Collembola: actors of soil life

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An unsuspected diversity of invertebrates swarms under our feet when we walk on the ground in a forest, meadow or garden. Invisible communities are active in the soil as in a parallel world, with the difference that this world is very real and well connected to the above ground level. It is indeed essential to plants that grow above it. Among the invertebrates living in the soil, Collembola (or springtails) are important because of their abundance and therefore their ability to impact the functioning of an entire ecosystem. They have a wide variety of forms and live in a wide variety of habitats. Their main role is to regulate the microorganisms responsible for the decomposition of organic matter and the recycling of nutrients that will be used by plants for their development. Unfortunately, many human activities can affect the communities of Collembola. These include, for example, soil pollution by metals, pesticides, etc., but also human practices such as the introduction of exotic plants or the use of waste to fertilize the soil.

1. Soil invertebrates, shadow workers

	Invertebrates	Size	Abundance	Diet
Macrofauna	Earthworms Millipedes Centipedes Spiders Isopods Gastropods Beetle larvae Diptera larvae Other insects	L : 4 to 80 mm ⌀ : 2 to 20 mm	100 to 1000 ind./m^2	Carnivorous Saprophagous Microphagous less common
Mesofauna	Mites Springtails Enchytraeids Protura	0,2 to 4 mm	10 000 to 100 000 ind./m^2	Microphagous, saprophagous, or carnivorous
Microfauna	Protozoan Rotifers Nematodes Tardigrades	4 to 200 µm	in the order of 1 000 000 ind./m^2	Microphagous dominant

Table 1.Invertebrates, sizes, abundances (in a temperate meadow) and dominant diets in each of the three soil fauna size classes. Ind.: individuals; L: length; ø: diameter. Saprophagous: a diet consisting of dead organic matter of plant or animal origin. Carnivory: a diet consisting of live animals. Microphagous: a diet consisting of bacteria, fungi and/or unicellular algae. [Source: From Gobat et al. [1]]

An incredible diversity exists in the soil, under our feet without us even suspecting it. Indeed, most of the major zoological branches are represented in soil fauna. There is a wide variety of sizes and shapes, from protozoa, the smallest animal organisms, to earthworms, which are among the largest individuals (Table 1). Soil invertebrates are classified into three categories according to their size and role: microfauna (4 to 200 µm long), mesofauna (0.2 to 4 mm long) and macrofauna (4 to 80 mm long) (Table 1).

From the point of view of general ecological characteristics, macrofauna and mesofauna invertebrates have **terrestrial life**. Small white grubs, cousins of earthworms, potworms, have an **aquatic life** - like microfauna invertebrates - because they live in the water retained in the pores of the soil. These invertebrates have developed strategies to resist dryness in dry periods such as slowed life or encysting.

The major role of soil fauna is to contribute to the **decomposition** and **mineralization of organic matter**, thus ensuring the **circulation of nutrients** (nitrogen, phosphorus, potassium, etc...) and their availability for plant development at the surface. **Soil structuring** is another fundamental action of soil invertebrates.

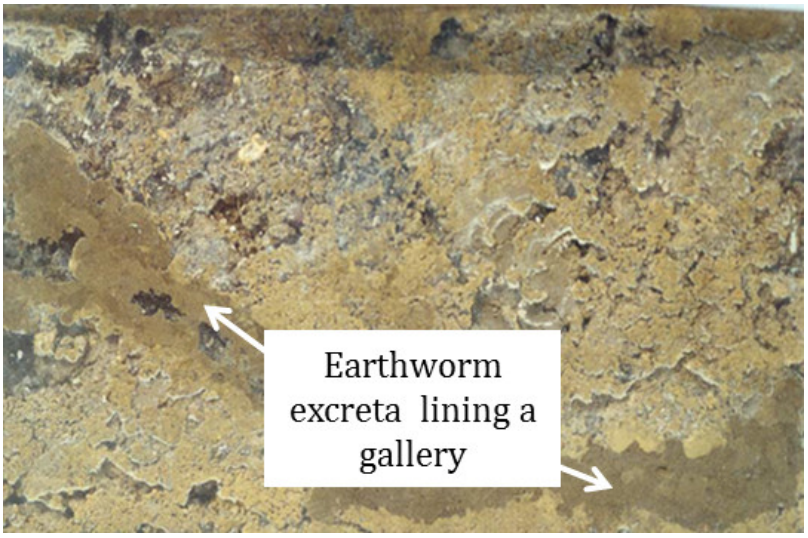

Figure 1. Ejecta lining a gallery of the anecic earthworm Aporrectodea giardi in an experimental device. These excreta are made up of an intimate and stable mixture of organic and mineral matter. This photo also indicates the burial of organic matter because the excreta are darker in colour, and therefore richer in organic matter than the horizon in which they are found. [Source: photo © Sandrine Salmon]

Some earthworms live deep but rise to the soil surface to feed on litter (earthworms belonging to the anecic category). To a lesser extent, some macroarthropods (termites, diplopods) bury organic matter at depth (Figure 1). They also contribute to the formation of stable aggregates by mixing the fragmented and more or less decomposed organic matter with the mineral matter in

their digestive tract. These earthworm species also create a huge network of galleries, which can increase the macroporosity of soils{ind-text}Percentage of soil pores larger than 50 µm.{end-tooltip} from 20 to 100%.

All these activities facilitate the circulation of water and air in the soil. They thus improve the water regime and soil aeration. They also stabilize its structure, which is generally beneficial to plants.

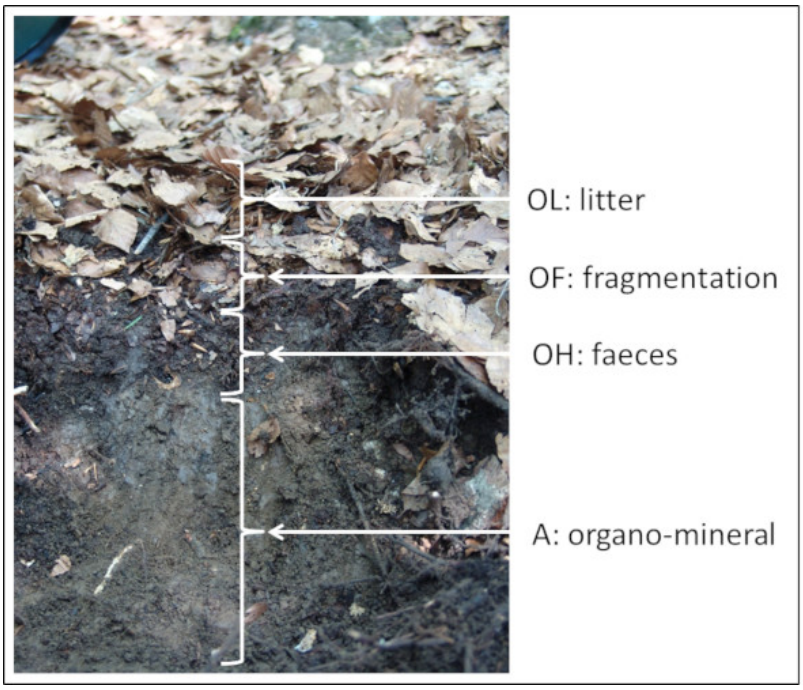

Figure 2. Soil profile in a beech forest in the Pyrenees showing the different horizons containing organic matter (humus). [Source: photo © Sandrine Salmon]

The action of anecic earthworms on soil structure and properties is remarkable and often results in the formation of a single horizon{end-text}Soil layer, homogeneous and parallel to the surface. A horizon is described according to various physico-chemical criteria: thickness, particle size composition (clays, silts, sands, stones), degree of alteration of the bedrock, acidity{end-tooltip} of humus (*i.e.* a single layer): the organo-mineral horizon "A", consisting of their excreta and galleries. Nevertheless, the action of other invertebrates (Enchytraeidae and arthropods) is particularly useful and visible in soils without this category of earthworm, generally acid soils. It can then be observed that the humus layer consists of different horizons: litter (OL), fragmented litter (OF), invertebrate faeces layer (OH), organo-mineral horizon (A) (Figure 2).

In the following sections we will get to know one of these wildlife groups, the Collembola. Like mites, Collembola (or springtails) are small arthropods that are very abundant in the soil. They contribute to the functioning of terrestrial ecosystems. However, unlike mites or earthworms, their names are generally unknown to the general public.

2. Collembola, a diversity of forms and habitats

Figure 3. Photo of a Collembola (Desoria sp., Isotomidae) showing the furca, a jumping organ, and the ventral tube, involved in water and ion regulation. [Source: photo © Sandrine Salmon]

Collembola appeared very early in the evolutionary history of living organisms, 400 million years ago, before insects. Like insects, they have three pairs of legs (hence the name hexapods) but unlike insects, they are Entognaths, *i.e.* their mouth parts are hidden inside a cavity, moreover they are without wings. They also have several specific organs that are essential in their interactions with the environment (Figure 3):

the *furca*, which is a jumping element operating as a spring lever;

the *ventral tube* that allows them to regulate their ionic and hydric balance by absorbing water from the soil with the ions it contains.

There are four orders of Collembola that differ in morphology:

Entomobryomorpha (cylindrical body, segmented with long appendages);

Poduromorpha (cylindrical body, segmented, with short appendages);

Symphypleona (spherical bodies with long appendages);

Neelipleona (spherical bodies with short antennas);

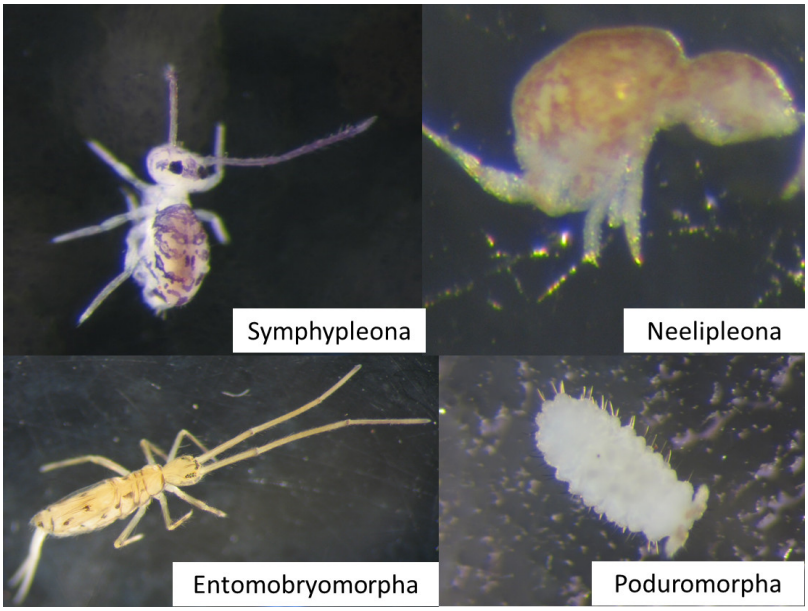

Figure 4. The four orders of Collembola: Symphypleona, Neelipleona, Entomobryomorpha, Poduromorpha. [Source: photos © Sandrine Salmon]

The **number of** Collembola **species** discovered in the world and described to date is **8600** [2] but there are still many more to be discovered. Collembola are, along with mites, the main representatives of microarthropods in the soil. There are *10,000 to 100,000 in a square metre of soil*. While they are most abundant in the soil, they are also found in many other environments: the herbaceous stratum, canopy in tropical regions, coastal sands, caves, on the surface of ponds, and even on the frozen ground of Antarctica [3]. In the soil, species are distributed from the surface to all layers containing organic matter.

Collembola species have **morphological and physiological adaptations to habitat depth and closure**:

Large, pigmented species with highly developed locomotor organs (legs, furca; e.g. Entomobryomorpha, Figure 4) and sensory organs sensitive to air (sensory silk) and light (eyes) are selected in open environments (e.g. meadow) and on the soil surface [4].

In the forest, and at depth in the soil, small, blind, unpigmented or poorly pigmented species with small locomotor appendages dominate (e. g. Poduromorph, Figure 4). The latter often also have a particular sensory organ, sensitive to chemical molecules, the post-antennal organ that compensates for the absence of other sensory organs.

Most species feed on microorganisms (fungi, terrestrial microalgae, bacteria), most often fungal filaments. Others consume dead plant organs, or excreta from other invertebrates. Others pierce the walls of plants and fungi and suck up the liquids they contain. Finally, a very small proportion is predatory of Nematodes, Rotifers, Tardigrades or other Collembola. It is essentially through their **trophic activity**, *i.e.* their search for and consumption of food, that **Collembola will perform different functions in the soil** and this is what we will discover in the following section.

3. Collembola, small but active

Like most soil wildlife stakeholders, Collembola have a direct and indirect effect on the **decomposition of organic matter and the recycling of nutrients**.

Some species, by consuming dead plant organs (leaves, root needles, etc.), or excreta from other invertebrates, contribute to the fragmentation of dead plant matter and the mineralization of organic matter, as well as to the **surface structure of the soil** (OF and OH layers of humus, see Figure 2).

However, a larger part of the fragmentation of dead plant organs is exerted by macrofauna, and mineralization is largely (70-80%) provided by microorganisms. It is therefore mainly **indirectly** that the activity of collembola on the mineralization of organic matter and the recycling of nutrients will be carried out, **by regulating soil microorganisms** (bacteria and fungi):

By consuming microorganisms in a moderate way, Collembola **stimulate the growth of their populations** and consequently the mineralization of organic matter. But depending on the species present, the filaments of the fungi can be consumed in excess by Collembola, thus preventing the excessive development of certain species, in particular pathogenic fungi.

Figure 5. Heteromurus nitidus (Entomobryomorpha, Entomobryidae) with bristles on the body capable of fixing and transporting fungal spores. [Source: Photo © Sandrine Salmon]

Collembola also **spread** fungal spores and bacteria, either through their intestinal transit or by attaching them to the body's bristles (Figure 5).

Finally, their faecal pellets provide a **favourable habitat for** the development of microorganisms.

By consuming phytopathogenic fungi, Collembola can limit fungal diseases in plants [5]. By stimulating the development and activity of mycorrhizal fungi, they can also promote the absorption of phosphorus by cultivated plants or regulate the root architecture of certain plants.

Finally, although the activity of springtails is generally beneficial to humans and crops, it is important to note the existence of two species considered harmful because they consume cultivated plants (usually alfalfa and clover seedlings). These are *Sminthurus viridis* and *Bourletiella hortensis*. But *Sminthurus viridis*, originated from Europe, is mainly a pest in alfalfa crops in Australia, where it has been accidentally introduced by humans and where it probably does not have a predator [3].

4. How do human activities disrupt Collembola?

The anthropogenic disturbances that can affect springtail communities are so diverse and varied that not all of them can be addressed in this article. Most often, it concerns soil contamination by pollutants such as metals in high concentrations, pesticides, polycyclic aromatic hydrocarbons (PAHs).... Human practices such as the introduction of exotic plants into a country, the use of waste to fertilize the soil, soil compaction or forest fragmentation can also be harmful, not to mention of course the destruction of soil caused by urbanization. And no! Collembola don't live in concrete!

4.1. Effect of metals

Soils polluted by metals are very diverse. Examples include former marshalling yards (cadmium, copper, nickel, lead, zinc), former foundries (iron, zinc, cadmium, copper) or former mines (silver, lead, zinc...) [6], but also agricultural soils (copper) [7] or urban parks (cadmium from road traffic). Soil pollution by high concentrations of metals can reduce the abundance and diversity of springtails. In all cases, it modifies communities, *i.e.* **the species usually present are replaced by others**. This generally results, at the regional scale, in a **high degree of homogenization** of communities, which are then dominated by a small number of metal-tolerant species. The risk of this homogenization of communities is the loss of biodiversity at the regional scale.

4.2. Effects of waste

The use of organic waste can be very beneficial for fertilizing agricultural soils, forest plantations or for the remediation of degraded soils. This type of amendment improves soil structure and water retention, and increases the concentration of nutrients and organic matter. This waste can be either agricultural waste of plant (compost) or animal (manure) origin, sludge from sewage treatment plants or waste of industrial origin, or a mixture of these various wastes. The problem is that these wastes can ultimately prove to be unfavourable to communities of springtails, or even very harmful since they can **greatly reduce the abundance of certain species and their reproduction rate**. They often have metal or ammonium concentrations high enough

to become toxic, even when metal levels are below legal standards [8].

4.3. Effect of pesticides

Collembola are often the object of collateral damage resulting from the treatment of crops with insecticides to eradicate insect pests. Thus, it has already been shown that the application of insecticides to fields in conventional agriculture causes a decrease in the abundance and diversity of Collembola. There is also a **change in community structure** due to the fact that some species are more sensitive than others [9]. A study of the features of collembola (eye development, furca, antennae, pigmentation and silks) showed that **species adapted to depth are the most vulnerable**. This is probably because these species cannot escape their environment when treatments are applied, unlike surface species that can gain refuge and then return. It should also be noted that **compaction of agricultural soils** can be as **harmful to** soil invertebrates as insecticide pollution.

4.4. Effects of "alien" plant species

A species is said to be **exotic when it is observed in a geographical area from which it does not originate, unlike native plants** (see When invasive plants also wander in the fields)**. Alien species are generally introduced by humans into a geographical area that is not part of their natural range**. These species have therefore not co-evolved with other species that inhabit the same environment, which can cause a disruption of the ecosystem where they are introduced. For example, they can cause local extinction of native species. The invasion of a habitat by exotic plant species has already shown significant effects on soil characteristics such as a change in the quantity and quality of organic matter [10].

They can also directly impact animal communities in the soil. Thus, the planting of Eucalyptus to replace Oaks in Portugal **has led to a decrease in the species richness of Collembola and the replacement of specialist species by generalist species** capable of colonising a large number of environments. The planting of *Pinus radiata* in Australia [11] has also resulted in the replacement of several native springtail species with exotic springtails.

4.5. Consequences of the homogenization of communities and the decrease in specific wealth

All these factors that alter springtails communities are also harmful to other soil invertebrate groups.

When the abundance and/or diversity of fauna decreases, it can no longer properly perform its functions such as nutrient recycling or pathogen regulation (see section 3). Indeed, the functions performed by soil organisms are spread over a large number of species. When several species disappear, the functions that these species used to perform are no longer performed. This can affect the functioning of the ecosystem. For example, if nutrient recycling is not done properly, it becomes difficult for plants to grow on the surface, which ultimately leads to soil erosion.

Also, the replacement of local species by generalist species and the resulting large-scale homogenization of communities alter the resistance and resilience of ecosystems (see What is Biodiversity?). In other words, in the event of a disturbance of the ecosystem, it will not be able to resist or return to its original state. Let us take as an example of disruption the arrival of a phytopathogenic fungus. If the fungivorous species that feed on this fungus have disappeared from the ecosystem, its development is no longer regulated, and the plant species attacked can be completely decimated.

Consequently, we must protect our soils by limiting urbanization, pollution (by pesticides, excess fertilizers, waste, metals), and soil compaction (by deep and intense ploughing or skidding equipment).

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References and notes

Cover image. Two specimens of Caledonimeria mirabilis, a species of collembola endemic to New Caledonia. [Source: Photo © Cyrille d'Haese]

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