Trophic resources of the edaphic mesofauna: a worldwide review of the empirical evidence

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Abstract

Ecosystem sustainable use requires reliable information about structure and functioning. Accurate knowledge of trophic relations is central for the understanding of ecosystem dynamics, essential to develop sustainable use practices. This review gathers the information available worldwide about the trophic resources within the soil mesofauna. From over 130000 hits of the initial search on soil mesofauna, only a total of 78 published works relate particular species, genera, and families to particular trophic resources, the majority of them dealing with soils of the Paleartic region. Thirteen trophic resource categories were identified for six of the main orders of soil Acari and Collembola, using a combination of eight different methodologies. Out of 2717 records relating specific taxonomic groups to their trophic resources, 515 mention saprophytic fungi as a food resource, 381 cite nematodes, 308 mention bacteria, 286 litter and 256 cite mychorrizae. The available information is also highly skewed, for 68.16% of all the available information comes from Acari, and within these, 44.5% correspond just to Sarcoptiformes. For Collembola, the information available in the literature is much scarce the majority of it from Arthropleona. This review shows the general lack of information relating species, genera, and families of the soil mesofauna to specific trophic resources, with Collembolans largely unexplored in this regard. It also highlights the studies mostly come from European soils, with the use of trophic resources by the mesofauna of majority of the soils in most of the world still largely unknown.

Keywords: trophic web, soil sustainable use, soil mesofauna, Acari, Collembola

Introduction

Only in the last few decades, sustainable use of the soil has come sharply into focus. The Ecosystem Millenium Assessment (2005), the report on Global Biodiversity and Ecosystem Services (IPBES 2019), and the recent State of Knowledge of Soil Biodiversity (FAO 2020) clearly state the importance of the soil ecosystem and the central role soil biodiversity plays. However, critical information is lacking on edaphic biodiversity and interaction webs for most soils.

The view about the edaphic biota has changed dramatically in recent years. Much of the work on taxonomic descriptions, richness, and biodiversity estimation, and microenvironments (Anderson 1978; Petersen and Luxton 1982), highlights the fragility and need for conservation of soils, and soil biodiversity (FAO 2020; Walker 1992). Gradually, the focus has shifted towards the study of the functioning of the soil ecosystem, in which the interactions between the biota and the edaphic environment affect its structure and functioning in a hierarchical manner, regulating the functioning of the edaphic ecosystem. (Barrios 2007; Behan-Pelletier and Newton 1999; Brussaard 1997; P. Lavelle et al. 2006) The relationships of species richness with ecosystem dynamics allow establishing causal relationships between the characteristics of the organisms present and the processes and services of the ecosystem (Hooper et al. 2005; Martín-López et al. 2007) in natural as well as in managed environments. (Wall et al. 2012).

The soil mesofauna is mainly constituted by microarthropods belonging to the Acari and Collembola subclasses that inhabit the upper soil horizons (Martinez and Narciso 2009), where complex communities are developed and maintained. These communities are influenced by a high microhabitats heterogeneity and the number of food resources available (Anderson 1977,

1978; Lavelle and Spain 1994), which provide a wide and varied set of ecological niches (Nielsen et al. 2010; Wallwork 1958a). The mesofauna, through its trophic relationships, contributes to the edaphic functioning through the processes of fragmentation of organic matter, the dynamics of the nutrient cycle, the transport of microflora propagules, and the regulation of microflora and microfauna populations that affect primary production. (Brussaard 1997; Cragg and Bardgett 2001; Lavelle 1996; Wall et al. 2012; FAO 2020).

The study of the flow of energy and matter in the soil ecosystem, groups edaphic organisms into functional guilds to understand the relationships with the functioning of the ecosystem. However, this approach leaves aside the understanding of how changes in the community influence the ecosystems (Thompson et al. 2012; Wall and Moore 1999). Thompson et. Al. (2012) suggest addressing this problem from the point of view of the trophic networks linking the flow of matter and energy and the diversity of a community. Thus, by studying the structure of the trophic networks, we can get a better understanding of the role of biodiversity in the functioning of the ecosystem. The methods used to obtain empirical evidence on trophic relationships of soil animals are generally used in both aquatic and terrestrial communities (JM Nielsen et al. 2018; Ruess and Chamberlain 2010; Tiunov 2007), but information about the latter is remarkably scarce in comparison.

Knowing the resources that microarthropods groups use as food is difficult due to their size and their cryptic environment. Furthermore, the observation of what an organism consumes at any given time does not indicate its potential diet (Nielsen et al. 2018). In this sense, the recognition of the food resources that are part of the diet of soil microarthropods must be based on empirical evidence, which constitutes the first step to establish the interactions between trophic species *sensu* Briand and Cohen (1984) and

the trophic resources that describe the trophic webs. (Briand and Cohen 1984; van Straalen 1998; Walter, Kaplan and Permar 1991).

Despite the increasing amount of descriptive works and lists of taxonomic groups, the information available worldwide is still largely fragmentary and incomplete, and the taxonomic resolution varies considerably between and within published works. The same happens with trophic relationships of the different taxonomic groups: information is still scarce. This data is necessary to elucidate these relationships to analyze and build webs of interactions that, in turn, could be used to assess the stability and conservation status of these ecosystems. (Barrios 2007; Briones 2014; Thakur et al. 2020).

Thus, the objectives of this review are to gather all the information currently available regarding the trophic resources used by mites and collembolans that inhabit soils, and establish trophic relationships and potential diets of these soil microarthropods.

Materials and methods

<u>Empirical evidence</u>

The recognition of the food resources that are part of the diet of soil microarthropods is based on the empirical evidence provided by the bibliography. These evidences are: [A] observations of consumption events in microcosm experiments where feeding preferences are studied (Hubert et al. 2001), selection of foods (Schneider 2005), physiological phenomena related to feeding (Saur and Ponge 1988) or studying trophic interactions (Schneider and Maraun 2009). [B] The observation of **intestinal contents** assumes that what is actually observed is what is consumed (Hartenstein 1962; Schneider et al. 2004; Wallwork 1958a). [C] Morphology and functioning **of mouthparts** related to food handling and processing (Buryn

and Brandl 1992; Kaneko 1988; Wallwork 1958b). [D] **Molecular analysis** of intestinal content (Heidemann et al. 2014; King et al. 2008; Read et al. 2006). [E] Analysis of digestive **enzyme activity** (OC Nielsen 1962; Siepel and Ruiter-Dijkman 1993). [F] Analysis of carbon and nitrogen **stable isotopes** (Potapov, Tiunov, and Scheu 2019; Tiunov 2007). And, [G] the study of **fatty acids** lipid profile as dietary markers (Pollierer, Scheu, and Haubert 2010; Ruess and Chamberlain 2010).

General review publications are also included in this review, provided that they collect information on the use of trophic resources from publications not readily available.

Bibliography search and database construction

A systematic search was carried out through Google Scholar using keywords related to the taxonomic groups of interest (mesofauna - collembola - acari), trophic relationships (trophic - trophic interactions - predation - diet - soil - food - soil food web), the empirical evidence (gut content - stable isotopes - food preferences - digestive - enzymes - lipids - fatty acids), and their combinations. The search yielded a total of 138,331 hits. This search was then successively refined, to take into account only those publications that provided evidence of the use of at least one trophic resource by soil mites and/or springtails, and was further restricted to publications that refer to specific levels of taxonomic resolution. The final database yielded a total of 78 citations (Electronic Supplementary Material, ESM I).

For the elaboration of the database from this search (ESM II), the taxonomic information (Mayr 1996) and trophic resources were obtained, from the papers and their published appendices (Thakur et al. 2020). To deal with the heterogeneous information provided by the empirical evidence, it was necessary to group the trophic resources to summarize their trophic and

ecological characteristics in the edaphic ecosystem. Once the trophic resources were defined, associations were made between the taxa and those resources.

Additional information can be found in the Electronic Supplementary Material.

Data analysis

The records were then analyzed by counting the associations between the taxa, the methods used and the trophic resources identified. We described trophic resources, their number of records, and their relationships with the different taxonomic levels. Then, the breakdown of each taxon was carried out within the taxonomic categories and their relationship with trophic resources. We calculated the proportions of the different methods and their relationship with the taxonomic level and trophic resources.

Finally, we estimated the potential importance of resources on the diet for the main orders of Acari and Collembola using the proportion of mentions between trophic resources and taxa included in such orders, that is, the sum of the proportion of mentions of a resource concerning the total mentions for a particular taxon. For example, if a species has ten records of the consumption of the same trophic resource, it is likely that the selection of this food item is a reflection of the use of the resource. Then if we gathered the information available from different species of the same genus, and the food items consumed by them, then we could assign it to the potential diet for the genus. Similarly, the resource use of the genera within a family can be thought of as reflecting the potential diet of the family.

That is, the diet of higher taxonomic hierarchies will be constituted by the sum of the resources used by the lower taxonomic levels.

The calculations, graphs, and tables were prepared using Excel and R.

Results

Only 21 articles from the 78 selected publications (ESM I) mention the countries in which the studies were carried out. Of these, 2 records belong to the Neotropical region, 3 to the Neartic region, 1 to the Australian region, 1 to the Eastern region, and the remaining 14 are all located in the Palearctic region. This is important to highlight because the species strongly vary depending on the biogeographic region it shows how incomplete still is the available information on this topic. It is also evident that knowledge about the trophic resources of Acari and Collembola was developed mainly in European countries and much work remains to be done worldwide. Only 49 of the publications mention the environments in which the studies were conducted. These authors analyzed 33 temperate forests, 3 tropical forests, 10 grasslands, 10 agroecosystems, and 1 desert. Regarding other environmental characteristics, 23 authors provide taxonomic information of the soil, 18 report on the pH, 10 mention the type of hummus. Other descriptions, environmental measures, and contributions of each bibliographic source can be found in ESM I.

Focusing on the use of trophic resources, a total of 2717 records were obtained from the empirical evidence (ESM II). To the species level, 127 records were Collembola species and 307 records were Acari species. The latter contributed 1848 of the 2717 total records (68.02%). At the genus level, 550 records were found, 21 genera belonging to Collembola and 115 genera belonging to Acari, out of a total of 53 and 234 genera of Collembola and Acari identified adding up genera and species within genera. The family level adds up to 240 records with 50 different families out of the total of 142 families identified in this review.

Methods for identification of trophic resources used

The method of observations in laboratory tests provide the main empirical evidence from the database with 1082 records (Figure 1).

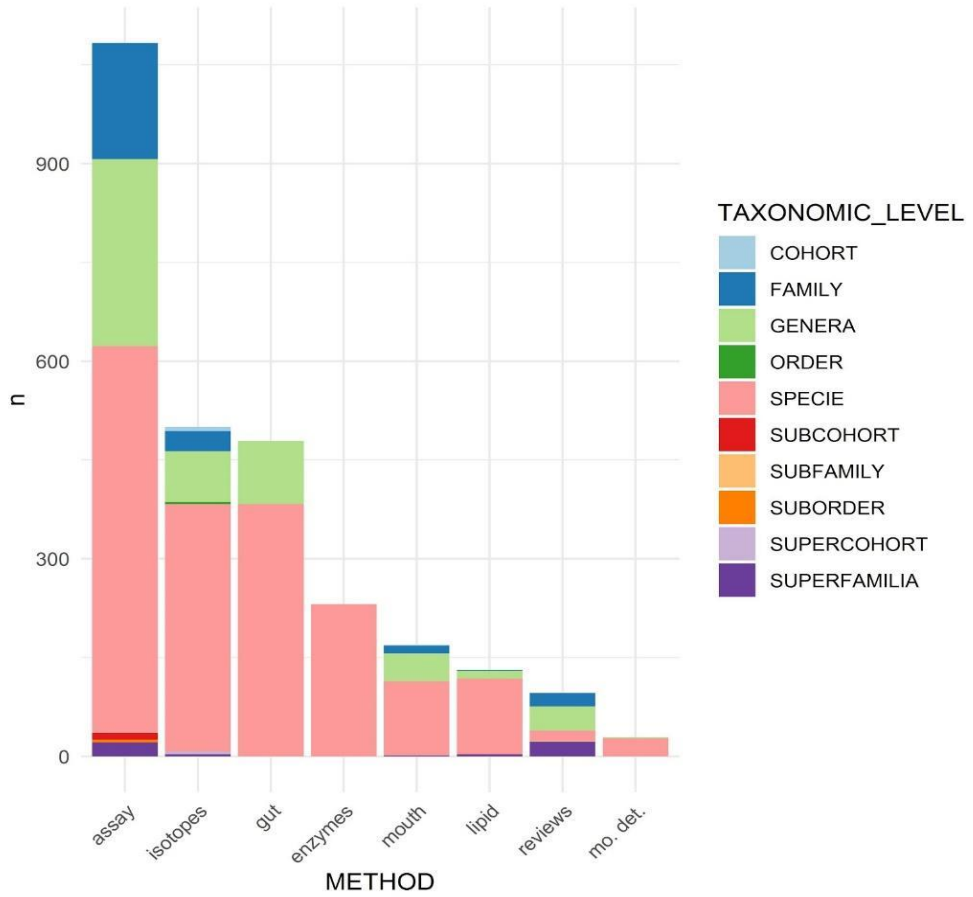

Figure 1. Methods used in the literature to assign trophic resources to soil mesofauna taxa. Colors within columns refer to the number of different taxonomic levels for which each method assigned at least one resource. Assay: laboratory tests and observations. Isotopes: stable isotopes. Gut: intestinal content. Enzymes: digestive enzymes. Mouth: mouthparts morphology. Lipid: lipid profile. Mo. Det: molecular detection of intestinal content. Reviews: general reviews by other authors.

Only 1.3% of the records describe feeding events for taxonomic levels higher than family. Mesofauna families constitute 17% of the observations in laboratory tests, with 85% of the total corresponding to the Prostigmata suborder, within which 27 different families are mentioned. In turn, 35 of the records correspond to the Prostigmata suborder that mentions 5 different

superfamilies (see ESM II). The evidence offered by observations in laboratory tests adds up to 83% for species and genera. The orders Mesostigmata (55.6%), Sarcoptiformes (26.7%) and Arthropleona (11.4%) are the ones with the higher presence in the literature.

Stable isotopes follow in importance adding up to 500 records. From these, 75% of the records mention species. Genera and family add up to 22% of the records, and the remainder of the taxa mentioned accumulate 3%. The observation of the intestinal content reaches 17.6% of the records, in which the species taxonomic level corresponds to 80% of the total records and the genus level to 20%. For this method there were no records associated with the order Mesostigmata, Acari. (see ESM II). The activity of digestive enzymes (231 records) in all cases reports down to the species level. For this empirical evidence the authors worked with the orders Sarcoptiforme (Acari), and Arthropleona and Symphypleona (Collembola). Intestinal contents analyses with molecular techniques for the detection of DNA is a tool of recent development and represents 1.1% of the total records.

Figure 2 shows the number of records for each trophic resource, and the empirical evidence that detects their relationships with them.

Laboratory tests mention the consumption of all thirteen trophic resources described in the available literature. The mention of nematodes is the single most important (225 records). Laboratory methods are the ones that most often mention collembola, mites, invertebrate larvae, invertebrate eggs, and enchytraeids as food resources. This method rarely mentions the consumption of humus and carrion.

The detection of digestive enzymes (Figure 2) assigns 24% and 20% of its contribution to saprophytic soil fungi and mycorrhizae, respectively. Litter and plant tissue participate together with 33% and bacteria are mentioned 17.75% of the times. The study of the lipid profile of 22 species of Collembola

and 12 species of Acari, allowed assigning bacteria (33.6%), saprophytic fungi (27.5%), leaf litter (17.6%,) and nematodes (16%) as the most important trophic resources.

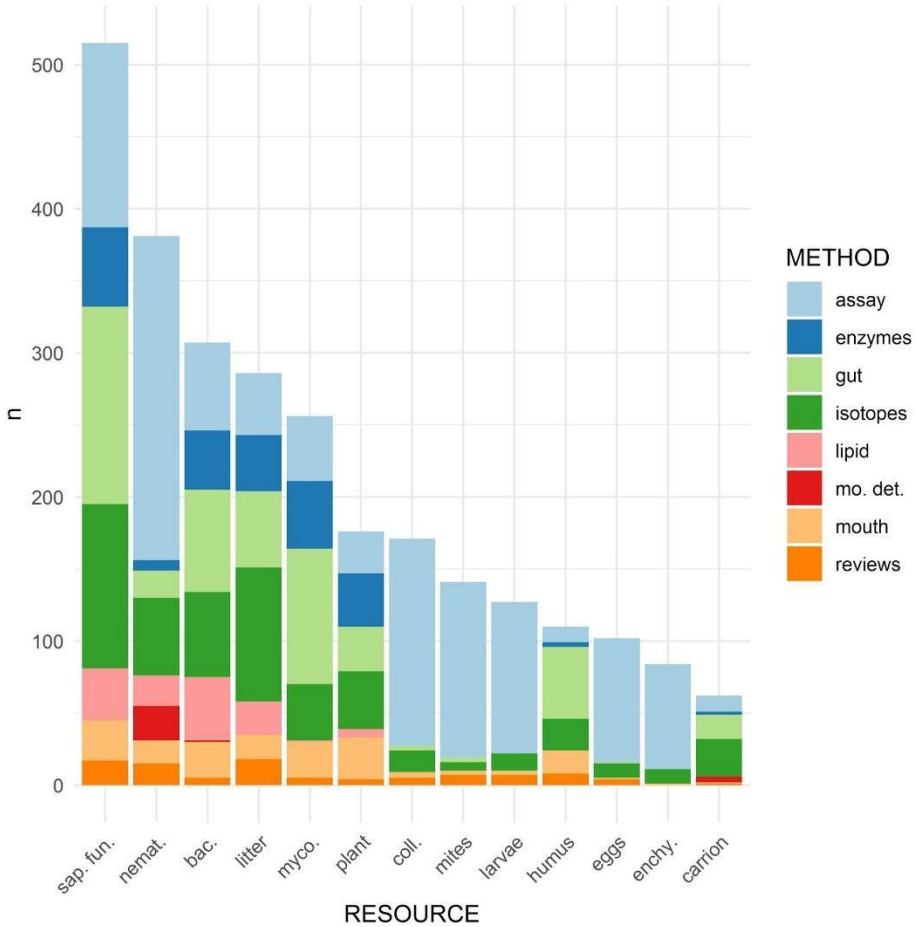

Figure 2. The number of records in the literature assigning each one of the 13 trophic resources to a mesofauna taxon as shown in Table 1. Colors in the columns refer to the method used to assign those trophic resources to a particular taxon. Methods as in Fig. 1.

Similar to laboratory tests, stable isotopes were associated with each and all of the trophic resources, saprophytic fungi are the main resource mentioned (114 times) followed by litter (93 mentions), bacteria (59 mentions), and nematodes (54 mentions).

From highest to lowest, the number of mentions of resources provided by the intestinal content analyses was: saprophytic fungi > mycorrhizae > bacteria

> litter > humus > plant tissue > nematodes > carrion > collembola - mites > invertebrate eggs.

Use of trophic resources by soil mesofauna

Table 1 shows the trophic resources identified divided into 13 categories.

Trophic Resource	Description	Number of consumer records			
		Total allocations by trophic resource, absolute values (percentage values). (2717 records)[1]	FAMILY	GENERA	SPECIE
Saprophytic fungi	They are ubiquitous soil fungi that break down organic matter.[c]	**515 (18,9)**	**16**	**93**	**396**
Nematodes	Soil nematodes and protozoa, tardigrades, rotatory and other edaphic microfauna.[e]	**381 (14)**	**45**	**115**	**211**
Bacteria	They include bacteria with enormous autotrophic and heterotrophic capacities.[b]	**308 (11,3)**	**9**	**63**	**227**
Litter	Dead plant tissue accumulated in the soil with different degrees of fragmentation and decomposition.[a]	**286 (10,5)**	**4**	**41**	**232**
Mycorrhizae	Symbiotic fungal hyphae with plant roots. [i]	**256 (9,4)**	**8**	**39**	**205**
Plant tissue	Includes non-vascular plants (mosses, lichens, etc.), live roots, and seedlings.	**174 (6,4)**	**1**	**15**	**154**
Springtails	Juvenile and adult springtails.	**171 (6,3)**	**47**	**42**	**73**
Mites	Soft-bodied, non-sclerotic, unshielded, or juvenile mites.[f]	**141 (5,2)**	**40**	**29**	**62**
Larvae	Soft-bodied invertebrate larvae.	**127 (4,7)**	**23**	**33**	**66**
Humus	Complex and amorphous organic matter with a high degree of decomposition: debris, fecal pellets, etc.[d]	**110 (4)**	**4**	**17**	**88**
Invertebrate eggs	Invertebrate eggs found by predators.[g]	**102 (4)**	**23**	**26**	**49**
Enchytraeids	Anatomically homogeneous, soft-bodied oligochaete annelids.[c]	**84 (3)**	**12**	**23**	**46**
Invertebrate carrion	Animal tissue, molts, invertebrate corpses, etc.[h]	**62 (2,3)**	**8**	**13**	**40**

[1]Supplementary material II [2]Supplementary material I [a]B. Berg y McClaugherty 2008 [b]Clark 1971 [c]Warcup 1971 [d]Ponge 1991 [e]Persson et al. 1980 [f]Krantz et al. 2009 [g]Chernova et al. 2007 [h]Rusek 1998 [i]Schneider et. al. 2005

Table 1 Basic description of trophic resources. Total allocations by trophic resource, absolute values (percentage values). Number of mentions of a trophic resource for the level of taxonomic resolution. [1]Supplementary material II [2]Supplementary material I [a]Berg & McClaugherty 2008 [b]Clark 1971 [c]Warcup 1971 [d]Ponge 1991 [e]Persson et al. 1980 [f]Krantz & Walter 2009 [g]Chernova et al. 2007 [h]Rusek 1998 [i]Schneider et al. 2005

It can be seen that the main resource mentioned corresponds to saprophytic fungi (18.9%) followed by nematodes (14%), bacteria (11.3%), and litter (10.5%), the records for mites, collembolans, enchytraeidae, larvae, and eggs accumulate 625 mentions (23.2%) and the lowest participation is for invertebrate carrion (2.3%). Table 1 shows in bold the number of records (in number and percentage) identified for each trophic resource, as well as the participation of each taxonomic level for which a resource was identified. Thus, for example, 515 total records (18.9%) of consumption of saprophytic fungi were identified, 16 of which were identified at the family level, 93 at the genus level, and 396 at the species level.

Interestingly, for the family level, the most numerous records correspond to trophic resources such as collembola, nematodes, larvae, enchytraeids, and mites, typical resources of predatory microarthropods that together add up to 190 records. In the same way, the predation detected at the genus level totals 268 records (48.82%). For the species taxonomic level, the main singular resource mentioned is saprophytic fungi with 396 records (21.42%), while total predation represents 27.42% (507 records).

Table 2 provides relevant information about how the consumption of the same trophic resources is composed in the six orders mentioned in the literature (3 orders of Collembola and 3 orders of Acari), identified according to whether they are mentioned at the family, genus, or species level. The number of times that each taxon is mentioned in the literature at the level of family, genus, or species is first identified, and the column below shows the mentions of resources consumed according to the records published for that taxon. Within the family taxonomic category, 23 families were mentioned in the order Mesostigmata (Acari). For the identity and more information about the families, genera and species mentioned in Table 2, see ESM II.

Trophic Resource	FAMILY						GENERA						SPECIE					
	M (23)	S (77)	T (31)	A (8)	N (1)	Sy (2)	M (64)	S (151)	T (19)	A (43)	N (2)	Sy (8)	M (79)	S (223)	T (5)	A (114)	N (1)	Sy (12)
Saprophytic fungi	5	66	9	7	1	1	5	116	8	35	1	6	2	145	3	86	0	6
Nematodes	21	31	27	7	0	1	56	45	8	26	0	2	62	58	0	33	0	2
Bacteria	4	57	6	8	1	1	4	92	5	31	2	3	3	107	0	50	1	5
Litter	3	42	1	6	1	2	3	79	0	27	1	6	2	97	0	48	0	6
Mycorrhizae	1	54	6	7	0	1	1	83	6	33	0	2	0	91	3	58	0	2
Plant tissue	3	43	2	7	0	1	3	72	1	18	0	5	2	92	0	24	0	7
Springtails	15	2	25	4	0	0	35	2	11	7	0	0	50	2	1	7	0	0
Mites	14	2	25	2	0	0	35	2	5	4	0	0	47	2	1	4	0	0
Larvae	14	3	12	2	0	0	38	3	0	4	0	0	54	3	0	3	0	0
Humus	2	27	3	7	1	1	2	43	0	16	2	1	0	44	0	26	1	1
Invertebrate eggs	16	2	12	1	0	0	36	2	0	2	0	0	42	2	0	1	0	0
Enchytraeids	14	2	7	0	0	0	34	2	0	0	0	0	40	2	0	0	0	0
Invertebrate carrion	1	18	2	4	1	1	1	23	0	12	1	1	1	23	0	11	1	1

Table 2. Nested boxes represent the main orders of Acari and Collembola. In parentheses the total number of taxa for the taxonomic category. Within the cells, the number of taxa associated with the trophic resource is shown.

At all the taxonomic levels considered, the order Sacroptiformes (Acari) is mentioned consuming mainly saprophytic fungi, bacteria and mycorrhizae. The records for the order Trombidiformes (Acari), show them mainly as predators, with 27 families consuming nematodes, 25 families consuming springtails, the same number for mites, and 12 families using invertebrate eggs and larvae. The use of litter, plant tissue and hummus were only associated with 1, 2 and 3 families of Trombidiformes respectively.

For Collembola, the information available on the trophic resources used is much scarce. At the family level, the order Arthropleona is mentioned in only 8 records, Neelipleona in only one record, and Symphypleona in only two records.

Considering the mentions at the genus level, the order Mesostigmata (Acari) is mentioned consuming nematodes in 56 of the 64 genera compiled for this order. Likewise, 38 genera consume invertebrate larvae, 35 genera consume mites or collembola, and 34 genera make use of the enchytraeids as a food resource. This information indicates predation as the main feeding strategy for this order of Acari. Saprophytic fungi, bacteria, plant tissue, and litter were

only mentioned by 5, 4, 3 and 3 genera respectively.

The information available at the species level for the order Symphypleona (Collembola), registered mentions for 12 different species, 7 of them provided evidence of consumption of plant tissue, 6 species consume saprophytic fungi and leaf litter, 5 consume bacteria and two species were associated with nematodes.

For Arthropleona (Collembola) the information at the species level indicates that they mainly consume saprophytic fungi with 86 of the 114 species records registered for this order mentioning this resource. Mycorrhizae, bacteria, and litter follow in importance. Nematodes are mentioned as a resource for 33 species. Adding up all the records at the three taxonomic levels (family, genus and species), the order Sarcoptiformes (Acari) accounts for 44.5% of the total records. Table 2 indicates that the literature mentions trophic resources for 77 families, 151 genera, and 223 species within this order. Ordering the information collected at the highest level of taxonomic resolution (species), the mentions of trophic resources for this order are: fungi > saprophytes > bacteria > litter > plant tissue > mycorrhizae. The nematode resource was associated with 58 species, hummus with 44 species, and carrion was recorded as a resource for 23 species. The associations that correspond to typical predator resources do not exceed 3 associations with species, except for nematodes.

Figure 3 is a bipartite diagram in which the thickness of each line gives visually information about the proportion in which the resources are associated with the main orders of microarthropods, according to the detail provided in Tables 1 and 2. The saprophytic fungus resource is the main constituent of the Arthropleona diet, along with bacteria, mycorrhizae and litter. Trombidiformes have a diet mainly based on microarthropods and nematodes and to a lesser extent saprophytic fungi.

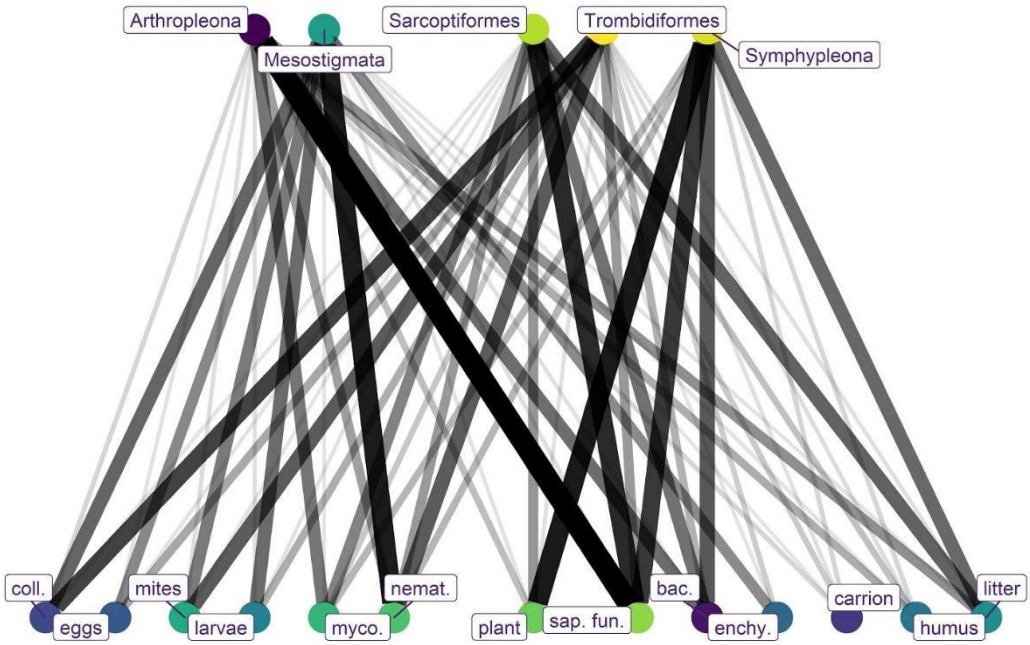

Figure 3. Bipartite graph showing the use of trophic resources by the main orders of Acari and Collembola. Upper nodes: Acari and Collembola orders as in Table 2. Neelipleona with only 8 records excluded. Lower nodes: trophic resources. The thickness and intensity of the lines give an idea of the proportion of mentions in the available literature about their use of trophic resources. Resource names as in Tables 1 and 2.

The Sarcoptiformes diet is mainly of saprophytic fungi, leaf litter, bacteria, and plant tissue. Nematodes are the main items mentioned as a secondary resource. Mesostigmata have a basically predatory diet, consisting mainly of nematodes, microarthropods, eggs, and worm-shaped prey. For the order Symphypleona, the diet is, from greater to lesser number of associations: plant tissue > saprophytic fungi > bacteria > litter.

Discussion

Until the 1960s, soil fauna considered only worms, and terrestrial ecologists considered the rest of the soil fauna as a “black box” of decomposers and detritivores (Briones, 2014). The information gradually collected over the following decades regarding the edaphic mesofauna is reaching the point

where it is possible to focus on integrative works. However, the available information is still scarce and mostly restricted to the most numerous or conspicuous groups of the soil mesofauna.

This review gathers the information currently available regarding the use of trophic resources by the edaphic mesofauna. This information, together with other characteristic features of the soil mesofauna, will allow building a food web interactions network, that could result in a better understanding of the structure and functioning of the edaphic biota (FAO 2020). Trophic networks will, in turn, allow for comparing the state of different soils, or the same soils under different intensities of anthropic impact (Pankhurst, Doube, and Gupta 1997; Pey et al. 2014; Thompson et al. (2012).

Estimating the diet of organisms provides the foundation for understanding trophic interactions by characterizing how trophic resources are used by consumers within the soil ecosystem. Furthermore, it provides much-needed information on their trophic niches, their nutritional physiology, and the flows of matter and energy throughout the soil ecosystem (JM Nielsen et al. 2018; Potapov et al. 2020). The empirical characterization of trophic interactions is challenging due to the spatial and temporal complexity of feeding patterns, and the limitations of the methods to identify and quantify the components of the diet (JM Nielsen et al. 2018; Pankhurst, Doube, and Gupta 1997; Walter, Kaplan, and Permar 1991).

For soil microarthropods, the evidence provided by laboratory work results in the most relevant approximation to know how these animals use trophic resources, their feeding behavior, their food preferences, and their development and growth in controlled environments. The results presented here show the importance of this method to better understand the use of trophic resources by these cryptic soil organisms. The method used to relate the isotopic signature of organisms and their resources is a recently

developed tool that is useful for detecting the importance and the changes in time or space of assumed trophic relationships, which means that we have to know in advance if the trophic relationship exists. This method can analyze a large number of species and an important variety of resources (Potapov, Tiunov, and Scheu 2019). The use of methods that allow tracing biomolecules along the food chain is advancing towards the development of strategies to interpret soil bulk volume analyzes. (Kühn, Schweitzer, and Ruess 2019; Ruess et al. (2007).

The trophic resources used by soil microarthropods can be determined in a complementary way by using different methods (Potapov et al. 2020; Walter, Kaplan, and Permar 1991). The most used resources are saprophytic fungi, nematodes, and bacteria. If we associate them with their nutritional characteristics, these trophic resources are rich in molecules with great nutritional value as determined in the dietary routes labeled by fatty acids, stable isotopes, or the ubiquitous enzymatic pathways of carbohydrases that hydrolyze nonstructural polysaccharides. (OC Nielsen 1962; Potapov, Tiunov, and Scheu 2019; Ruess and Chamberlain 2010).

We found that a large proportion of the resources are defined as taxonomic categories of species, genera, and families, which would be important to estimate the diets of higher taxonomic groups. The available information for low taxonomic levels could be used as a reference to address the problem of what the use of soil resources will be like by higher level taxonomic groups (Bedano 2007).

This information must be interpreted with caution, however, because within a taxonomic category, each species could apply different strategies to the problem of exploiting resources (Lavelle and Spain 2001; Moore, Walter, and Hunt 1988), as many taxa in the available literature are considered to be general consumers. We allowed a closer look at the complexity of the

interaction networks between the main orders of Acari and Collembola and the trophic resources present in the edaphic environment. Furthermore, this information suggests that the edaphic ecosystem might have a high level of homeostasis because of the high number of redundant species that exist in the edaphic system (Hättenschwiler, Tiunov, and Scheu 2005).

Moreover, the results presented here provide valuable new information about the different feeding strategies of the main groups of the soil mesofauna. At the same time, the still quite scant information available in this regard must be highlighted. Of the total number of publications retrieved in the bibliographic search, we found only 78 works providing information on the relationships between taxa of the edaphic mesofauna and their trophic resources. Even more scarce is the geographic information, with only 21 papers mentioning the country of origin of the data. The great majority of studies are from countries of the Palearctic region focusing on temperate forest soils. Likewise, it is illustrative to note that most of the works have been carried out in European countries.

It is also to be noted that the information available for Acari and Collembola is strongly asymmetric. Out of the total of 2717 records retrieved in the bibliographic search, 1848 (68.16%) correspond to Acari, and within this number, the majority (44.5%) correspond to Sarcoptiformes.

Finally, it is necessary to call attention to the need for more studies on the trophic relationships of the soil mesofauna. Out of a total of approximately 9000 described species of Collembola (Bellinger et al. 2020), it was only possible to find trophic information for just 127 soil inhabitant species. For Acari, out of the approximately 58,000 species described (Schmidt 2020), it was only possible to find references of trophic relationships for 307 soil species.

Further deepening on the knowledge of functional and trophic relationships

of the soil the fauna would allow for a better and more precise evaluation of the functioning of the edaphic ecosystem, the protection of the ecosystem services that the soil mesofauna provides, and the sustainable use of the soil.

Declarations

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