Community structure and species richness in the Mediterranean-type soil fauna

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Abstract. Recent results on community structure and species richness of the soil fauna of Mediterranean-type ecosystems are reviewed. Faunal composition, relative abundance of animal groups and trophic levels, spatial and temporal variation of the community structure together with species diversity are summarized. The effects of fire, grazing, agriculture and of other human activities on community structure are described. It is concluded that the soil fauna system of the Mediterranean-type ecosystems has a significant spatial, temporal and ecological complexity that can be better understood only by detailed species-level, long-term, seasonal and multi-sample studies.

Introduction

Ecological aspects of the soil fauna of Mediterranean-type ecosystems are poorly known. Only three large-scale reviews have appeared over the last 20 years (Di Castri, 1973; Di Castri & Vitali-Di Castri, 1981; Majer & Greenslade, 1988). Most of the specific articles that have appeared deal with the ecology of particular animal groups or species whilst few are concerned with the community as a whole. This chapter will attempt to summarize some of the results obtained from various Mediterranean-type ecosystems. It was not possible to make the coverage exhaustive because some results have been published in journals unavailable to me whilst other results were obtained using methods that made them incomparable with others. Some generalities about community structure and species richness will be attempted, however.

Faunal composition

The first element of community structure that is easily obtained from any study is the presence or absence of certain animal groups. In the case of soil fauna, the minimum taxonomic levels used in the articles reviewed are: phylum for Nematoda, Mollusca and Annelida, class for Myriapoda and order for Crustacea, Arachnida and Insecta. For many groups, the limited number of reports arises not because of their absence from the study area but from the use of selective methods or from the decision of the authors not to include them. For example, many authors do not include microarthropods; some others exclude ants and termites because of their highly contagious distributions. By looking at each site in detail one can note, however, a consistent absence of certain groups (Tables 4.1 and 4.2). For instance, Diplopoda, Thysanoptera and Psocoptera are absent from the two most arid areas studied, viz. the Mariut *Anabasis-Thymelaea* area in Egypt (Cancela da Fonseca *et al.*, 1984; Ghabbour *et al.*, 1977, 1985; Ghabbour & Shakir, 1980) and the asphodel desert in Greece (Pantis *et al.*, 1988).

Relative importance

The relative importance of the groups of soil animals can be estimated using either of two methods. One is to measure population density using

Table 4.1. Population densities in individuals/m² of soil invertebrates in various Mediterranean-type ecosystems

	A	B	C	D	E	F	G	H	I	J	K	L	M	N
Nematoda											0–93			
Mollusca												1.27		
Annelida												1.16		
Isopoda	0.18	0.03	3.68	5.69	0–3	27–107	17.6	4.4	2.8	6	0–64	2.29	12.5	3.8
Araneae	5.61	3.8	1.24	38.95	29–163	13–91	68.7	38.3	11.3	17.6	28–59	0.63	6.5	4.6
Pseudoscorpiones	0.17	0.08		68.77	43–158		133.5	30.1	14.1	14.3	0–257	1.78	13.9	8
Opiliones				1.36			1.2		0.3	0.3	0–24	0.09		
Scorpiones	0.05	0.03	0.04				0.4					0.02		
Solpugida			0.04											
Acarina	0.11	0.24	0.12			5–224	4966.4	5326.7			37468–121641	66.51	1067.6	803.9
Diplopoda				39.01	3–174	0.112	253.4	44.8	11.1	19	45–149	0.99	5.4	2.5
Chilopoda	0.09	0.02	18.33		0–13		37.1	12.2	0.7	3.7	44–179	0.86	1.3	0.7
Pauropoda											44–1592	0.01	2.2	0.8
Symphyla							2.2	18.8	0.1		306–1617	0.12	2.8	0.3
Collembola							1208.3	4530.4			1615–12788	14.44	190	40.1
Protura							0.3	1.1			87–567	0.04	4.7	3.8
Diplura							17.2	1	0.1		0–131	0.19	0.8	0.3
Thysanura	0.57	1.35	0.24	4.42	0–14	0–43	0.3	0.8	2.9	2.8	0–6	0.07	0.2	0.1
Orthoptera	0.05								1		0–2	0.01		
Dermaptera							0.3	0.2		0.1	0–22			
Embioptera				1.5			1.8	0.5	3.2	3	0–2			
Dictyoptera	5.3	5.27	11.56	16.21	3–16		1.8	1.3	1.9	0.3	0–2	0.06		
Isoptera											0–371			
Psocoptera					3–61	0–91	139	106.6	8.8		0–265	0.19	9.1	17.9
Hemiptera	2.8	3.19	2.56		13–181	37–123	22.8	71.9	5.5	13.7	3–539	0.98	39	16.7
Thysanoptera					61–189	11–21	116	324.5	10		4–105	0.31	4.5	7.8
Neuroptera	5.6	4.59	3.38				0.1	2				0.04		
Lepidoptera			0.6		0.27		1.7	3.2	32.7		20–95	0.53	3.7	3.8
Diptera	0.8	1.03	1.44		11–117	32–603	389.3	54.8	30.2		93–670	1.53	18	5.9
Hymenoptera	15.44	7.29	3.3		4–64	0–5					9–287	0.85	0.8	0.7
Coleoptera	9	5.43	31.5	25.58	13–355	117–464	50.8	112.5	7.4	5.1	408–744	5.03	13.9	8.9

A: *Anabasis* formation in Omayed, Egypt (Cancela da Fonseca *et al.*, 1984), B: *Thymelaea* formation in Omayed, Egypt (Cancela da Fonseca *et al.*, 1984), C: *Thymelaea* formation in Gharbaniat, Egypt (Ghabbour *et al.*, 1985), D: *Pinus halepensis* forest in Sophiko, S. Greece (Karamaouna, 1990), E: *Arbutus unedo* formation in Ikaria is., Greece (Magioris, 1989), F: *Quercus coccifera* formation in Ikaria is., Greece (Magioris, 1989), G: *P. halepensis* forest in Skopelos is., Greece (Radea, 1989), H: *P. halepensis* forest in N. Euboea, Greece (Marmari, 1991), I: *Q. coccifera* formation in Naxos is., Greece (Magioris, 1991), J: *Juniperus phoenicea* formation in Naxos is., Greece (Karamaouna *et al.*, 1993), K: *Eucalyptus marginata* forest in S.W. Australia (Postle, 1985), L: Sclerophyllous forest in Chile. Results expressed as percentages of total density (Di Castri, 1963), M: Sclerophyllous forest in Chile. Results expressed as number/dm³ (Di Castri & Vitali-Di Castri, 1981), N: Sclerophyllous mattoral in Chile. Results expressed as number/dm³ (Di Castri & Vitali-Di Castri, 1981).

a variety of techniques (Berlese–Tullgren funnels, Winkler–Moczarski apparatus, hand-sorting, etc.) and the other is to use pitfall traps of various sizes. In order to compare the results from various studies, it was decided for this review to use results obtained as individuals per m² for density measurements and individuals per trap per 30 days for pitfall results. All the results used refer to either the average or the minimum and maximum measurements obtained throughout at least one annual cycle.

The most important groups in all areas studied are Coleoptera, Araneae, Hemiptera, Diptera, Diplopoda and Pseudoscorpiones (Table 4.1). To these must be added Acarina, Collembola and ants that, although most probably the most abundant groups, are not always included because they require different methods. The drier areas of Egypt show a high density of Dictyoptera, Neuropteran larvae and Thysanura whilst within Coleoptera, family Tenebrionidae seems to dominate. These areas also show either a very low number or absence of Diplopoda, Chilopoda, Pseudoscorpiones and Psocoptera (Cancela da Fonseca *et al.*, 1984; Ghabbour *et al.*, 1985). These latter four groups have high densities in southwestern Australian forests of *Eucalyptus* (Postle, 1985). The Mediterranean areas of

Table 4.2. Number of animals caught in pitfall traps expressed as individuals/trap/30 days

	A	B	C	D	E	F	G	H	I	J
Mollusca				2						
Annelida					1					
Isopoda	0.4	0.1	0.5	7	11	54	0.1	1.4	6.8	0.2
Amphipoda							0.1	8.9		
Araneae	2	6.8	11.8	353	150	52	1.8	13.2	5.7	6.8
Pseudoscorpiones		0.1	0.4	2	2			0.9	0.1	0.8
Opiliones	2	1.8	6	11	28	22		1.1	0.2	
Scorpiones	0.1			5	2	7			0.1	0.1
Solpugida								1.4	0.5	0.5
Acarina				655	394	1	28.8	11.1		
Diplopoda		0.03	0.8	17	5	1	0.3	1.5	1.8	0.6
Chilopoda	0.9	0.04	0.6	29	7		0.1	0.8	0.1	0.1
Symphyla								0.2		
Collembola							143.2	47.6	0.7	4.9
Diplura	1.5									
Thysanura		0.2				11	1.2		0.2	3.6
Orthoptera		0.5		62	51		0.9	6.5	1.5	2.2
Dermaptera			0.5	2222	580	209	17.4	0.5		
Embioptera		0.04	0.1							
Dictyoptera		2.9	0.4	7	18	46	0.2	1.5		
Psocoptera		0.6					0.1	0.9	0.5	0.3
Hemiptera	3.6	2.2	4.9	65	9	17	0.4	10.8	2.3	3.6
Thysanoptera		0.03		2	1		0.3	0.2	1.9	0.2
Mecoptera				5						
Lepidoptera		0.2		3	8	1		0.3	1.1	1.3
Trichoptera					1					
Diptera		0.4					6.1	60	10.8	18.9
Hymenoptera	4.1			1264	894	693	32	149.3	6.2	7.6
Coleoptera	45.6	2.7		831	785	215	12.1	27.2	15.6	18.9
Siphonaptera			12.8					0.2	0.1	0.1
Strepsiptera								0.3		

A: Asphodel desert in C. Greece (Pantis *et al.*, 1988), B: *Quercus coccifera* formation in Naxos is., Greece (Magioris, 1991), C: *Juniperus phoenicea* formation in Naxos is., Greece (Karamaouna *et al.*, 1993), D: *Eucalyptus marginata* forest in Perth, S.W. Australia (Koch & Majer, 1980; Majer & Koch, 1982), E: *E. marginata* forest in Dwellingup, S.W. Australia (Koch & Majer, 1980; Majer & Koch, 1982), F: *E. marginata* forest in Manjimup, S.W. Australia (Koch & Majer, 1980; Majer & Koch, 1982), G: *Eucalyptus* forest in Mt. Lofty Ranges, S. Australia (Greenslade, 1988), H: Fynbos in Jonkershoek Valley, S. Africa (Donnelly & Giliomee, 1988), I: Xerophytic scrub mattoral in Fray Jorge Natnl. Park, Chile (Saiz, 1988), J: Thorny scrub mattoral in Fray Jorge Natnl. Park, Chile (Saiz, 1988).

Greece are characterized by high densities of Diplopoda, Pseudoscorpiones, Araneae and Coleoptera (Radea, 1989; Karamaouna, 1990; Magioris, 1989, 1991; Marmari, 1991; Karamaouna *et al.*, 1993) whilst in Chile, the dominant groups are Coleoptera, Hemiptera, Diptera, Psocoptera and Pseudoscorpiones (Di Castri, 1963).

Data from pitfall traps show similar tendencies (Table 4.2). Differences occur with the groups that move very slowly such as Diplopoda and hence are under-represented in the traps, or else are very active, such as Dermaptera (in Australia), Orthoptera and Opiliones.

Trophic levels

Looking at the main groups in the various trophic levels, one can see that detritivores are the most diverse. In the arid areas of Egypt, it is mainly the Dictyoptera together with Isopoda, Thysanura and Dipteran larvae that dominate at this level. In southwestern Australia, the dominant detritivore groups are Dipteran larvae, Isoptera and Diplopoda. In the Greek Mediterranean ecosystems and in Chile it is mainly Diplopoda and Dipteran larvae together with Isopoda.

Among the carnivores, Araneae and Pseudo-

scorpiones are present at high densities in all eco-systems. Neuropteran larvae are very abundant in Egypt whilst Chilopoda can be found in high numbers in certain cases.

Hemiptera seem to be the main phytophagous group in most Mediterranean-type areas. Finally, it must be noted that some groups that exhibit high densities, such as Psocoptera, Hymenoptera and Coleoptera, cannot be assigned to a parti-cular trophic level as they include species with different feeding habits.

The complexity of the soil communities can also be seen in the succession of one group by another at the same trophic level as environmen-tal conditions change. As climate changes from very wet to dry, the dominant macroarthropod decomposers on the island of Naxos, Greece, change from Diplopoda to Isopoda to Thysanura (Karamaouna *et al.*, 1993).

Spatial variation

In the majority of Mediterranean-type ecosystems there is significant spatial variation of the com-munity structure, caused mainly by the heterogen-eity of the environment. In the humid and arid areas, at the two extremes of Mediterranean-type ecosystems, this variation is less pronounced. The spatial heterogeneity is both horizontal and vert-ical. Horizontal heterogeneity is because of the patchiness of an environment that offers areas of open ground, ground under stones, thin or thick litter of various quality, ability to retain water or availability of space, litter under thick or sparse cover, stones in litter under cover, thick or sparse understorey vegetation, etc. Vertical heterogene-ity includes the above-ground vegetation, litter, stones and the soil which, at least in calcareous areas, is full of cracks and fissures and may retain in the deeper layers a relative humidity of 100% for most of the year (Ghabbour, 1979). The soil may have a more abundant fauna with higher densities than litter but litter has more species (Postle, 1985; Postle *et al.*, 1991). Bigot and Bodot (1972) have shown that because of the interdependence of invertebrates of the canopy, the litter, the stones and the soil, we cannot really speak of four different communities but of one, characteristic of the dominant plant species.

Spatial variation is accentuated by seasonal va-riation which causes significant micromigrations from one microhabitat to the other.

Temporal variation

Contrary to what was believed earlier (Di Castri & Vitali-Di Castri, 1981), there does not seem to be a common pattern of temporal variation in community structure in Mediterranean-type eco-systems. If we look at total arthropod densities or biomass, in some areas there are two peaks, one in spring and one in autumn, with a maximum in some areas in the spring and in others in the autumn. In other areas, only one peak is observed and this can be either during winter or summer. There are many reasons for this lack of a common pattern. In Australia, the summer season is by no means as dry as that experienced in similar cli-matic zones in the Northern Hemisphere. Summer rainfall is erratic and enables the domin-ant plants to produce new shoots. This may be a relict from a subtropical climate during the Terti-ary (Edmonds & Specht, 1981). In areas with mild winters, such as South Africa, many animal groups can produce high densities during winter, correlated with rainfall (Donnelly & Giliomee, 1988).

The temporal pattern becomes more com-plicated if we look at trophic levels or animal groups. Depending on which trophic level is more abundant, we see different temporal patterns. Herbivores are more closely connected with plant growth rate and therefore are expected to be in higher densities during the peak of the growth season. Decomposers are usually more abundant during the wetter but not the colder months. Therefore, if the summer is not completely dry, they may be active throughout. Predators and parasites depend less on seasons because there is always an amount of food available to them (Edmonds & Specht, 1981).

Individual groups show a large variety of tem-poral patterns. For example, from pitfall results, spiders in South Australia have one peak in early spring (Greenslade, 1988), in southwest Western Australia one peak in spring (Koch & Majer, 1980), in central and southern Greece one peak in early summer (Karamaouna *et al.*, 1993) or

one peak in autumn (Pantis *et al.*, 1988), whilst in S. Africa one peak in spring (Donnelly & Giliomee, 1988). Hemiptera in South Australia have one peak in the summer (Greenslade, 1988), in southwest Western Australia in spring and autumn (Majer & Koch, 1982), in central and southern Greece in spring (Karamaouna *et al.*, 1993) or in summer (Pantis *et al.*, 1988) and in S. Africa in the spring and autumn (Donnelly & Giliomee, 1988).

If we go deeper to the family or species level, temporal differences become more marked. In the central Aegean ecosystem dominated by *Juniperus*, the two peaks of Coleoptera – one in spring and one in the autumn – arise because of two families: Carabidae are abundant during spring and Staphylinidae during autumn. Within the Scarabaeidae, the spring peak was because of the abundant presence of two species whilst the autumn peak was because of the abundance of a third species (Trihas & Legakis, 1991). In the *Eucalyptus* forests of Western Australia, there is a wide array of responses to season, with some species being active throughout the year, some confined to a particular season and some to the cooler, warmer or the moister months (Postle *et al.*, 1991).

It can therefore be concluded that although temporal variation in the total number of soil invertebrates or even of one group may give a general idea of phenology, one has to go to the species or at least to the guild level in order to understand the ecological importance of temporal and spatial variation.

One final note of caution must be mentioned. It is unwise to compare phenologies of quantitative densities with phenologies of trapped animals. As concurrent samples have shown for the island of Naxos, Greece, for some groups there was a difference between peaks of up to two months because of a differential effect that environmental conditions may have on population density and activity (Karamaouna *et al.*, 1993).

Effects of environmental factors

The general trend that is known to occur in soil communities in Mediterranean-climate areas is that organic matter is responsible for spatial vari-

ation of the community structure at a given time whilst seasonal variations in temperature and water availability are responsible for temporal population changes (Di Castri & Vitali-Di Castri, 1981). A number of other factors has been shown to play a role in structuring soil communities. Wind action in exposed litter under *Thymelaea* bushes in Egypt causes both dispersal of litter and therefore diminishing organic matter and desiccation of the soil (Ghabbour *et al.*, 1984). The open, uncovered ground in overgrazed maquis ecosystems has both higher temperatures and reduced organic matter (Magioris, 1991). Therefore, in the more arid Mediterranean areas, temperature and water availability play a significant role in the spatial structuring as well as the composition of soil communities.

Interesting conclusions can be drawn by studying the combination of results from pitfall traps and quantitative samples. In winter, high humidity favours high densities, whilst low temperatures decrease mobility. In spring and early summer, low humidity has a negative effect on the presence of many species, whilst increasing temperatures increase their activity (Karamaouna *et al.*, 1992).

Effects of fire

Fire is an important factor in Mediterranean-type ecosystems as it is both a recurring natural phenomenon and a human-induced disturbance. Few studies have been concerned with the effects of fire on the soil invertebrate fauna. The basic conclusions can be summarized as follows.

Total density, species diversity and composition at the class or order level decrease after fire but recover with few exceptions after 2–7 years (Springett, 1971, 1976; Abbott, 1984; Majer, 1980b, 1984, 1985a,b; Sgardelis, 1988).

The soil animals that are more affected by fire are surface-active invertebrates, litter invertebrates (Majer, 1984, 1985a,b), particularly decomposers and especially those associated with the early stages of decomposition (Sgardelis, 1988), fungal feeders and juveniles (Springett, 1979). The impact of burning on these animals has important implications for the rate of nutrient cycling because many of them help regulate de-

composition of litter (Majer & Abbott, 1989). The time of recovery of these animals depends on the rate of recovery of the organic horizons and therefore of the vegetation (Sgardelis, 1988).

The fauna may be influenced by direct physical effects of fire but more significantly by longer-term changes in factors such as food availability, shelter and environmental conditions (Majer, 1984).

Fires late in the summer or in the autumn are less detrimental for soil and litter invertebrates than in spring or early summer as most groups are already taking measures to avoid the hot period of the year (Majer, 1980, 1985a,b).

Unburned plants, logs, patches of litter and areas under stones are important refuges for fauna in burnt areas (Whelan et al., 1980; Majer, 1980; Sgardelis, 1988). The phenology of many soil animal groups was still disturbed at least one year after the fire (Sgardelis, 1988).

There are significant differences in reaction to fire between taxa: immediate density reduction, delayed density reduction, temporary absence, density stimulation or no reaction (Majer, 1984). Results obtained from fire impact studies depend significantly on the intensity of fire studied, the type of experimental design or the taxonomic treatment used in the study (Majer, 1985a,b). Therefore, what are needed in these kinds of studies in Mediterranean-type ecosystems are adequate pre-fire data, adequate site replication, samples taken over a long period and animal identifications to species level (Majer, 1985a,b).

Effects of grazing

Although grazing is an important human activity in Mediterranean-type ecosystems, its effect on soil fauna has been little studied. It seems that the basic effect of overgrazing is to reduce densities of most taxa (Magioris, 1991). However, although protection from grazing may induce an increase of density in most taxa, some, especially the detritivores, are negatively affected, thereby allowing the herbivores to be the dominant groups (Cancela da Fonseca et al., 1984; Magioris, 1991). This may be because of the increase of phytomass and the absence of animal dung. Litter fauna is more

significantly affected by grazing whilst animals living in soil are less disturbed.

Under conditions of overgrazing, although the Mediterranean-type ecosystems are disturbed, their biota adapt to this stress by using seasonal and annual mechanisms of adjustment (Cancela da Fonseca et al., 1984). Some groups may use both grazed and ungrazed areas during their life cycles. Therefore, a system of periodic or alternate grazing may promote diversity (Magioris, 1991). This partial protection may be more beneficial than complete protection since it favours soil fertility, increases the rate of mineral turnover and does not exaggerate the density of herbivores which may endanger the vegetation in the long run (Cancela da Fonseca et al., 1984).

Effects of agriculture

With the intensification of agricultural practices in Mediterranean-type ecosystems, true detritivores of the original system, capable of dealing with the available plant and animal litter and adapted to the mediterranean climate, are replaced by other mesic detritivores adapted to changes in litter quality (less animal and more plant) and also adapted to the changed physical and chemical soil conditions. Meanwhile, the increase in plant biomass encourages the appearance and proliferation of cryptic phytophages (agricultural pests), occupying the niche of the removed large herbivores. Carnivores also change accordingly (Ghabbour et al., 1985).

Other effects

The effects of mining and subsequent rehabilitation on soil fauna have been studied principally in Mediterranean-type ecosystems in Australia. Highest densities were observed in areas revegetated with a diverse mixture of native plants mainly because of the formation of a species-rich understorey compared with the relatively simple monoculture of revegated areas (Majer & Abbott, 1989).

Trampling by humans in Mediterranean pine forests basically causes both a reduction in population density and changes in the phenology of

various groups. The most affected groups are the detritivores, some of which may be completely absent from heavily trampled areas. Most of the predators have lower densities and disturbed phenologies, whilst for taxa such as Dipteran larvae and Collembola, their phenology is not affected. Coleoptera seem to be sensitive indicators of the effects of trampling (Marmari, 1991).

Species richness

The patchiness of Mediterranean-type ecosystems is reflected in the high diversity of soil animal species compared with neighbouring temperate and arid regions. This high diversity has posed problems for the detailed study of these animals because identification to species level is hampered by the lack of specialists in systematics and the cost in time to sort the high number of samples needed to cover environmental heterogeneity. It is therefore not surprising that very few studies have gone to specific level.

Species richness follows in general the spatial and temporal patterns of abundance of soil animals. There are, for example, more species in humid areas than in arid ones (Di Castri & Vitali-Di Castri, 1981; Saiz, 1988). However, although the abundance of invertebrates is higher in soil than in litter, the diversity is higher in litter and diminishes progressively from the surface downwards (Postle, 1985; Saiz, 1988; Postle *et al.*, 1991). Species diversity also shows greater seasonal fluctuations in litter than in soil (Lions, 1977).

Less disturbed sites are richer in species than more disturbed sites and more diverse habitats are richer in species than more uniform ones (Gross, 1985). Sites at high elevations may have more (Di Castri & Vitali-Di Castri, 1981) or less species (Marcuzzi, 1966) than those at lower elevations and coniferous formations such as *Pinus halepensis* may have less species than sclerophyllous formations (Marcuzzi, 1968), although there are cases of coniferous formations having more abundant populations than sclerophyllous formations (Radea, 1989; Marmari, 1991). Lateritic soils may have more species than loamy soils (Postle *et al.*, 1991).

Conclusions

It is still too early to be able to have a detailed view or to construct a functional model of community structure for Mediterranean-type soil fauna. Whole areas of ecological research have yet to be explored, such as trophic interrelationships and connectance, effects of competition and predation on community structure, effects of invasive plants and animals, factors affecting species richness, fluxes of energy, relationships with other components of the mediterranean ecosystems, and many more. The most important element that arises from all recent work is the spatial, temporal and ecological complexity of this system, that can be better understood only by detailed species-level, long-term, seasonal and multi-sample studies and with the cooperation of scientists from all five areas of mediterranean climate in order to exchange information and to establish common sampling, statistical methods and techniques.

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