

THE FUNCTIONAL GROUPS OF INVERTEBRATES ACCORDING TO THEIR TROPHIC PREFERENCE

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Abstract. Soil species of invertebrates interact differently with their environment. The feeding mode is one of the most important relationships between organisms, and its quality and distribution shape the structure of soil food webs. The soil food web model analysis is a useful approach for understanding nutrient cycling and energy flows between soil communities, as well as establishing relationships between soil food web dynamics and ecosystem stability. Soil mesofauna and macrofauna break down dead organic matter into smaller pieces thereby increasing the surface area for decomposition and facilitate decomposition by soil bacteria and fungi that begin mineralizing organic nutrient forms into inorganic nutrients essential for plant growth. Depending on the trophic preference, the species are divided into trophic groups: microbivores (nematodes, collembola, mites that feed on microorganisms: fungi, algae, bacteria), herbivores (nematode species, collembola, some mites that feed on plant material), omnivores (nematode species, collembola, some mites that increase connectivity in food webs because they feed on multiple resources), predators (do not change soil structure or plant productivity directly, but have an indirect effect on ecosystem functions through the impact on populations of other organisms), detritivores (most soil species are part of the decomposition process by feeding on dead organic matter (detritus)). Species that feed on similar resources are functionally equivalent, that is, they exert similar top-down forces on their prey. A large diversity of soil ecological niches, both in size and in the range of provided resources, leads to significant functional differentiation of subterranean soil invertebrates. This differentiation leads to changes in the trophic network, so changes in the rhizosphere, in the structure of the vegetal carpet, thus there are changes in the provided ecosystem services (including in the food provided by certain agricultural crops).

Keywords: soil invertebrates, trophic preferences, trophic food webs.

Rezumat. Grupele funcționale de nevertebrate în funcție de preferințele trofice. Speciile de nevertebrate din sol interacționează diferit cu mediul lor de viață. Modul de hrănire este printre cele mai importante relații dintre organisme, iar calitatea și distribuția sa modelează structura rețelelor trofice ale solului. Analiza modelului rețelei trofice a solului este o abordare utilă pentru înțelegerea ciclului nutrienților și a fluxurilor de energie între comunitățile de sol. Fauna de sol are rolul de a descompune materia organică moartă în bucăți mai mici, crescând astfel suprafața de descompunere și facilitând descompunerea de către bacteriile și ciupercile din sol care încep să mineralizeze formele de nutrienți organici în nutrienți anorganici esențiali pentru creșterea plantelor. În funcție de preferințele trofice, speciile sunt împărțite în grupe trofice: microbivore (nematode, collembole, acarieni care se hrănesc cu microorganisme: ciuperci, alge, bacterii), ierbivore (specii de nematode, collembole, unii acarieni care se hrănesc cu material vegetal), omnivore (specii de nematode, collembole, unii acarieni care cresc conectivitatea în rețelele trofice pentru că se hrănesc cu resurse multiple), prădători (nu modifică direct structura solului sau productivitatea plantelor, dar au un efect indirect asupra funcțiilor ecosistemului prin impactul asupra populațiilor altor organisme), detritivore (majoritatea speciilor de sol fac parte din procesul de descompunere prin hrănirea cu materie organică moartă (detritus)). Speciile care se hrănesc cu resurse similare sunt echivalente din punct de vedere funcțional, adică exercită forțe similare de sus în jos asupra pradei lor. O mare diversitate a nișelor ecologice ale solului duce la o diferențiere funcțională semnificativă a nevertebratelor din sol. Această diferențiere duce la modificări în rețeaua trofică, deci modificări în rizosferă, în structura covorului vegetal, astfel apar modificări în serviciile ecosistemice oferite.

Cuvinte cheie: nevertebrate din sol, rețeaua trofică, preferințe trofice.

INTRODUCTION

Functional traits are morphological, biochemical, physiological, structural, phenological or behavioral characteristics of organisms that influence their life cycle. The grouping of species in relation to their common functional characteristics is an idea that dates back a long time (CLEMENTS, 1916; GLEASON 1926), but is still widely used in ecology studies (LALIBERTE' et al., 2012; NOCK et al., 2016).

Invertebrates play crucial roles in soil matter and energy cycles. Some of them are consumers of primary producers (e.g. herbivores, fungivores, granivores) and the remains of other plant and animal species (they feed on fallen leaves on the ground, the excretions of other species or even their bodies after death). They are also food for higher trophic levels (predators, parasites and parasitoids) and are recognized as ecosystem engineers (MANU, 2011). Therefore, knowledge of the functional traits of invertebrates is key to understanding multitrophic processes and ecosystem functioning. Information in current databases on invertebrate functional traits is often obtained from studies and observations, with no uniform methodology chosen for measurements. Furthermore, functional traits such as species temperature tolerance and drought resistance are often missing or inferred from the abiotic conditions of the habitats in which they were observed and not directly measured on individuals (MORETTI et al., 2017). To be able to work with the immense diversity of invertebrates, soil biologists have classified them into guilds or organisms that have similar trophic niche requirements. They are also called functional groups because they have similar ecological functions.

Trophic interactions shape most of the ecosystem services provided by the soil (carbon sequestration, nutrient cycling, biological control, etc.). These ecological processes that take place in the soil support the growth of plants and

their health, they also support above-ground biodiversity, but also the stability and resilience of ecosystems. By modeling energy flows and the transfer of nutrients between soil organisms, we can better understand the relationship between trophic groups and the functioning of ecosystems (LE GUILLARME et al., 2023). To know the ecosystem services provided by soil invertebrates, the first step is to discuss the trophic preference of the main invertebrate functional groups.

The environment is the main aspect that shapes the interactions between species. It also has a major impact on how they feed. Trophic interactions are essential relationships between species because food quality and quantity shape the structure of soil food webs (KUMAR et al., 2021). Knowing the structure of feeding relationships between invertebrate functional groups, we can have some information about the ecosystem services provided by these soil organisms. For example, by analyzing the soil food web model we obtain information about nutrient cycling and energy flow between soil communities. We can also link soil food chain dynamics to ecosystem stability. Soil has three phases: solid (soil matrix), liquid (soil water with dissolved substances) and gas (air in soil pores). As an adaptation to these properties, soil invertebrates have developed a dual nature combining the characteristics of terrestrial and aquatic species. These include high integumental permeability, skin respiration, relatively low resistance to cold, reduced sensitivity to high concentrations of carbon dioxide, saprophagy like aquatic animals. For many species of terrestrial invertebrates, soil is a transitional environment during their evolution (WOLTERS, 1991). Soil invertebrates intervene in soil processes and properties through several activities: incorporation (physico-chemical modification through processes of digestion and synthesis of body tissue), transport (defecation, excretion of body substance) and restructuring (change of environment caused by feeding and movement, but also by the secretion of enzymes or mucus). These simple basic activities can lead to extremely different effects, depending on species-specific and environmental characteristics (WOLTERS, 1991).

Soil mesofauna and macrofauna have the role of breaking down dead organic matter into smaller pieces thus increasing the decomposition surface and facilitating decomposition by soil bacteria and fungi that begin mineralizing organic nutrient forms into inorganic nutrients essential for plant growth. The consequence of this process is that soil fauna regulates microbial populations. Mineralization continues with the action of organisms such as protozoa and nematodes that feed on bacteria and fungi (BARRIOS, 2007). For the proper functioning of underground systems, trophic interactions are very important.

They are considered by most scientists to be key factors in biogeochemical cycles. Trophic interactions play a major role in litter decomposition and C and N cycling (ERKTAN et al., 2020). Feeding relationships include several categories: predator-prey (CHASE et al., 2002), between species that use the same resource, mutualism - where two organisms benefit from each other (plants and mycorrhizal fungi) (NEHER & BARBERCHECK, 1998; STRECKER, 2021), symbiosis and others. The concept of a food web refers to a map of feeding relationships between species in which energy flows and dynamics are highlighted (DE RUITER et al., 2005). Trophic level represents the energy flow that occurs when an organism feeds on another organism (WALTER et al., 1991; NEHER, 2010; NGUYEN et al., 2022). The structure of trophic interactions determines the sensitivity of food webs to perturbations, but rigorous assessments of the effects of plant diversity on network topology are lacking (GILING et al., 2019).

The trophic network is also known under the definition of an ecological network with nodes represented by the species in the ecosystem and where the links are of the prey-predator type. The direction of the connection represents where the energy comes from and where it goes (ROONEY & McCANN, 2012; LAYMAN et al., 2015). This network illustrates the complete architecture of the ecosystem functioning as a whole (CONTI et al., 2020). Research on the relationship between plants and soil invertebrates has shifted to a more practical approach that uses species functional characteristics and food web characteristics related to the provision of ecosystem services (MARIOTTE et al., 2018). An important step included in this approach is the emphasis on energy flow between species in the food web (building an energy flow network) (SCHEU, 2002).

This energy flow provides information about control between species (e.g. in the case of the prey-predator relationship). Some invertebrate species have a flexible diet. For example, in the conditions of urban agglomerations, food options decrease significantly, the adaptation possibilities for most species disappear, which in the absence of flexibility could lead to a decrease in the number of species in urban ecosystems (KOROLEV & BRYGADYRENKO, 2014). Invertebrate abundance and biomass are correlated with soil volume and decrease from bottom to top in the food web. Unlike surface networks, soil networks are both longer and more complex (NEHER, 2001). In communities with a large number of species as in the case of those in the soil, the formation of trophic groups is very likely (SCHEU, 2002).

The aim of this work was to create a synthesis of the literature that includes information from part of the articles published on the topic of trophic relationships that are established within the different functional groups of soil invertebrates.

MATERIALS AND METHODS

The method of carrying out this work included several stages. Initially, keywords were established that were closely related to the topic addressed, namely: soil invertebrates, invertebrate trophic preferences, soil trophic networks. With the help of these words, databases with free access to scientific papers were queried. An Excel database was then created containing the information detailed from the content of these works and based on it this literature review was carried out.

RESULTS AND DISCUSSION

Placing a species accurately in a particular trophic category is difficult (SCHEU, 2002), because, depending on what resources are available, some invertebrates may vary their food choice from algae to fungi, detritus or other invertebrate species (SCHEU, 2002; MANU et al., 2013). Plant species and organic wastes provide habitat for subterranean invertebrates. They have a great influence on the soil biota directly (supply of organic matter (WOLTERS, 2000)) and indirectly (shading, soil protection, water and nutrient supply) (NEHER, 2001). A great diversity of species is found in soil interconnected by trophic links that form complex food webs (BROSE & SCHEU, 2014; ERKTAN et al., 2020). The food web structure contains several trophic groups namely: primary producers, consumers and detritivores.

Mesofauna is found at all levels of the food web and directly influences both primary production (by providing plants with organic matter resulting from shredding) and indirectly through their contribution to the decomposition and mineralization of nutrients (NEHER, 2001). Soil organisms play an important role in aboveground community dynamics and in the functioning of the terrestrial ecosystem. However, most studies have considered soil biota as a black box or focused on specific groups, while little is known about soil food webs (MORRIËN et al., 2017). Depending on the trophic preference (NEHER and BARBERCHECK, 1998; STRECKER, 2021), the species are divided into trophic groups: microbivores (they feed on microorganisms: fungi, algae and bacteria).

This category includes species of nematodes, collembola, mites (NEHER & BARBERCHECK, 1998; SCHNEIDER & MARAUN, 2004); herbivores (they feed on plant material, namely some nematode species, collembola, some mites) (NEHER & BARBERCHECK, 1998); omnivores (increase the degree of connectivity in food webs because they feed on more resources (OGITA et al., 2021); predators (some species can be both predator and prey, do not change soil structure or plant productivity directly, but have an indirect effect on ecosystem functions by impacting the populations of other organisms (MANU et al., 2013); detritivores (most soil species are part of the decaying food web, according to their trophic group, soil organisms function as primary decomposers by feeding predominantly with dead organic matter (detritus)) (STRECKER, 2021).

This classification implies that several species feed on similar resources, thus being functionally equivalent, that is, they exert similar top-down forces on their prey. The concept of trophic groups simplifies the structure of food webs. In soil ecology, the use of the trophic group concept is useful due to the high diversity of soil species (STRECKER, 2021). Another result identified following the critical analysis of the specialized literature is that the same invertebrate communities from soil, may have different functions in the ecosystem in relation to the different trophic spectrum, as for example: ants are a group of thermophilic and predatory insects that feed on other ants, termites, collembola, mites and other insects. They are one of the most abundant taxa of insects and are considered soil engineers due to their effects on soil properties and their influence on resource availability to other organisms, including microorganisms and plants.

They are both primary food for many small vertebrates and top predators in soil food webs (JOUQUET et al., 2006). Carabidae and Staphylinidae are mainly predators, feeding on Collembola, Diptera, Coleoptera, Aphids, Earthworms and other prey. Most pasture beetles are saprophagous. In contrast, some Carabidae species feed on the seeds of certain plant species (HONEK et al., 2007), and others feed on the microorganism-rich liquid fraction of animal excreta (STAVERT et al., 2014).

Coleoptera are essential in the first stage of decomposition of organic matter, because they fragment into smaller pieces, facilitating the release of nutrients and prevent mineral loss, returning nutrients to primary producers and associated soil microorganisms (STAVERT et al., 2014). Oligochaetes (earthworms) feed on dead organic matter. Earthworms can ingest large amounts of litter and/or soil and are classified as detritivorous species. While they ingest soil and organic matter, they also ingest bacteria and fungi.

They have the potential to influence the functions of soil in a variety of ways, including tunneling, detritus consumption, and by regulating the composition and activity of lower trophic level organisms (i.e., fungi and bacteria). Earthworms can also feed on plant residues, which are usually colonized by soil microflora and microfauna. In particular, protozoa and fungi are considered an important food source. The intestinal contents of earthworms have fungal hyphae and propagules, which are partially digested. They are suitable hosts for saprotrophic soil fungi, fast-growing zygomycetes and plant pathogens (*Fusarium*). Earthworms use fungal community composition as a cue to detect fresh organic resources in the soil (RUESS & LUSSENHOP, 2005).

Isopods feed mainly on dead plant material and to some extent on dung, animal remains and live plant material. Thysanoptera feed on juices from leaves, flowers and plant shoots; some feed on mosses and fungi, while others are predators of small arthropods. In grasslands, the mite trophic spectrum is very wide, from polyphagous to highly specialized species, parasites, herbivores, fungivores, microbivores, detritivores and omnivores (MANU et al., 2015). Although mites are essential in the food web, enchytreids are probably the "keystones" for the decomposition process. Several enchytreid species are fungivorous (DASH & CRAGG, 1972; DASH et al., 1980), but there is no information on whether they select specific fungal species (RUESS & LUSSENHOP, 2005).

Macrofauna that feed on fungi include enchytreids, dipteran larvae, millipedes, centipedes, thysanurans, and earthworms. Enchytreids are 80% microbivores (bacteria and fungi) and 20% saprophages (DIDDEN et al., 1997). Nematodes are well known to function as key players in terrestrial food webs. They can reach densities of several

million individuals per square meter of soil, and their communities often comprise more than 100 species. The structural diversity of nematodes reflects the variety of ecological niches they occupy (DE DEYN et al., 2004).

They feed on bacteria and thereby mobilize the nutrients and minerals bound in the microbial biomass, thereby regulating nutrient cycling. Other nematodes feed on fungi, algae, plants or live as omnivores and predators. Nematodes are, in turn, food for other species, predominantly microarthropods, and provide an important link between the microbial and faunal food webs. In conclusion, nematodes form a key link between soil bacteria, fungi and roots, the main energy and matter flows in soil food webs (MENZEL et al., 2018). Some nematodes can be omnivores and feed on algae, bacteria, fungi or even other nematodes. Collembola, although they generally feed on microorganisms, can also feed on nematodes. There are also mites that feed on both microorganisms and decaying plant matter (NEHER & BARBERCHECK, 1998); Collembola feed on various microorganisms in the soil, for example, fungi, bacteria, actinomycetes and algae.

They can feed on fungi on the surface of decaying leaves, faecal material and soil particles. Many collembolans are very flexible in diet and change their trophic preferences according to food availability. Food selection is influenced by substrate type or physiological factors such as nutritional status of fungal hyphae or odour, and the chemical quality of a food resource can influence collembola productivity. By shredding and dispersing spores, collembola have a significant impact on the soil fungal community (CHAMBERLAIN et al., 2006). All these invertebrates are dependent on each other and compete with each other (MULDER, 2006; MANU et al., 2016).

Microarthropods can be predators of smaller microarthropod species (enchytreids) and for their eggs, nematodes and others (NEHER & BARBERCHECK, 1998). A variety of soil ecological niches, both in size and range of resources provided, leads to significant functional differentiation of soil organisms.

CONCLUSIONS

The soil food web can have four to eight trophic levels, with many organisms being omnivores. Some authors have used this food web concept to show that webs with many omnivores are more stable. The number of trophic levels led to experiments to determine whether the control of numbers at each level is given by predators (top-down) or resources (bottom-up). The absence of top-down effects in decomposition systems may be due to omnivores and the occurrence of refugia (tiny soil pores that protect some bacteria and fungi from being consumed).

Moreover, bacteria and fungi are able to compensate for the consumed biomass by accelerating their turnover rate. Availability and disturbance of soil resources are widely recognized as key drivers of invertebrate community structure.

However, the relative importance of different invertebrate functional traits in determining species abundance following changes in soil resource availability and disturbance remains understudied, particularly in long-term experiments.

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