|
| | | | Geophage, Bioturbator | Detritivore, Coprophage Decomposer | Phytophage, Xylophage, Pest | Carnivore, Predator, Parasite | Fungivore, Microbivore |
| **Phylum Annelida** | | | | | | | |
| Class Clitellata | | | | | | | |
| Subclass Hirudinea | | | | | | | |
| Order Arhynchobdellida | Land leeches | 92 | | | | X | |
| Subclass Oligochaeta | | | | | | | |
| Order Crassiclitellata | Earthworms | 5,753 | X | X | | | X |
| **Phylum Arthropoda** | | | | | | | |
| Subphylum Chelicerata | | | | | | | |
| Class Arachnida | | | | | | | |
| Order Amblypigi | Whip-spiders | >279 | | | | X | |
| Order Araneae | Spiders | 52,311 | X | | | X | |
| Order Ixodida | Ticks | 742 | | | | X | |
| Order Opiliones | Harvestmen | 6,637 | X | | | X | |
| Order Pseudoscorpiones | Pseudoscorpions | 4,525 | | X | | X | |
| Order Ricinulei | | 103 | | | | X | |
| Order Schizomida | | 376 | | | | X | |
| Order Scorpiones | Scorpions | 2,838 | X | | | X | |
| Order Solifugae | Camel spiders | 1,211 | X | | | X | |
| Order Uropygi | Vinagroon scorpions | 126 | | | | X | X |
| Subphylum Crustacea | | | | | | | |
| Class Malacostraca | | | | | | | |
| Order Amphipoda | | | | | | | |
| Family Talitridae | Sandfleas | 157 | X | X | | | |
| Order Isopoda | Woodlice, pillbugs, | | | | | | |
| Suborder Oniscidea | sowbugs | 3,936 | X | X | | X | X |
| Subphylum Hexapoda | ND | | | | | | |
| Class Diplura | | 1,008 | | X | | X | |
| Class Insecta | | | | | | | |
| Order Archaeognatha | Bristletails | 548 | | X | | | |
| Order Blattodea: Blattoidae, etc | Cockroaches | 5,022 | X | X | X | | X |
| Termitoidea | Termites | 3,111 | X | X | X | | X |
| Order Coleoptera | Beetles | 389,487 | X | X | X | X | X |
| Order Dermaptera | Earwigs | 2,055 | X | X | X | X | |
| Order Diptera | Fly larvae | 157,971 | X | X | X | X | X |
| Order Embioptera | Webspinners | 466 | | X | X | | X |
| Order Grylloblattodea | Icebugs | 41 | X | X | | X | |
| Order Hemiptera | | | X | X | X | X | |
| Suborder Auchenorrhyncha | Cicadas | 3,478 | X | | X | | |
| Suborder Heteroptera | True bugs | 40,444 | X | | X | X | |
| Suborder Stenorrhynca | Ground pearls | 107 | | | X | | |
| Order Hymenoptera | | | | | | | |
| Family Apidae. | Bumblebees, solitary bees, stingless bees | 5,662 | | | X | | |

**Table 1** continued.

| Taxonomic classification | Common name | No. species* | Feeding preferences & Functional groups/ | | | | |
|---|---|---|---|---|---|---|---|
| | | | **Geophage, Bioturbator** | **Detritivore, Coprophage Decomposer** | **Phytophage, Xylophage, Pest** | **Carnivore, Predator, Parasite** | **Fungivore, Microbivore** |
| Family Formicidae | Ants | 16,735 | X | X | X | X | X |
| Family Vespidae | Wasps, hornets | 4,932 | X | | | X | |
| Order Lepidoptera | Butterflies, moths (larvae, pupae) | 137,441 | | | X | X | |
| Order Mantodea | Praying mantis | 2,547 | | | | X | |
| Order Mantophasmatodea | Gladiators | 26 | | | | X | |
| Order Mecoptera | Scorpion flies | 737 | X | X | X | X | |
| Order Neuroptera | | | | | | | |
| Family Myrmeleontidae | Antlions | 2,090 | X | | | X | |
| Family Chrysopidae | Lacewings | 1,415 | | | | X | |
| Order Orthoptera | | | | | | | |
| Family Gryllidae | Crickets | 6,329 | X | | X | | |
| Order Psocodea | Booklice | 11,972 | | X | X | | |
| Order Thysanoptera | Thrips | 6,174 | | X | X | X | |
| Order Zygentoma | Silverfish | 594 | | X | | | X |
| Subphylum Myriapoda | | | | | | | |
| Class Chilopoda | Centipedes | 3,327 | X | | | X | |
| Class Diplopoda | Millipedes | 12,946 | X | X | X | | X |
| Class Symphyla | Garden centipedes | 204 | | X | X | X | X |
| **Phylum Mollusca** | | | | | | | |
| Class Gastropoda | Slugs and snails | 24,937 | X | X | X | | X |
| **Phylum Mollusca** | | | | | | | |
| Class Gastropoda | | | | | | | |
| Order Mermithida | Mermithid | 640 | | | | X | |
| **Phylum Nematomorpha** | | | | | | | |
| Class Gordioidea | | | | | | | |
| Order Gordioida | Horsehair worms | 351 | | | | X | |
| **Phylum Onycophora** | Velvet-worms | 222 | | | | X | |
| **Phylum Platyhelminthes** | | | | | | | |
| Class Rhabditophora | | | | | | | |
| Order Tricladida | Flatworms, land planarians | 910 | | | | X | |
| **Total** | | 888,742 | 24 taxa | 22 taxa | 20 taxa | 32 taxa | 13 taxa |

*The number provided is, when possible, the best approximation of the species associated with soils and the surface-litter layer, or involved in bioturbation. When not possible, the number represents all the known species of a particular taxon, in some cases also aquatic taxa. Fossil and/or extinct species were removed from the estimates, whenever this information was known. Sources of the species estimates: Hirudinea: Sket & Trontelj (2008); Crassiclitellata: Brown et al. (2024c); Amblypigi: World Amblypygi Catalog (2022); Araneae: World Spider Catalog (2024); Ixodida: Guglielmone et al. (2019); Opiliones: Kury et al. (2021); Pseudoscorpiones: World Pseudoscorpiones Catalog (2022); Ricinulei: World Ricinulei Catalog (2022); Schizomida and Thelyphonida (Uropygi): Clouse et al. (2017); Scorpiones: Rein (2017); Solifugae: World Solifugae Catalog (2022); Uropygi: World Uropygi Catalog (2022); Coleoptera and Symphyla: Zhang (2013); Talitridae: Lowry & Myers (2019); Oniscidea: Svavarsson (2011); Diplura: Sendra et al. (2021); Archaeognatha and Zygentoma: Mendes (2018); Blattoidae, Nocticolidae, Corydiidae, Cryptocercoidae, and Blaberoidae: Beccaloni (2014); Isoptera: Krishna et al. (2024); Dermaptera: Hopkins et al. (2024a); Diptera: Courtney et al. (2017); Embioptera: Hopkins (2024a); Grylloblattodea: Zhou et al. (2023); Auchenorrhyncha: Dmitriev et al. (2022); Heteroptera: Henry (2017); Stenorrhynca: EFSA Panel on Plant Health et al. (2019); Apidae and Vespidae: Aguiar et al. (2013); Formicidae: AntWeb (2024); Lepidoptera: Beccaloni et al. (2024); Mantodea: Otte et al. (2024); Mantophasmatodea: Hopkins (2024b); Mecoptera: Bicha (2018); Myrmeleontidae and Chrysopidae: Oswald & Machado (2018); Gryllidae: Cigliano et al. (2024); Psocodea: Hopkins et al. (2024b); Thysanoptera: Mound (2018); Chilopoda: Bonato et al. (2016); Diplopoda: Sierwald & Spelda (2024); Gastropoda: MolluscaBase (2024); Mermithida: Hodda (2013); Gordioida: Zhang (2011); Tricladida: Sluys (2019); Onycophora: Oliveira et al. (2024).

**Table 2.** Soil and surface litter megafauna (vertebrate) taxa, their common names, worldwide species richness estimates (from various sources), and their effects on soil functions (modified and expanded from Brown & Gabriac, 2022 and Brown et al., 2018). References for the number of species are provided in the footnote.

| | | | Feeding preferences & Functional groups/ | | | | |
|---|---|---|---|---|---|---|---|
| **Taxonomic classification** | **Common name** | **No. species*** | **Geophage, Bioturbator** | **Detritivore, Coprophage Decomposer** | **Phytophage, Xylophage, Pest** | **Carnivore, Predator, Parasite** | **Fungivore, Microbivore** |
| **Phylum Chordata** | | | | | | | |
| Subphylum Vertebrata | | | | | | | |
| Class Amphibia | | | | | | | |
| Order Anura | | | | | | | |
| Family Hemisotidae | Shovelnose frogs | 9 | X | | | X | |
| Family Microhylidae | Narrow-mouth frogs | 745 | X | | | X | |
| Family Myobatrachidae | Australian ground frogs and burrowing frogs | 227 | X | | | X | |
| Family Rhinophrynidae | Mexican burrowing toad | 1 | X | | | X | |
| Family Scaphiopodidae | Spadefoot toads | 7 | X | | X | | |
| Order Gymnophyona | Caecilians | 222 | X | | | X | |
| Order Urodela | | | | | | X | |
| Family | Mole salamanders, | 32 | X | | | | |
| Ambystomatidae | Tiger salamander | | | | | X | |
| | Lungless salamanders, | 516 | X | | | | |
| Family Plethodontidae | woodland salamanders | | | | | X | |
| | True salamanders, Fire | 139 | X | | | | |
| Family Salamandridae | salamander, Newts | | | | | X | |
| Class Aves | Kiwis | 5 | X | | | X | |
| Order Apterygiformes | | | | | | | |
| Order Charadriiformes | Auks, Puffins | 25 | X | | | X | |
| Family Alcidae | | | | | | | |
| Order Passeriformes | Lyre-birds | 2 | X | | | | |
| Family Menuridae | | | | | | | |
| Order Procellariiformes | Petrels, Shearwaters | 98 | X | | | X | |
| Family Procellariidae | | | | | | | |
| Order Strigiformes | Burrowing owls | 3 | X | | | X | |
| Family Strigidae | | | | | | | |
| Class Mammalia | | | | | | | |
| Order Afrosoricida | Golden-moles | 21 | X | | | X | |
| Family Chrysochloridae | Tenrecs | 31 | X | | X | X | |
| Family Tenrecidae | | | | | | | |
| Order Artiodactyla | Boars, hogs, pigs | 18 | X | | X | X | |
| Family Suidae | Peccaries, javelinas | 3 | X | | X | X | |
| Family Tayassuidae | | | | | | | |
| Order Carnivora | Coyotes, foxes, dogs | 39 | X | | | X | |
| Family Canidae | Meerkats | 35 | X | | | X | |
| Family Herpestidae | Skunks, stink badgers | 14 | X | | | X | |
| Family Mephitidae | Badgers, weasels | 69 | X | | | X | |
| Family Mustelidae | Brown bear, grizzly | 3 | X | | X | X | |
| Family Ursidae | bear, sloth bears | | | | | | |
| | Armadillos | 22 | X | | | X | |
| Order Cingulata | | | | | | | |
| Order Diprotodontia | Bettongs, potoroos, rat | 12 | X | | X | X | X |
| Family Potoroidae | kangaroos | | | | | | |

**Table 2** continued.

| Taxonomic classification | Common name | No. species* | Feeding preferences & Functional groups/ | | | | |
|---|---|---|---|---|---|---|---|
| | | | Geophage, Bioturbator | Detritivore, Coprophage Decomposer | Phytophage, Xylophage, Pest | Carnivore, Predator, Parasite | Fungivore, Microbivore |
| Family Vombatidae | Wombats | 3 | X | | X | | |
| Order Eulipotyphla | | | | | | | |
| Family Erinaceidae | Hedgehogs, gymnures | 34 | X | | | X | |
| Family Soricidae | Shrews | 483 | X | | | X | |
| Family Talpidae | Moles | 65 | X | | | X | |
| Order Lagomorpha | | | | | | | |
| Family Leporidae | Hares, rabbits | 77 | X | | X | | |
| Family Ochotonidae | Pikas | 34 | X | | X | | |
| Order Macroscelidea | Elephant shrews, sengis | 20 | X | | X | X | |
| Order Monotremata | | | | | | | |
| Family Tachyglossidae | Echidnas | 4 | X | | | X | |
| Order Peramelemorphia | | | | | | | |
| Family Peramelidae | Bandicoots | 27 | X | | X | X | |
| Family Thylacomyidae | Bilbies | 2 | X | | X | X | X |
| Order Pholidota | Pangolins | 8 | X | | | X | |
| Order Proboscidea | | | | | | | |
| Family Elephantidae | Elephants | 3 | X | | X | | |
| Order Rodentia | | | | | | | |
| Family Bathyergidae | Blesmols, African mole-rats | 26 | X | | | X | |
| Family Chinchillidae | Vizcachas | 7 | | | | | |
| Family Cricetidae | Voles, ground-rats, pack-rats, lemmings | 872 | X | | | X | |
| Family Ctenomyidae | Tuco-tucos | 67 | X | | X | X | |
| Family Echimyidae | Spiny-rats | 117 | X | | X | X | |
| Family Geomyidae | Pocket gophers, gophers | 42 | X | | X | X | |
| Family Heterocephalidae | Naked mole-rat | 1 | X | X | X | | |
| Family Muridae | Bandicoot rats, Norway rats | 871 | X | | X | X | |
| Family Sciuridae | Groundhogs, woodchucks, marmots, ground-squirrels, | 376 | X | | X | X | |
| | chipmunks, prairie-dogs | 38 | | | | | |
| Family Spalacidae | Mole-rats, Blind mole-rats | 1 | X | | X | X | |
| Order Tubulidentata | Aardvark | | | | | | |
| Class Reptilia | | | X | | | X | |
| Order Squamata | | | | | | | |
| Clade Amphisbaenia (six families) | Worm-lizards | 203 | X | | | X | |
| Family Anguidae | Slow-worms | 88 | X | | | X | |
| Family Dibamidae | Skinks | 27 | X | | | X | |
| Family Helodermatidae | Gila monster | 1 | X | | | X | |
| Family Pygopodidae | Snake-lizards | 47 | X | | | X | |
| Family Varanidae | Lizards, monitor lizards, Komodo dragon | 88 | X | | X | X | |

**Table 2** continued.

| Taxonomic classification | Common name | No. species* | Feeding preferences & Functional groups/ Geophage, Bioturbator | Detritivore, Coprophage Decomposer | Phytophage, Xylophage, Pest | Carnivore, Predator, Parasite | Fungivore, Microbivore |
|---|---|---|---|---|---|---|---|
| Infraorder Alethinophidia | | | | | | | |
| Family Atractaspididae | Burrowing asps | 69 | X | | | X | |
| Family Colubridae | Snakes, burrowing snakes worm-snakes | 2,119 | X | | | X | |
| Family Loxocemidae | Mexican burrowing snake | 1 | X | | | X | |
| Family Pareidae | Snail-eating snakes | 46 | X | | | X | |
| Infraorder Scolecophidia | Blind snakes, thread snakes | 474 | X | | | X | |
| Order Testudines | | | | | | | |
| Family Testudinidae | Tortoises | 47 | X | X | X | X | |
| **Total** | | 8,625 | 59 taxa | 2 taxa | 21 taxa | 53 taxa | 2 taxa |

*The number provided is, when possible, the best approximation of the species associated with soils or involved in bioturbation. When not possible, the number represents all the known species of a particular taxon, including those that are aquatic (e.g., salamanders, frogs). Sources of the species estimates: Amphibians: AmphibiaWeb (2024); Aves: Billerman et al. (2022) and Gill et al. (2024); Mammalia: Mammal Diversity Database (2023); Reptilia: Uetz et al. (2023).

the best assessment methods worldwide, to promote adequate monitoring practices.

Therefore, the present study was undertaken to evaluate country-level and global knowledge and expertise on large soil fauna, by assessing the most studied taxa, potential uses and study/sampling methods using bibliographic information and data science tools. It is not a traditional review of literature, scientometric or meta-analysis, but rather an overview of the main actors (countries) in terms of scientific output related to a series of topics (key-word searches) concerning the main soil macroinvertebrate and vertebrate taxa.

## 2. Material and Methods

### 2.1 Publications on soil macroinvertebrates and vertebrates

Bibliographic information of publications evaluating selected soil animal groups (macrofauna and megafauna), as well as different applications of these groups in research and sampling/study methods used for macroinvertebrates worldwide was obtained from the largest databases of academic disciplines, Web of Science (WoS). Search terms considered only eight of the main soil macrofauna groups (Table 3) , as there is an abundant literature on soil macroinvertebrates (e.g., Phillips et al. 2024), and this would allow focusing on some of the more abundant and widely collected taxa (Lavelle et al. 2022). On the other hand, much less information is available on soil disturbing vertebrates animals, so the search items considered a much larger range of taxa (Table 4). For soil macrofauna, the search was conducted in March 2022 and considered only articles published between January 2011 and February 2022. For vertebrate megafauna, the search conducted in May 2024 considered articles published between January 2014 and December 2023. This would allow for an assessment of the more active working groups and professionals publishing on these topics worldwide. A set of additional search terms were applied to obtain some of the main applications of these animals, and sampling methods for soil macrofauna. Terms formed by two words were used with quotation marks to keep the meaning of the words together, and asterisks were used to consider plurals and various word endings for each taxon. The Boolean operator “OR” was used, indicating the presence of any of the search terms used. For all searches, the word “soil” was used together with the search terms of the topics listed in Tables 3 and 4. The search results were downloaded as Excel spreadsheets with the complete records to feed the database.

## 2.2 Database construction

In order to store, organize and facilitate the use of the data obtained in WoS within the R statistical program (R Core Team, 2021), a database was developed in PostgreSQL, a free and open-source relational database management system (RDBMS) (EDB - Enterprisedb - PostgreSQL), as described by Silva and Malaquias (2021). Detailed information on how to model a database with all data normalization rules and relational logic can be found in Silberschatz et al. (2019). The database is constituted by entities (tables) that are interrelated (Figure S1). It is important to note that the data were not normalized because the ultimate goal was to generate datasets, applying custom SQL (Structured Query Language) queries, for use within R.

## 2.3 Data analysis

The database in PostgreSQL was connected with R, enabling analysis of the resulting WoS data through 227 SQL customized queries (Figure 1). For macrofauna, the queries were performed with keywords of interest, as shown in Table 3, in the fields (columns of table fao.a3_ data_wos) article_title, abstract, author_keywords and keywords_plus. Following this strategy, the queries were carried out with R within the data records (bibliographic information obtained in WoS) stored in the PostgreSQL database (Figure 1) only within the selected groups/ topics of interest (Tables 3 and 4). For the customized queries, specific words were used to detect the topic of interest using the title, keyword list or abstract fields. Then, the quantitative results were expressed as the number of unique records (publications). Duplicate records were eliminated considering the publication title. Microsoft Excel version 2019 was used to build tables, graphs and maps. For soil vertebrates, the InCites plug-in of the Clarivate WoS program was used to generate maps.

For soil macroinvertebrates, the records retrieved were validated by checking manually the correspondence of publication contents (using the title and abstract) to the query keywords (Table 5). Only queries with > 80% match and over 100 records were validated for further analysis after removing unmatched records. The exception was biological control (78% match), which was considered due to its relevance for food, fiber and energy production. Other keywords were not included for further analysis due to the very low number of publications or because correspondence was random or weak. The number of publications per keyword query and countries were based on the information available in the field for all authors' addresses within each article. Hence, the number of publications in a given topic (query) corresponded to the number of publications with authors of the country of affiliation provided, and not necessarily the place where the study was performed. This approach permitted

**Table 3.** Topics used as main search terms for macrofauna in the Web of Science platform, together with the term "soil", considering the period January 2011 to February 2022.

| Macrofauna search terms | Number of publications |
|---|---|
| Macrofauna | 323 |
| Ants; formicid* | 1,614 |
| Chilopoda | 499 |
| Coleoptera | 2,411 |
| Diplopoda | 907 |
| Earthworm* | 7,411 |
| Spider* | 723 |
| Termite* | 1,059 |
| **Total** | **14,947** |

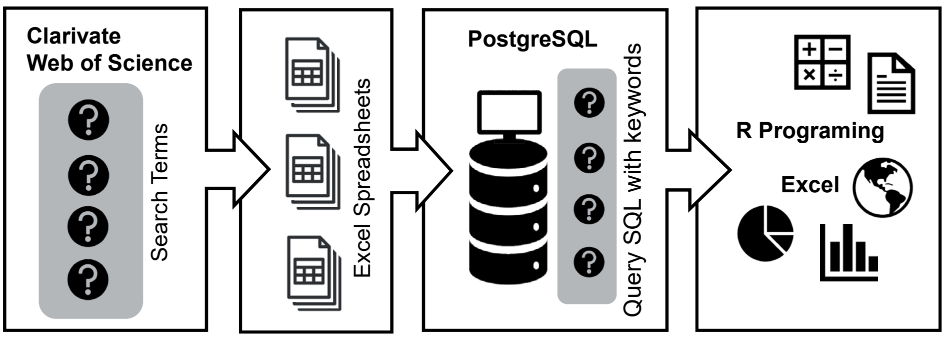


**Figure 1.** Diagram showing the steps from literature review until data analysis with the R statistical program. Excel spreadsheets downloaded with the bibliographic records from searches in Web of Science are stored in the PostgreSQL database. Posteriorly, the database is consulted through custom queries and data analysis is performed within the R and Excel programs which generate reports and graphs.

identifying country potential expertise in each topic consulted at national, regional and global levels. The countries were classified according to the FAO list.

Software for bibliometric analysis was available when this work started, but the analysis was based only on the first author of the publications rather than the full author list. Because the searches needed to consider all authors, a customized data science tool was built to obtain this information. Analysis of the data retrieved from WoS using a PostgreSQL database and customized queries allowed estimation of the most studied macrofauna and megafauna groups and their

**Table 4.** Search terms related to soil bioturbating vertebrates and the number of publications obtained from WoS searchers from the period of January 2014 to December 2023.

| **Search terms** | Publications | **Search terms** | Publications | **Search terms** | Publications |
|---|---|---|---|---|---|
| Snakes | **442** | Squamata | **54** | Burrowing owl | **9** |
| Moles | **437** | Megafauna | **51** | Gymnophiona | **9** |
| Elephants | **281** | Armadillo | **41** | Wild pig | **9** |
| Frogs | **273** | Shrew | **39** | Soricidae | **8** |
| Lizard | **217** | Prairie dog | **29** | Aardvark | **7** |
| Boars | **192** | Hedgehog | **28** | Lyrebird | **5** |
| Hogs | **147** | Skink | **21** | Amphisbaena | **4** |
| Voles, Lemmings, Pack Rats | **133** | Pangolin | **20** | Golden-mole | **3** |
| Gophers | **117** | Echidna | **16** | Meerkat | **3** |
| Salamand* | **107** | Stink badger* or Skunks | **16** | Snake-lizard | **2** |
| Pikas | **100** | Caecilians | **15** | Spiny Rats | **2** |
| Aves | **83** | Peccary | **15** | Vizcachas | **2** |
| Toad | **79** | Tuco-Tucos | **14** | Urodela | **2** |
| Rodentia | **75** | Bilby | **13** | Tenrec | **1** |
| Badgers and Weasels | **75** | Bandicoot | **11** | Pholidota | **1** |
| Mole-rat | **70** | Wombat | **10** | Gila monster | **0** |
| Ground squirrel or Marmot | **69** | Talpidae | **10** | Sengis | **0** |
| Tortoise | **55** | Cingulata | **10** | Total | **3,432** |

uses as well as the countries with more expertise based scientific output (publications), considering all authors. However, some difficulties were encountered during system construction like the lack of, or insufficient standardization of the information extracted from the WoS platform. Abbreviations or names of institutions varied for the same institution, making estimation of the main institutions working with soil fauna impractical at the time the database was built.

## 3. Results

### 3.1 Studies on macrofauna worldwide

Soil macroinvertebrates studied by authors affiliated to 151 countries (out of 199) between 2011 and 2022 (Table S1). USA had the highest number of publications (2,394) followed by China (1,715), Germany (892), Brazil (885) and the United Kingdom (815) (Figure 2; Table S1). In the Asian continent, India (790) followed China, in sixth place, and in the African continent, South Africa stood out (16th place globally) authoring 307 publications. In general, Northern hemisphere countries authored more publications, while Brazil and Australia (479) stood out in the Southern hemisphere. There was a clear knowledge gap in the African continent as several countries as none or at most three publications (Table S1).

Earthworms were by far the most studied invertebrate in the world, with more than seven thousand publications (Table 3) with authors affiliated to 127 countries (Figure 3). Beetles were studied in 94 countries with three times less publications than earthworms, followed by ants (Formicidae) in 94 countries, termites (Isoptera) in 96 countries, millipedes (Diplopoda) in 67 countries, spiders (Arachnida) in 79 countries and centipedes (Chilopoda) in 59 countries (Figure 3, Table S3).

USA concentrated most of the authors publishing on beetles (623 publications), termites (218) and spiders (119). Overall, this country had almost five times more publications on beetles than Germany, Brazil, United Kingdom, China and Italy and 2-3 times more publications on termites than Brazil, South Africa, Australia, France, India, China and Germany. Similarly, publications on spiders were 2-3 times more frequent in USA than Germany, China, Australia, United Kingdom and Brazil. It is noteworthy that publications with authors from many African countries were absent for all the major macrofauna groups evaluated. While the Russian Federation had many publications on millipedes (163), centipedes were less commonly studied worldwide. Most studies were published by authors affiliated to UK institutions (66), followed by Italian, German and Chinese institutions. Most of the African countries lacked studies on centipedes, as well as several Asian and South American countries (white colors in Figure 3).

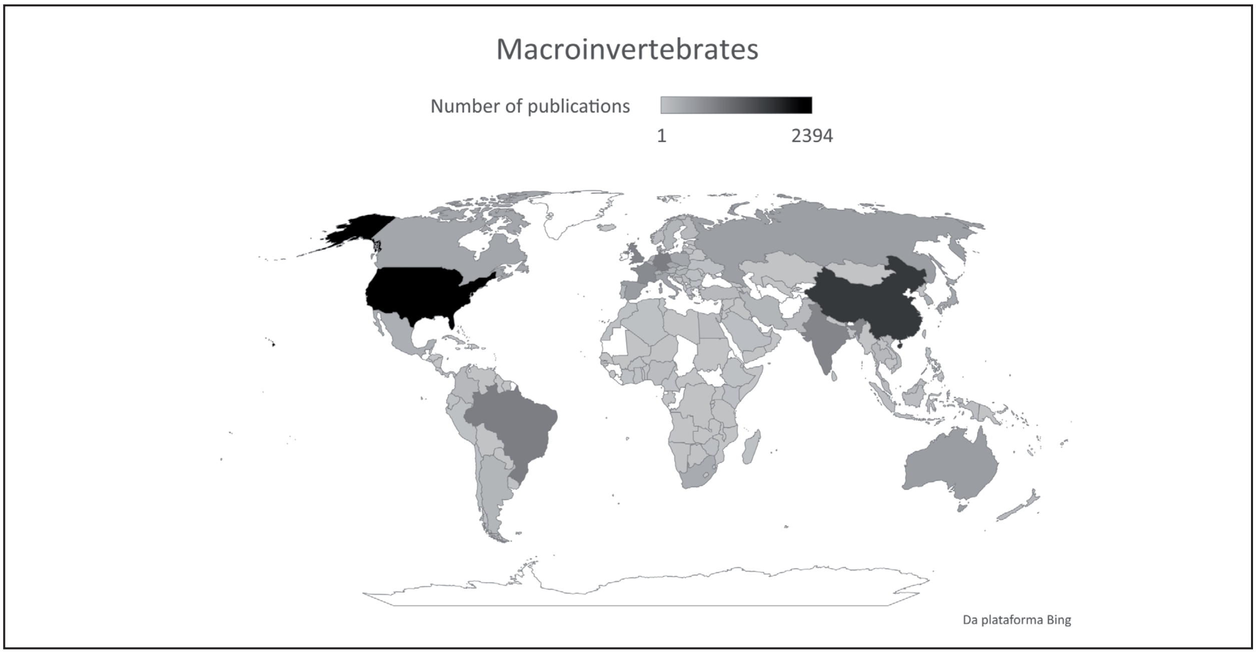


**Figure 2.** Worldwide distribution of the countries with authors publishing on macroinvertebrates between January 2011 and February, 2022 (left). The color intensity represents the increasing number of publication records, where blank is absence of records and darker colors refer to higher numbers.

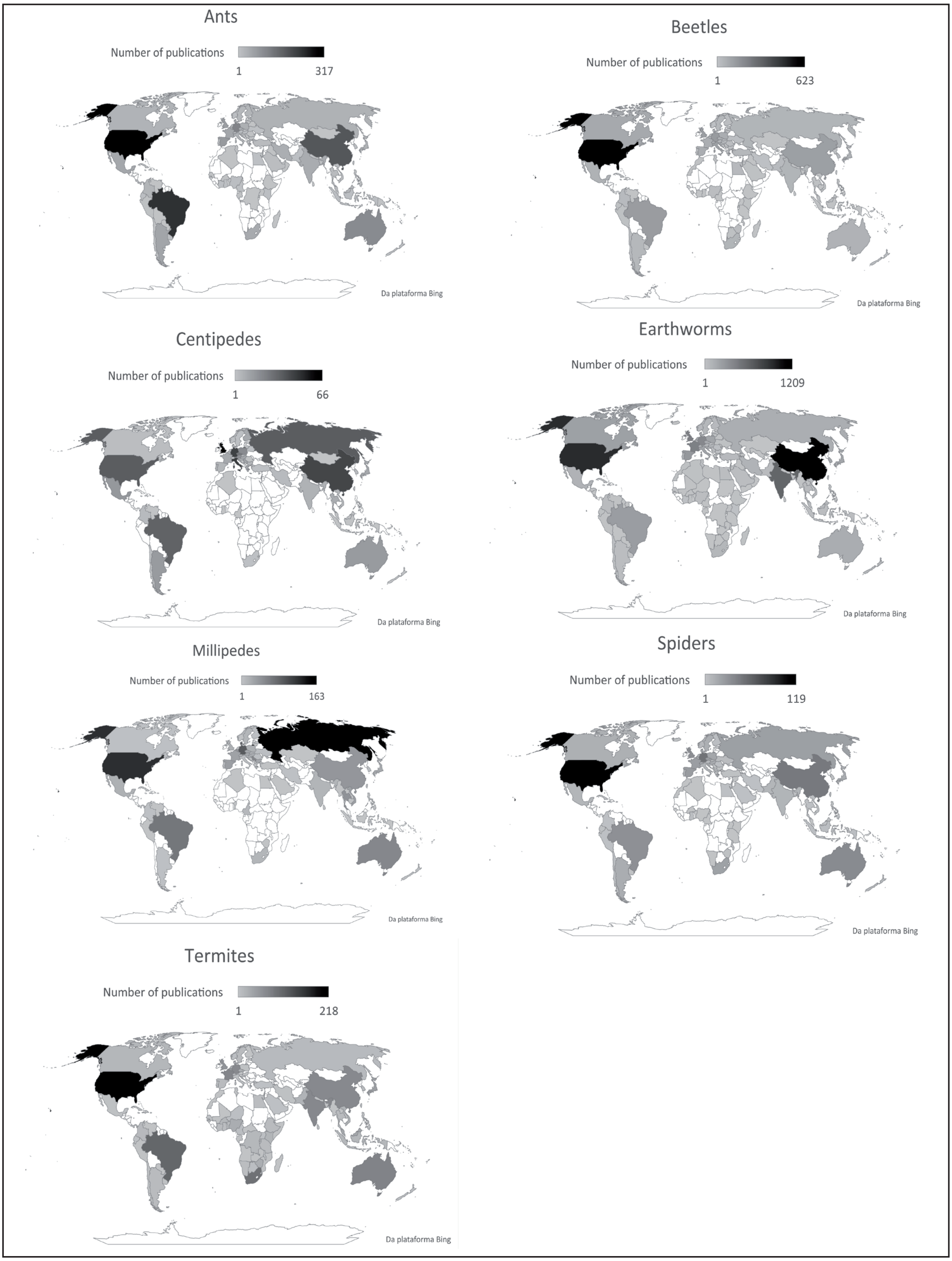


**Figure 3.** Worldwide distribution of the countries with authors publishing on earthworms, beetles, ants, termites, millipedes, centipedes and spiders between 2011 and February, 2022 in WoS. The color intensity represents the increasing number of publication records, where blank is absence of records and darker colors refer to higher numbers.

### 3.2 Uses and sampling methods with soil macrofauna

Soil macroinvertebrates were used in a variety of contexts, sometimes considering the whole community (macrofauna) in ecological approaches assessing soil biodiversity, although specific groups were also frequently targeted, mainly as bioindicators (Figure 4, Table S4). Macroinvertebrates were studied as indicators in agricultural and natural sites or in some kind of soil pollution or monitoring context in almost 2,000 publications from 99 countries, while soil quality was assessed in almost 600 publications by authors from 92 countries (Figures 4 and 5). Earthworms were the most commonly used invertebrate as bioindicator and in soil quality, being mentioned in 69% and 63% of the publications (Figure 4). Beetles were the second most mentioned in the use as bioindicators (13%), followed by ants and spiders, while ants (10%), termites and beetles (48%) followed earthworms in studies on soil quality. Carabids were the most studied beetle as bioindicators.

Authors affiliated to China published the most articles (264) using macroinvertebrates as bioindicators, followed by Brazil (135), France and Germany (each with >100; Figure 5). Although the topics soil quality and indicators might appear correlated, USA was the top country (88) publishing on soil quality but was 97th on publications (n=1) related to bioindicators (Figure 5, Table S5). China was the second country with the most publications (59) on soil quality, followed by France, Brazil and India.

Taxonomic studies and inventories were most commonly performed with millipedes (43%), followed by earthworms (22%), and beetles (13%) (Figure 4, Table S6). Authors affiliated to Russia had the most publications

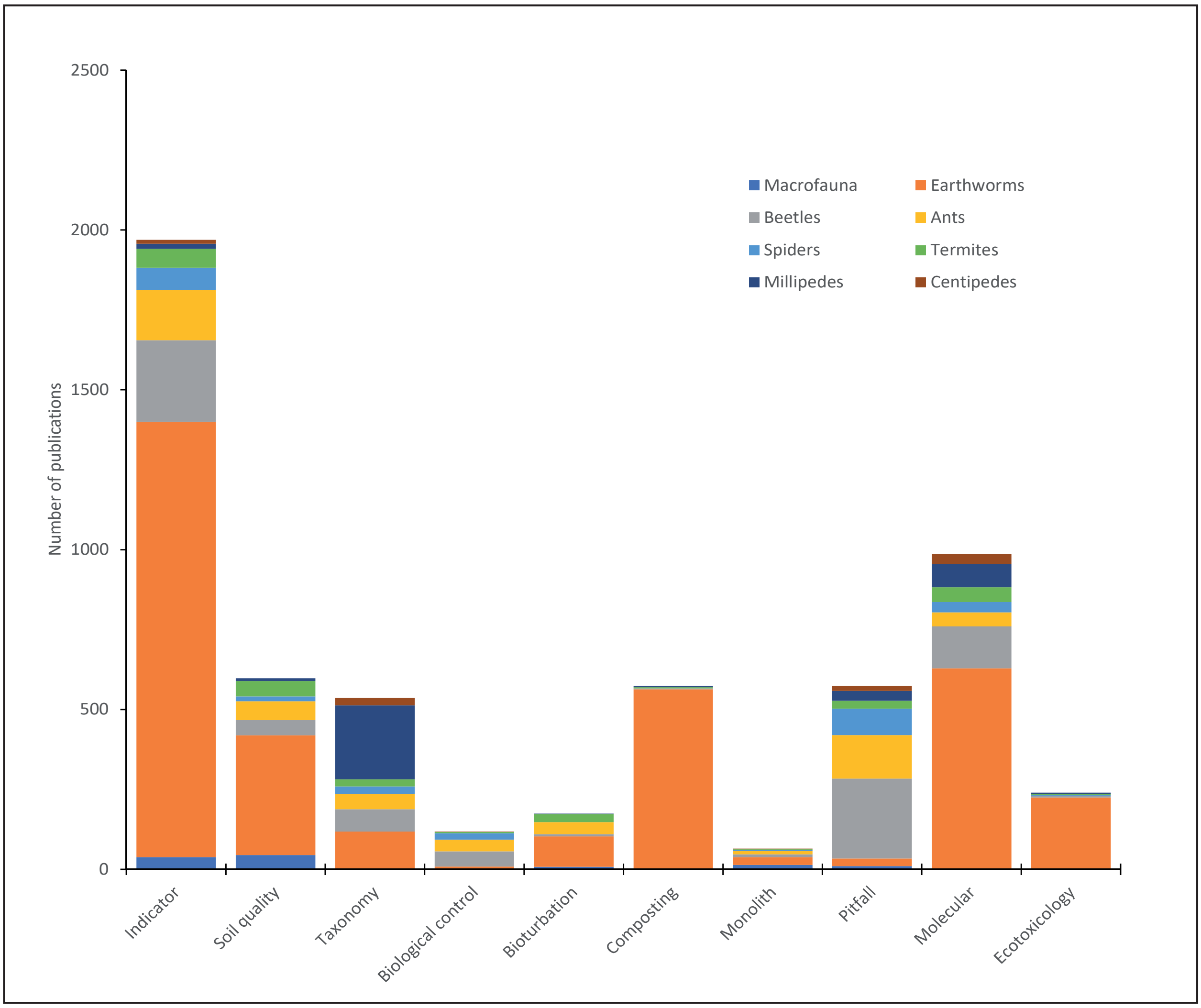


**Figure 4.** Number of publications on various applications and methods with eight soil macrofauna taxa (earthworms, beetles, ants, termites, millipedes, spiders, centipedes) and the overall macrofauna community recovered from the WoS between January 2011 and February 2022.

on taxonomy (120), followed by the USA (93), Denmark (51) and Brazil (48) (Figure 5). South Africa was the most prominent country in taxonomy in the African continent, although it ranked only 21st (19 articles) among the 73 publishing countries.

Analysis of the topic of biological control was difficult because many publications were on the control of herbivorous invertebrate pests rather than the use of macroinvertebrates as biological control agents. Beetles were the most mentioned in publications on this topic (40%), followed by ants (31%) and spiders (17%) (Figure 4, Table S7). Authors affiliated to the USA had the most publications on biological control with more than five times the number of articles compared to China (28) and Brazil (27) (Figure 5).

Soil macrofauna are also important for decomposing organic residues and in bioturbation, and publications on these topics were conducted from 57 and 44 countries, respectively. Bioturbation was mostly associated to earthworms (55%), but also to ants (22%), termites (14%), beetles (4%) (Figure 4, Table S8), with France and the USA as the countries with the most publications overall (41 and 34, respectively). On the other hand, publications on composting were more common than bioturbation and almost exclusively associated to earthworms (98%), with India and China publishing the most (181 and 114 publications, respectively), with 4 to 6 times more than the other countries (Figure 5, Table S9).

Regarding the methods used to study soil macrofauna, molecular approaches, including barcoding, sequencing, eDNA, -omics and genetics, were the most mentioned with publications from authors affiliated to 81 countries. China (265) and the USA (177) had the highest scientific output with 2-3 times more publications than some European countries and India (Figure 6, Table S10). Molecular approaches were mainly associated with earthworms (64%), followed by beetles (13%) and millipedes (8%) (Figure 4).

**Table 5.** Query keywords, number of retrieved publications and percentage of publications validated by checking manually whether the articles corresponded to the keyword topics.

| Query keywords | Publications | Validated |
|---|---|---|
| bioindicator or indicator or monitoring or pollution | 1,949 | 97.8% |
| soil health or soil quality or soil fertility | 865 | 99.3% |
| taxonomy or inventory | 1,264 | 97.9% |
| biological control | 527 | 78% |
| Bioturbation | 194 | 97.9% |
| Composting | 594 | 99.2% |
| TSBF* or monolith | 83 | 93% |
| Pitfall or Provid* or trap | 706 | 84% |
| DNA or sequencing or metabarcoding or barcoding or molecular technique | 1,560 | 95.3% |
| ecotoxicology or toxicology | 385 | 99.5% |

*TSBF is the abbreviation used for the Tropical Soil Biology and Fertility Programme of UNESCO, that developed a widely used method handbook for soil biology and fertility analysis in the tropics (Anderson & Ingram 1993); Provid is a technique similar to the pitfall traps developed by Antoniolli et al. (2006).

**Table 6.** Number of publications and countries of origin related to various potential uses of soil vertebrates, as recovered from the WoS searches from January 2014 to December 2023.

| Search terms used | Publications | Countries |
|---|---|---|
| soil health or soil quality or soil fertility | 551 | 79 |
| bioindicator or indicator or monitoring or pollution | 441 | 68 |
| education | 291 | 72 |
| pharmaceutical or antimicrobial or antibiotic or hormone or medic* | 132 | 40 |
| bioturbation | 61 | 28 |
| taxonomy or inventory | 48 | 50 |

Publications on pitfall traps came from authors affiliated to 124 countries and were mostly used in USA (701) and China (432), followed by Germany (274), Brazil (240) and the UK (239) (Figure 6, Table S12). South Africa (81) ranked only 13th overall. Beetles (44%), followed by ants (24%) and spiders (14%), were most frequently associated with pitfall traps (Figure 4). Soil monoliths, on the other hand, appeared associated to fewer countries (90) than the traps, being prevalent in Brazil (39), Colombia, France and USA (14) (Figure 6, Tables S11 and S12). The most sampled invertebrates with hand sorting of soil monoliths were earthworms (37%), and the overall macrofauna community (22%), followed by ants (15%) (Figure 4).


**Figure 5.** Worldwide distribution of the countries with authors publishing on macrofauna including bioindicators, soil quality, taxonomy, biological control, bioturbation and composting between 2011 and February, 2022 in WoS. The color intensity represents the increasing number of publication records, where blank is absence of records and darker colors refer to higher numbers.

Ecotoxicological studies were more commonly associated with authors affiliated to China (34 publications), followed by Brazil and the UK (28 and 27, respectively) (Figure 6, Table S13), and earthworms (94%) were the most studied soil invertebrate in this context (Figure 4). Most (70%) of the publications studied the earthworms of the genus *Eisenia*.

### 3.3 Soil vertebrate studies worldwide

A total of 3,432 publications dealt with vertebrate megafauna including authors from 115 countries overall (Figure 7; Table S2). Most of the publications were from institutions in the USA (399) and China (312), which together had >20% of all publications (Figure 7). Of the top 20 countries publishing most articles, ten were in Europe, while three were in Asia (China, Japan, India), two in Latin American and the Caribbean (Brazil, Argentina) and North America (USA, Canada), and only in the African continent (South Africa), in North Africa and the Near East (Iran), and in Oceania and the Pacific (Australia).

Considering the four main animal Classes (Table 2), most publications were on mammals (especially rodents and Eulipotyphla), followed by reptiles, amphibians and birds (Table 4). In reptiles, most publications were on snakes (442), while in Eulipotyphla, the vast majority were on moles (437), and together these two taxa represented more than 25% of all publications. All other taxa represented each less than 10% of all publications, with elephants, frogs, lizards and boars each representing around 6-8% of the total.

Most of the research on the soil megafauna was published in a biological and ecological context, with functions and uses receiving significant attention (Table 6). Their role in soil fertility, quality or health was most mentioned in publications (551), followed by their use as bioindicators (441), coming from 79 and 68 countries, respectively. Their use in educational activities

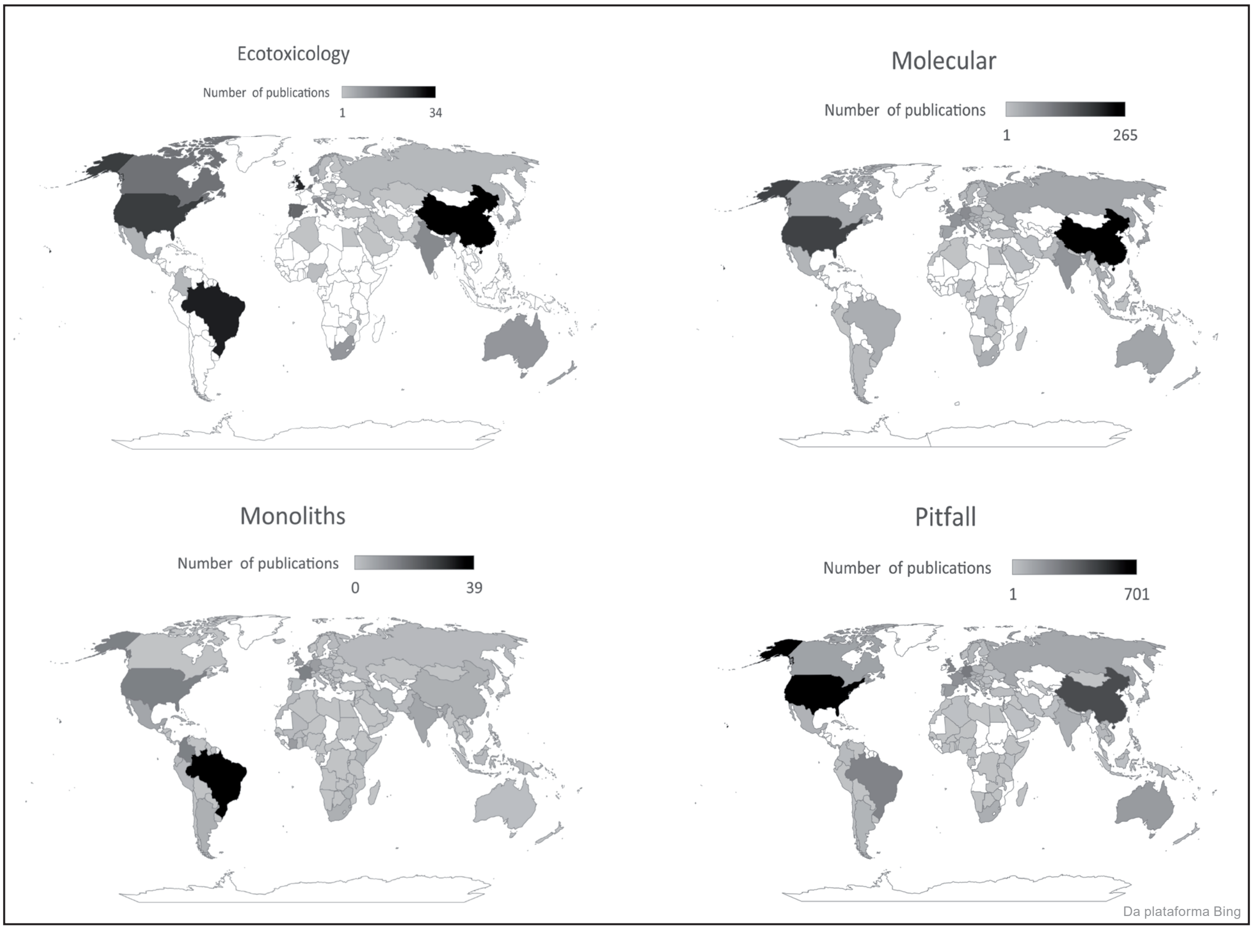


**Figure 6.** Worldwide distribution of the countries with authors publishing on methods for analyzing and studying macrofauna such as molecular and genetic approaches, sampling of soil monoliths/ TSBF, pitfall traps and ecotoxicological approaches, between January 2011 and February, 2022 in WoS. The color intensity represents the increasing number of publication records, where blank is absence of records and darker colors refer to higher numbers.

(291 articles) was also important and their use for pharmaceutical or medicinal purposes were also quite popular, while surprisingly, fewer publications were related to inventories or taxonomy or even bioturbation.

## 4. Discussion

### 4.1 Soil macrofauna research worldwide

Publications on the overall soil macrofauna community, or of a specific taxonomic group came from every continent except Antartica, but the expertise (expressed as publication numbers) was not evenly distributed. In the temperate region, expertise was concentrated in more developed countries such as in Canada and the USA, Europe and China, while in the tropical region, it was mainly in India, Brazil and Australia. Africa appeared as a major gap in publications on all topics related to soil macrofauna, except in South Africa where expertise was detected for several taxa and uses. There were 48 countries without records of studies on soil macrofauna and 21 countries with only one record, representing overall 35% of the world's countries. When compared to the FAO's Hunger map (https://www.fao.org/interactive/hunger-map-light/en/) the picture is inverted, with the number of publications lowest (or zero) in the countries with higher hunger index, mainly in Africa (12 countries). Similarly, within Oceania 12 countries lacked publications, and in the American continent 11 countries, mostly small ones (in surface area). Conversely in Asia and Europe seven and six countries, respectively, lacked publications. Therefore, any global monitoring scheme will require substantial efforts to reach out and build capacity for soil macroinvertebrate assessments in these countries.

Studies with macroinvertebrates as indicators of soil quality in an agricultural context were more frequent in major agricultural exporting countries like the USA, China, Brazil, India and France (Figure 6), but examples of the use of macroinvertebrates as indicators in soil quality assessment were found worldwide. For instance, Lavelle et al. (2022) analyzed the global data on macrofauna communities sampled under native vegetation and croplands worldwide using the hand sorting (TSBF) method, proving the usefulness of this technique in a wider monitoring program. In fact, the global initiative SoilBON has implemented a worldwide monitoring of soil invertebrate diversity including the TSBF sampling method in their design (Potapov et al. 2022). However, although more than ten thousand sites across the world have been sampled using this method

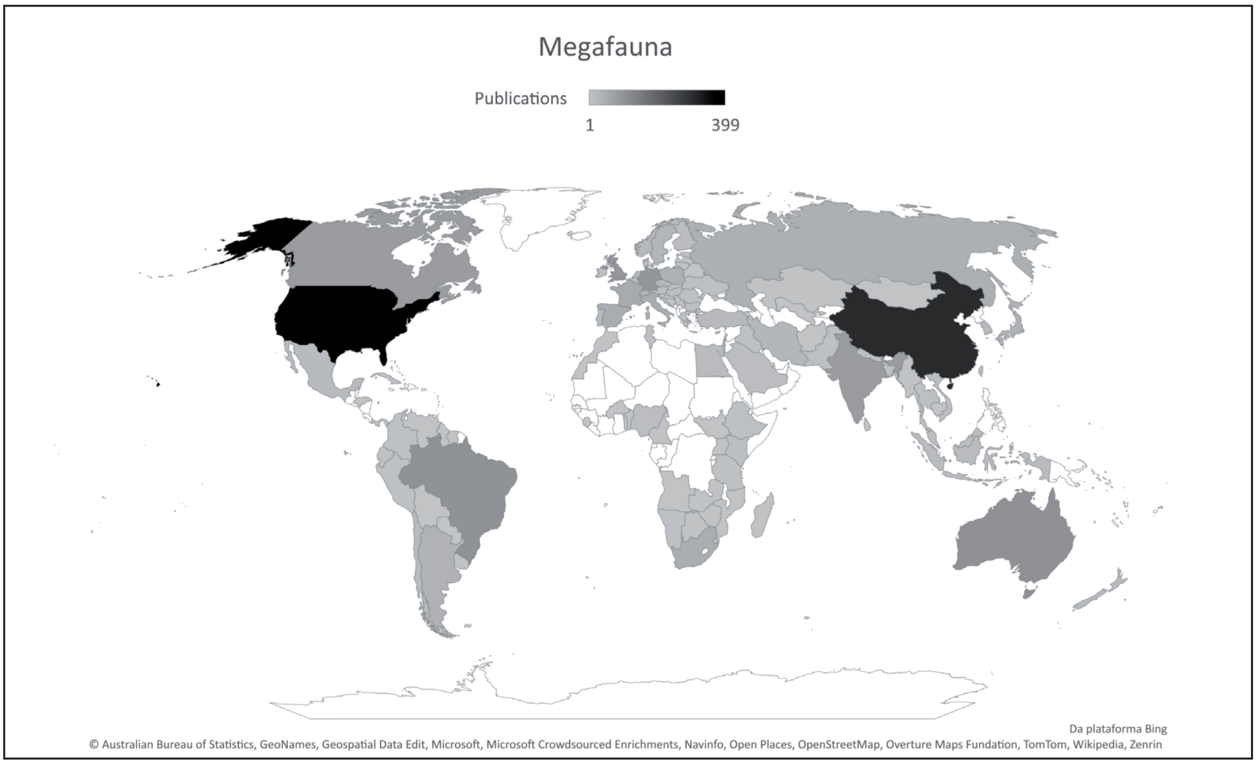


**Figure 7.** Worldwide distribution of the countries with publications on vertebrate soil bioturbating megafauna between January 2014 and December 2023. The color intensity represents the increasing number of publication records, where blank is absence of records.

(Mathieu et al. 2025), there is still low coverage in North Africa and the Near East, and in Western Asia as well as many Pacific islands confirming trends observed here, and highlighting the need for additional research on soil macroinvertebrates in these regions (Guerra et al. 2020).

Pitfall traps, a well consolidated technique to measure activity and populations of surface-active macroinvertebrates (Woodcock 2005) were more common worldwide (Hohbein & Conway 2018) than hand sorted soil monoliths (TSBF), agreeing with results of a recent online global soil biodiversity survey (Brown et al. this issue). Both methods are simple but only the monoliths have been internationally standardized so far (ISO 23611-5, 2011). Pitfall standardization was proposed by Brown & Matthews (2016) and Hohbein & Conway (2018), and represents an important step towards implementation of global monitoring schemes using this technique.

Of all the invertebrates evaluated, earthworms were the most studied, likely due to their multiple uses such as in ameliorating soil conditions (e.g., Cunha et al. 2016, Liu et al. 2019, Fonte et al. 2019), in soil restoration and remediation (e.g., Ratsiatosika et al. 2021, Xiao et al. 2022), environmental protection (e.g., Pelosi et al. 2014, Sanchez-Hernandez et al. 2020), in soil health assessments (e.g., Bünemann et al. 2018, Bartz et al. 2024) and as a supply of pharmacological/medical substances (Afreen & Aslaaf 2020). As observed by Xiang et al. (2015), China and the USA were the top publishing countries on earthworms, while India stood out in the tropical region. Several African countries, however, did not have any publications on earthworms, a phenomenon also observed for other invertebrates.

The release of noxious chemicals like pesticides, metals, pharmaceuticals, nanoparticles, microplastics, residues, wastes and others into the environment threatens soil biodiversity and its ecosystem functions (Wang et al. 2020, Beaumelle et al. 2021). In fact, ecotoxicological studies using macroinvertebrates have contributed greatly to the understanding of the impacts of these substances and materials on soils (Gunstone et al 2021, Pelosi et al. 2013). Expertise on soil ecotoxicology was higher in developing countries like China and Brazil (Duan et al. 2016, Niva et al. 2016), which was unexpected, although the analyses was restricted to macroinvertebrates. Interestingly, in a global survey, ecotoxicological methods were used only by a small part of the researchers studying macrofauna (13%) (Brown et al. this issue).

Despite the ecosystem services that beetles, ants and termites provide in natural and agricultural ecosystems, they are more often considered pests due to the herbivorous behavior of some species (Orgiazzi et al. 2016). In fact, the topic "biological control" used in the present analysis retrieved publications both on macroinvertebrates as pests and as agents of biological control. Furthermore, the validation rate of publications on the topic was comparatively low suggesting it was a tricky keyword (Table 5). Fewer publications on this topic compared to other uses agreed with the low proportion of respondents of a global survey (24%) studying soil fauna use in biological control (Brown et al. this issue). Almost half of the publications were on beetles, as predatory ground beetles have long been studied as biological control agents in agroecosystems (Cividanes 2021) and are also weed seed consumers (Kulkarni et al. 2015), while wireworms – larvae of click beetles - can be serious subterranean pests requiring control (Nikoukar & Rashed 2022).

Ants have beneficial and harmful effects (Diamé et al. 2017, Wills & Landis 2018, Pérez-Rodríguez et al. 2021, Anjos et al. 2022), and these social or eusocial insects, together with the termites are major soil bioturbators, moving soil to build nests, mounds and galleries which can change soil hydraulic properties (Kristensen et al. 2019, Viles et al. 2021). Dung beetles are also important bioturbators and soil engineers, though they do not impact the soil in the same way (Cheik et al. 2022). However, despite the importance of soil macrofauna for this ecological function, bioturbation studies with macroinvertebrates were few in number, and also were little studied (5%) by the respondents of a global survey (Brown et al. this issue), revealing an important research niche deserving further attention by the scientific community. Ironically, bioturbation studies have Charles Darwin as the precursor, who was convinced about the importance of soil biota for soil functioning (Feller et al. 2003). Despite that, the mechanisms underlying bioturbation and interactions with plant growth and soil biodiversity remains unclear (Meysmann et al. 2006).

Regarding composting, there was an outstanding number of publications on earthworms probably due to the widespread use of this animal in vermicompost production to improve soil fertility (Blouin et al. 2019) and to remediate contaminated soil (Poornima et al. 2024). Interestingly, Asian countries such as India, Malaysia and China had more publications on composting with soil macroinvertebrates than Western countries (Table S8). Considering the vast amounts of organic residues produced and improperly processed worldwide (UNEP 2021), enhancing composting, reuse and recycling of these wastes is a global priority, where earthworms and other soil fauna can play an important role.

Despite the importance of termites in recycling litter, our results showed a much lower expertise on these invertebrates worldwide when compared to earthworms, and more associated to temperate countries (Figure 3). In contrast, when litter consumption of soil fauna biomass was globally analyzed by Heděnec et al. (2022), soil fauna has been estimated to consume 48.6% of litter in a year, more in tropical and temperate regions than in arid or colder places, and higher in grasslands than forests. Earthworms and bioturbation were found to be more predominant in temperate biomes, while termites processed litter more in tropical and arid biomes. This information strongly suggests the need to enhance knowledge on termites in tropical and arid regions.

Millipedes, spiders and centipedes were the least studied macroinvertebrates among the groups analyzed, although millipedes stood out among these due to contributions from Russia, with a high number (75% of total) of publications by Golovatch and colleagues (e.g., Golovatch & Liu 2020). Millipedes are also useful as bioindicators (Tudose & Rîșnoveanu 2023) and in composting (Antunes et al. 2016). Centipedes were the least studied macroinvertebrate, though they are bioindicators of heavy metal bioaccumulation (Mitić et al. 2022) and have important pharmacological properties including antibacterial metabolites (Ali et al. 2019). Spiders were the third most frequently used macroinvertebrate in biological control, one of the two topics where earthworms were not at the top, although they are also useful bioindicators (Rosa et al. 2019). These relatively poorly explored uses of soil macrofauna taxa highlight the vast potential for additional studies on this untapped biological resource (Anderson 2009, Jiménez et al. 2001).

Finally, the use of molecular tools in soil macroinvertebrate studies was substantially high, surpassing publications on pitfall traps. Tools such as DNA metabarcoding have become increasingly popular to assess diversity and ecological patterns (Young & Hebert 2022, Zhu et al. 2020), though there are still many opportunities and challenges to improve their use with soil fauna (Recuero et al. 2024). Among these challenges are the reduction in analysis costs, the building of open reference libraries for identification, and the building of capacity and infrastructure in many countries that currently lack these resources.

### 4.2 Soil megafauna research worldwide

The number of publications (3,432) and countries (115) publishing on soil vertebrates was lower than for macroinvertebrates, although a similar geographic under-representation was observed, with Northern Africa and the Near East and many Pacific islands with no publications on the topic. As seen also with many macrofauna taxa, China, the USA and many European nations as well as Australia, Canada and Brazil were among the top 10 most publishing nations overall.

The scientific output related to the many vertebrate taxa tended to confirm results obtained in a recent global survey (Brown et al. this issue), where 81 respondents who worked with soil megafauna focused mostly on rodents, and around ¼ of them on birds or snakes. However, the inclusion of many other mammals (e.g., hogs, boars, peccaries, elephants, marsupials, carnivores), as well as additional reptiles (skinks, lizards, turtles) and amphibians (toads, frogs) in the present study greatly expanded the taxonomic range, number of contributions and authors worldwide working with soil bioturbating vertebrates.

Interestingly, the two mammals with the highest number of publications were moles that live permanently within the soil and elephants, that live solely above ground although both cause significant bioturbation, particularly in prairie or grassland soils (Questad and Foster 2007, Haynes 2012, Alexander et al. 2020). In fact, around one-half of all mammal species are at least partly (and many completely) fossorial (Voorhies 1975), and Table 2 lists 3,385 (51%) out of total of 6,611 species (Mammal Diversity Database 2024), though estimates for some taxa include all species, and not just burrowing ones, so estimates are slightly inflated.

Most (70%) of the soil mammal megafauna are fossorial rodents (2,357 species) that make burrows in the soil, and a considerable number of them spend a large part of their time within the soil, like mole-rats, voles, gophers and prairie dogs. Not surprisingly, over 500 publications were recovered in the searches considering all the rodent taxa. These ecosystem engineers can move considerable amounts of soil (commonly up to 25 $m^3$ $ha^{-1}$ $yr^{1}$; Übernickel et al. 2021), and their burrows frequently serve as nesting or resting sites or refugia for other animals (Übernickel et al. 2021). Tunnel lengths from 9 m for the East African root rat (Katandukila et al. 2014) up to 49 m for the South American tuco-tuco (Übernickel et al. 2021) were reported.

Most vertebrate taxa are also major players in the soil food chain by consuming large amounts of plant material or predating on other animals, although few above to below ground foodweb studies include soil and above-ground vertebrates (Setälä 2005, Potapov et al. 2024). This is clearly a research gap that must be filled, particularly considering a recent study (Potapov et al. 2024) surprisingly showing that most of the energy fluxes in rainforests were channeled in belowground food webs rather than in aboveground animal food webs. Furthermore, by moving large quantities of soil and depositing feces within the soil or on its surface, soil bioturbating vertebrates contribute both to soil physical changes and enhanced nutrient cycling (Meysmann et al. 2006, Platt et al. 2016). In fact, most studies on soil bioturbating vertebrates recovered in the WoS searches focused on their roles in soil health, fertility or quality, while bioturbation was not that common as a research topic, despite its importance for soil functioning and health.

Several carnivorous mammals dig into the soil to obtain food and for nesting (e.g., coyotes, foxes), and the badgers and weasels are known for being rather “feisty” or irritable, while the meerkats are known for their cooperative breeding and important burrowing behavior (Strandburg-Peshkin et al. 2020). However, the largest burrowing carnivores are the grizzly bears, known to collect insects, earthworms and other invertebrates for food (Sawyer et al. 2022). Less than 100 articles were recovered in WoS on carnivores, and although the searches originally included bears, the difficulty in separating out conflicting keywords with other meanings made it impractical to sort through the >17 thousand records on this taxon in the WoS. Although there are 8 known bear species (Mammal Diversity Database, 2024), only three of them are consistently major soil burrowers: the brown, grizzly and sloth bear, the latter of which is a major termite and ant forager that developed morphological adaptations for feeding on these insects (Joshi et al. 1997). The digging activities of these animals affect vegetation dynamics, nutrient cycling, and the populations of invertebrates and vertebrates that serve as their prey or that use their dens (Kurek et al. 2014, Conway 2018).

A considerable number of bird species (>250) are soil movers or fossorial (Voorhies 1975), using it mainly for nesting or protection (Orgiazzi et al. 2016), and affecting soil foodwebs by modifying the distribution of organic resources as well as topsoil physical and chemical (mainly by feces or guano deposition) properties (Smith et al. 2011, Peña-Lastra 2018, Otero et al. 2021). For instance, puffins developed strong beaks to dig holes in the soil for nesting (Badikova & Dzerzhinsky 2014), and ecosystem engineering lyre-birds can move an estimated 200ton $ha^{-1}$ of soil and surface litter per year (Ashton & Bassett 1997, Maisey et al. 2018). In fact, many species of seabirds like petrels, auks, and penguins can also be important ecosystem engineers, moving soil particularly for nesting purposes (Voorhies 1975, Smith et al. 2011). On the other hand, many burrowing owls, despite their name, tend to be more opportunistic users of burrows previously created by bioturbating mammals like ground squirrels, prairie dogs, badgers, skunks, foxes, coyotes, and armadillos (Conway 2018), rather than burrowers themselves. Despite their immense popularity and the large number of bird-watchers worldwide, scientific output on birds related to soils was not very high (<100 papers), indicating an important research gap related to avian impacts on soils.

In Australia and New Zealand, most rodents and many marsupials like bandicoots, bilbies, bettong, moles, potoroos, rat kangaroos, and wombats (Fleming et al. 2014), as well as kiwis (Jolly 1989), and echidnas (Clemente et al. 2016, Davies et al. 2019) are important soil bioturbators, threatened by land use and climate changes. Despite their importance as ecosystem engineers, and the fact that the loss of many of these digging animals in Australasia may lead to significant changes in ecosystem functioning (Fleming et al. 2014), there were relatively few publications on these animals (40 articles on mammals), highlighting the need for further research and conservation efforts in the region.

Considering the amphibians, caecilians are the ones that are mainly terrestrial and fossorial (only a few are aquatic), while most of the anurans and salamanders are aquatic, and only a few frogs or toads are bioturbators and the Urodela tend to mostly use burrows made by others (Voorhies 1975). Nevertheless, most of the publications recovered in the WoS were on the latter two taxa rather than on the caecilians, which is likely related to the number of specialists on these taxa worldwide. All these animals are important invertebrate predators and some are particularly useful in biocontrol of insect pests (e.g., frogs and salamanders; Hocking & Babbitt 2013, Tripathi et al. 2024). A few members of the Hylidae (tree-frogs) and Dicroglossidae (Forked-Tongue Frogs) families are burrowing species, particularly the 14 *Cyclorana* species in Australia (AmphibiaWeb 2024, Tracy et al. 2007) and the 10 *Sphaerotheca* species in SE Asia (Deepak et al. 2024). However, these are a minority, among the more than 1,000 species of the former family and >200 species in the latter (AmphibiaWeb 2024). Interestingly, some toad and frog species can spend many months buried in the soil, sometimes at great depths (>1 m) waiting for seasonal rains (Voorhies 1975) or for the soil to warm up in cold climates (Berman et al. 2023), while others in more humid environments move around considerably foraging mainly for insects like termites and ants (e.g., the Mexican burrowing toad; Trueb & Gans 1983).

Of all four megafauna classes evaluated, reptiles represented the one with the second most publications, and also the second most speciose (37% of all species), with snakes leading the scientific output and being the most biodiverse. In fact, many snakes burrow into the soil (particularly the asps), generally using reinforced trunk muscles and skull (Deufel 2017). The amphisbaenians, typically considered true soil burrowers (Martín et al. 2021) surprisingly had very few publications related with the soil. The lizards were the second taxon with the highest output, and many species dig burrows as refuge from harsh environmental conditions, from predators, or for nesting. Even the largest species in the world, the Komodo dragon and the monitor lizard are significant soil movers (Doody et al. 2021, Jessop et al 2004). Finally, the tortoises were the third reptile with the highest scientific output. These important ecosystem engineers (Kinlaw & Grasmueck 2012) include 47 terrestrial species creating burrows inhabited by up to more than 300 other vertebrate and invertebrate species (Jackson & Milstrey 1989).

The importance of wild boars, hogs, pigs and peccaries as invasive species or as ecosystem engineers (Beck et al. 2010, Risch et al. 2021) was evident from the relatively large number of publications retrieved on these ungulates overall (>350). These animals are avid invertebrate (and small vertebrate) predators (Coleman et al. 2001, Wilcox & van Vuren 2009), and invasive feral pigs (particularly *Sus scrofa*) ma be threatening endangered animal and plant species in native ecosystems worldwide, particularly on islands (Risch et al. 2021). Complex interactions were observed among soil disturbances caused by wild boar rooting, cattle raising activity and earthworm communities, particularly affecting endogeic worms (Bueno & Jimenez 2014). On the other hand, their wallowing, like that done by other ungulates like the bison, creates circular depressions in the landscape, that become water-ponds frequently used by other animals, particularly during the rainy season (Baruzzi & Krofel 2017). In native neotropical forests, peccary wallowing may be beneficial to certain amphibians (Beck et al. 2010), while in other ecosystems, invasive pigs may have mostly negative impacts (Marshall et al. 2020).

Many soil bioturbating vertebrates can be associated to human and veterinary health issues, like mole rats, a large number of small rodents, snakes, lizards, tortoises, salamanders, frogs, armadillos, and pangolins, due to their role as pest, parasite or disease carriers (e.g., Khatri-Chhetri et al. 2016, Scholz et al. 2016, Retief et al. 2017, Koeppel et al. 2021, Liu et al. 2023) They can also be potential sources of pharmaceuticals like anti-venoms, anti-coagulants, or anti-microbial substances (Hocking & Babbit 2013, Chen & Lu 2020, Assis et al. 2020, Vasconcelos et al. 2021), and useful for studies on gene inheritance, ageing, eyesight and skin regeneration (e.g., Braude et al. 2021). These potential uses were reflected in the results of the WoS searches (132 publications). Finally, the high number of publications related to education is likely related to the fact that many of these animals are easily visible, often quite charismatic, and many of them can be maintained in captivity.

It cannot be denied that the approach used in the present study is limited. The obligatory inclusion of the word soil in the abstract means that many publications that dealt with soil vertebrate and invertebrate animals may not have been included, particularly for some soil burrowing vertebrates that are not fossorial. This is further supported by the low number of results with the term bioturbation including vertebrates. A more in-depth review might be necessary, and should be undertaken in each country wishing to better assess the biodiversity, role and importance of these animals in their soils. Clearly, there are still many facets of these animals that remain to be elucidated concerning the world's soils, and it is likely that further research will reveal important unknown and unexplored species, functions in foodwebs and potential uses.

### 4.3 Database in PostgreSQL and customized queries

The present analysis using customized queries cannot be considered an accurate means of reviewing bibliography on particular topics, and is not a conventional bibliometric or scientometric analysis. It does not consider the citations or impact factors, but only the number of publications on a topic in each country considering all the authors' addresses, meaning that several countries can be affiliated to a single article. Nonetheless, this study allowed the analysis of thousands of publications, a task that would have been too tedious to perform manually. Some results might differ from other reviews at first sight because our focus was on the topics studied and the authors address (country) in each publication, which was limited only to journal articles in the period of 2011-2022 (macrofauna) and 2014-2023 (megafauna). For example, Lavelle et al. (2022) showed Colombia was the most prominent country considering the amount of sampling sites for macroinvertebrates using monoliths, but in the present work, Colombia figured in second place after Brazil, possibly because data from other types of publications (theses, book chapters, books) and other specific databases (Scielo, Scopus, etc.) were not used in the present analysis, as well as the strategy not based on sampling sites. In another case, Xiang et al. (2015) performed a scientometric study showing USA and China as the top countries publishing on earthworms, which agrees with our results because similar bibliographic data available in public platforms were used. On the other hand, in our analysis, Brazil appears in the 8th place while in Xiang et al. (2015) it does not appear in the ranking of the top 13 countries because different criteria and time-periods were used in their analysis. Hence, our results are limited by the tools and database (WoS) used, although they provide comparable estimates of the expertise on particular topics and taxa related to soil macro and megafauna present in a given country.

The data science tool used in the present work was also employed in other publications in this special issue (Correia et al., Jesus et al., Brown et al.). It proved efficient in estimating scientific output on specific topics and revealing country expertise based on the authors' addresses. Recent advances in analytical tools linked to the WoS platform, such as the InCities plugin from Clarivate Analytics, have enhanced bibliographic analysis of extracted data. This tool was used for the more recent soil megafauna data (2014-2023) and allowed the creation of global maps and better estimates of scientific output by country and topics, although more profound analyses were not performed here.

## 5. Conclusions

Macroinvertebrates and soil vertebrates are important natural resources in soils globally, with the former representing a large part of known and estimated biodiversity, and both moving massive amounts of soils, and often acting as ecosystem engineers. Their roles in global foodwebs and in soil quality, health or fertility assessment means that they are essential components of terrestrial ecosystems, contributing to ecosystem services and sustainable development goals. Nonetheless, our analysis revealed a globally unbalanced distribution of knowledge and research on these animals. First of all, the number of publications on taxonomy and inventories was insufficient given the vast diversity and potential numbers of undescribed species, particularly in the tropics and among macroinvertebrates. To date, a detailed global estimate of the richness of macrofauna species that inhabit the soil for at least part of their life cycle has not been undertaken, despite the recent estimates of Anthony et al. (2023). Clearly, further work on taxonomy and biology of macroinvertebrates is warranted. This knowledge will pave the way toward their conservation, sustainable use and monitoring of soil biodiversity worldwide.

Next, our global analysis of scientific publications revealed the geographic imbalance of knowledge on many taxa. Overall, the USA and China were the two countries with more expertise on soil macrofauna worldwide. Regionally, China and India lead in Asia, Australia in Oceania, Brazil in Latin America, South Africa in Africa and, in Europe, France, United Kingdom, Germany and Italy were generally within the top 10 depending on the topic, for both macrofauna and the soil burrowing vertebrates. There was an evident knowledge gap with few experts working in many countries in the African continent as well as from the Near East and many island nations throughout the world. These gaps must be taken into consideration for future efforts involving any global monitoring of soil animals, such as that proposed in the Global Soil Biodiversity Observatory (Parnell et al. this issue).

Earthworms were the most studied soil macroinvertebrate worldwide and mostly used as bioindicators, confirming the global importance and wider spread acceptance of this group for soil quality monitoring, due to its size, relative ease of capture and association with fertile soils by farmers globally. Pitfall traps were the most common sampling method for soil macrofauna while monoliths with hand-sorting were mainly used in South and North America. However, pitfall traps have not yet been standardized globally and would need to be so before they can be included in any global monitoring effort. Furthermore, sampling methods should consider specific conditions of the site. In places where hand sorting of soil monoliths are not appropriate, other methods should be applied, keeping in mind that pitfall traps will only trap surface-inhabiting animals, and not those living permanently in the soil, such as endogeic earthworms.

Of the many soil burrowing vertebrate taxa, snakes, moles, elephants and frogs were the ones with the highest number of publications, though this did not necessarily reflect their relative roles in soil bioturbation or in ecosystem engineering, but rather more likely their relative interest as a research topic (charisma), the number of specialists, and their multiple uses not fully associated with soils (pharmaceutical, etc.). The number of publications on some of the major bioturbators (Platt et al. 2016, Sun et al. 2021, Albertson et al. 2022) like armadillos, gophers, prairie dogs, mole-rats, tuco-tucos and ground-squirrels was not proportionate to the amount of soil displaced (Platt et al. 2016), highlighting the need for further efforts to understand the role of these important ecosystem engineers to soil functioning in natural and anthropically disturbed ecosystems.

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