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25.4 Macroarthropods

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25.4.1 Introduction

The macroarthropods are those large enough to be sampled as individuals, in contrast to the microarthropods that are sampled by extraction from a fragment of habitat (Section 25.3; Dindal, 1990; Borror et al., 1992; Arnett, 1993). Although smaller macroarthropods overlap in size with the larger microarthropods (Figure 25.2), the distinction between them is a practical one, based on method of sampling. A functional difference lies in their impact on soils. Macroarthropods are capable of restructuring soil profiles or relocating large amounts of soil, whereas microarthropods typically inhabit (and do little to modify) the existing pore spaces in soil (Coleman et al., 2004). Two insect groups, ants and termites, are responsible for major disruptions of soil profiles and have thus been classified as ecosystem engineers (Jones et al., 1997; Jouquet et al., 2006), while other macroarthropods may cause some disturbance. Examples include emergence tunnels of periodical cicadas (Insecta: Homoptera) (Whiles et al., 2001), or chimneys made by terrestrial crayfish (Crustacea: Decapoda) in hydric soils (Welch et al., 2008).

The macroarthropods in soil systems are a highly diverse group. Most terrestrial insect orders contain species that live in the soil at some phase of their life cycle. Transient species (some Lepidoptera), are those that overwinter or pupate in surficial soil layers. Other temporary residents such as midges and other flies spend their immature stages in the soil but emerge as adults to feed elsewhere. Permanent soil residents, such as predaceous beetles, remain in the soil or on soil surfaces. Spiders (Araneae) and centipedes (Chilopoda) are numerous and important predators in soil systems (Kastan, 1978; Camatini, 1979; Kevan and Scudder, 1989; Foelix, 1996). Detrivores include millipedes (Diplopoda) and sowbugs (Isopoda) (Shachak et al., 1976; Camatini, 1979; Snider and Shaddy, 1980). Scorpions (Scorpionida) and windscorpions (Solifugae) are important predators in desert systems (Crawford, 1981; Williams, 1987). Ants fall into several feeding guilds, and are diverse, abundant, and nearly ubiquitous in tropical and temperate ecosystems (Keller and Gordon, 2009). Several groups of macroarthropods (e.g., Coleoptera, Diptera, Lepidoptera) are considered pests in agricultural systems and can cause significant economic impacts either through crop and forage damage, or through expenses associated with their control (e.g., McCracken et al., 1995; Jackson and Klein, 2006; Doğramaci and Tingey, 2009).

25.4.2 Biology and Ecology

The major groups of macroarthropods likely to be found in soil and litter samples are listed in Table 25.7. The list is not inclusive

TABLE 25.7 Major Groups of Macroarthropods

Class	Order	Common Name(s)
Arachnida	Araneae	Spiders
	Scorpiones	Scorpions
	Opiliones	Phalangids, harvestmen
	Pseudoscorpiones	Pseudoscorpions
	Solifugae	Windscorpions
Malacostraca	Isopoda	Sowbugs, pillbugs, woodlice, roly-polies
Diplopoda	Ten orders	Millipedes
Chilopoda	Four orders	Centipedes
Hexapoda	Hymenoptera	Ants, wasps
	Isoptera	Termites
	Coleoptera	Beetles, rove beetles, tiger beetles, white grubs, wireworms
	Diptera	Flies, clusterflies, midges, leatherjackets, maggots
	Lepidoptera	Armyworms, potato tuberworms
	Homoptera	Cicadas, leafhoppers
	Dermaptera	Earwigs
	Diplura	Diplura
	Protura	Protura
	Neuroptera	Antlions
	Twenty-one other orders	

because, aside from representatives of the minor orders of arachnids and insects not listed, samples may also include representatives of major orders not usually considered to be soil fauna. Grasshoppers and crickets are frequently found on the soil surface and in pitfall traps. Even caterpillars that have descended from plant canopies to pupate in soil will be sampled. In fact, nearly every free-living group of terrestrial arthropods may occasionally enter soil food webs as prey items.

The majority of the scientific literature deals with individual taxa in detail, rather than providing overviews of entire macroarthropod faunas. Where general overviews do exist, they attempt broad syntheses, often without detailed information about macroarthropods (Dindal, 1990; Borror et al., 1992). The biology and importance of some ecological groups, such as root feeders, remain poorly known (Hunter, 2001; Blossey and Hunt-Joshi, 2003; Coleman et al., 2004; Johnson and Murray, 2008).

Macroarthropod fauna vary considerably between and within types of ecosystems. Several workers have suggested that macroarthropods can be used as indicators of soil quality in agricultural or pollution contexts (Linden et al., 1994; Kuperman, 1996; Lobry de Bruyn, 1997), and others have indicated that belowground arthropod herbivores have potential for use as biological control agents for invasive plant species, but this potential is largely unexplored relative to aboveground insect herbivores (Blossey and Hunt-Joshi, 2003). Forested ecosystems in general contain macroarthropod fauna dominated by millipedes, spiders, flies, and beetles (Table 25.8). Numbers and biomass tend to be greater in hardwood than in evergreen forests, where microarthropod abundance is high (Section 25.3). Spiders, carabid beetles, and crickets are abundant in pitfall traps placed in agricultural areas (Blumberg and Crossley, 1983; House and Stinner, 1983). Most species of macroarthropods may be more sensitive to cultivation than other soil fauna, and as a result, investigations have neglected the sensitive species in favor of the abundant ones (Wolters and Ekschmitt, 1997). Spiders are the most abundant and probably the most important of the predaceous macroarthropods in terms of their impact on food webs (Ekschmitt et al., 1997; Lawrence and Wise, 2004; Wise, 2004). The ranges of macroarthropod population sizes vary widely. Considerable overlap in abundance of macroarthropod taxa among different ecosystems has been found for millipedes and centipedes, although arable land tends to contain the lower part of the range. The ranges listed in Tables 25.8 and 25.9 illustrate the differences that occur between habitat types and seasons. Adjacent forest, grassland, and agricultural lands often have markedly different species within more general taxonomic groupings such as spiders (Reichert and Lockly, 1984; Draney, 1992). The range in measured abundance is also somewhat affected by method of sampling, and the size-based definition used to delineate "macroarthropod" (Table 25.8, Figure 25.2), and additional difficulty in establishing accurate density estimates arises from the nonrandom, often highly aggregated nature of macroarthropod distribution.

25.4.2.1 Social Insects

Collectively, ants and termites are responsible for major modifications of soil. Termites are typical insects of tropical and subtropical regions and may be dominant in arid or semiarid ecosystems (Lee and Wood, 1971; Bryan, 1978; Hölldobler and Wilson, 1990; Stork and Eggleton, 1992; Bolton, 1994; Arriaga and Maya, 2007). The following soil modifications are brought about by the activities of termites: (1) physical changes of soil profiles, (2) changes in soil structure, (3) changes in the nature and distribution of organic matter, (4) changes in the distribution of plant nutrients, and (5) construction of subterranean galleries (macropores). Ants are more widely distributed than termites, occurring in most terrestrial habitats, and exhibit a variety of trophic behaviors including herbivory (foliar and seed feeding), omnivory, and many are predaceous. Their colonies are smaller than those of termites, but they are responsible for the same kinds of soil modifications. In tropical systems, leaf-cutter ants are among the most important arthropod herbivores with dramatic effects on incorporation of organic materials to belowground pools, and these ants have been implicated as affecting forest plant community dynamics when they reach high abundances (particularly in forest fragments where their predators are absent) (Terborgh et al., 2001). As predators, ants may have a considerable impact on herbivorous insects. The importance of ants as predators of insect pests has been well demonstrated in a variety of stable forest ecosystems. Close, evidently coevolved, relationships exist between some plant and ant species, but in relatively unstable, annual agroecosystems, less is known of the importance of the ants.

TABLE 25.8 Ranges and Mean Abundance (Number m^{-2}) of Selected Major Macroarthropod Taxa Reported from Differing Ecosystems Worldwide

Habitat Type	Location[a]	Diplopoda	Diptera (Larvae)	Araneae	Coleoptera (Larvae)	Chilopoda	Method[b]	Sources
Grassland	KS	~5–74	—	~35	~5–30	3–6	HS	Blair et al. (2000), Callaham et al. (2003)
Upland pine	FL	241–276	8–12	12–19	43–82	4–8	TF	Frouz and Ali (2004)
Upland hardwood	FL	23–66	~8	16–31	27–47	4–16	TF	Frouz and Ali (2004)
Spruce forest	FIN	—	—	~700	~371	—		Siira-Pietikäinen et al. (2003)
Mediterranean pine	ISL			40–214			BF	Broza and Izhaki (1997)
Beech forest	FRA	30–40	12–23	16–27	43–52	~46	HS	Aubert et al. (2002)
Mixed forest	FRA	15–17	15–56	15–20	37–41	18–21	HS	Aubert et al. (2002)
Clear-cut with slash	SWE	39	238	289	224	—	TF	Bengtsson et al. (1997)
Clear-cut no slash	SWE	74	106	152	133	—	TF	Bengtsson et al. (1997)
Pasture	FRA	0	—	11	62	16	HS	Decaëns et al. (1998)
44 year fallow	FRA	1	—	13	17	58	HS	Decaëns et al. (1998)
Maple forest	FRA	3	—	6	15	63	HS	Decaëns et al. (1998)
Pine forest	FRA	0	—	7	0.5	39	HS	Decaëns et al. (1998)
Planted birch in forest soil	FIN	0–6	133–208	129–196	338–606	55–95	HSM	Huhta (2002)
Planted birch in agricultural soil	FIN	0–8	126–265	101–156	220–367	2–10	HSM	Huhta (2002)
Natural birch	FIN	0–80	173–360	247–340	220–814	20–91	HSM	Huhta (2002)
Deciduous forest	CAN	139	1003	—	288	—	HSM	Paquin and Coderre (1997)
Mixed forest	CAN	64	299	—	277	—	HSM	Paquin and Coderre (1997)
Coniferous forest	CAN	32	32	—	85	—	HSM	Paquin and Coderre (1997)
Atlantic forest	BRA	~20–320	~100–380	~50–100	~100–230	~10–50	BTF	Pellens and Garay (1999)
Eucalypt plantation	BRA	~0–320	~40–100	~10–120	~100–200	~0–2	BTF	Pellens and Garay (1999)
Acacia plantation	BRA	~0–100	~20–240	~0–100	~230–770	~0–10	BTF	Pellens and Garay (1999)
Norway spruce forest	ITA	24	0	—	835	287	DF	Salmon et al. (2006)
Regenerating spruce	ITA	47–119	287–454	—	239–287	478–957	DF	Salmon et al. (2006)

Notes: When data are presented as a range, this indicates that the authors were reporting mean densities from different sites of similar vegetation or were reporting densities from the same site from different seasons. When data are preceded by "~," this indicates that numbers were estimated (or recalculated) from graphical data and not transcribed directly from tabular data in source materials or derived from multiple sources.

[a] KS, Kansas; FL, Florida; FIN, Finland; ISL, Israel; FRA, France; SWE, Sweden; CAN, Canada; BRA, Brazil; ITA, Italy.

[b] HS, hand sorting; TF, Tullgren funnel; BF, Berlese funnel; HSM, hand sorting under dissecting microscope; BTF, Berlese–Tullgren funnel; DF, dry funnel, all as reported by authors in source materials.

TABLE 25.9 Abundance and Biomass of Macroarthropod Taxa in Three Ecosystems

	Arable Land		Temperate Grassland		Temperate Deciduous Forest	
Taxon	N m^{-2}	mg m^{-2}	N m^{-2}	mg m^{-2}	N m^{-2}	mg m^{-2}
Isopoda	5 (0–25)	15	1200 (500–7900)	1600	286 (96–1850)	93
Diplopoda	200 (70–400)	—	— (500–7900)	1250	55 (210–700)	618
Chilopoda	100 (40–220)	—	60 (63–387)	140	187 (50–790)	265

Source: Wolters, V., and K. Ekschmitt. 1997. Gastropods, isopods, diplopods and chilopods: Neglected groups of the decomposer food web, p. 265–306. *In* G. Benckiser (ed.) Fauna in soil ecosystems. Marcel Dekker, New York.

Numbers in parentheses indicate ranges of abundance estimates.

25.4.2.2 Myriapods

The many-legged arthropods (myriapods) are abundant in undisturbed soils of many types, but less abundant in agricultural systems (Table 25.8). Millipedes are major saprovores, feeding upon decomposing organic matter in a variety of ecosystems. Although moisture dependent, they are among the macroarthropods of desert ecosystems (Crawford, 1979). Millipedes, which are important in Ca cycling in forests, have a calcareous exoskeleton and may process 15%–20% of Ca inputs into forest floors (Coleman et al., 2004). Some millipedes are obligate coprophages, feeding on their own microbially enriched fecal matter, while others excrete noxious chemicals as a defense mechanism against predation.

Centipedes are ubiquitous and active predators in soil and litter habitats, able to run rapidly and capture small prey such as microarthropods (especially collembolans). Most are 3–5 cm in length, but tropical centipedes may exceed 30 cm. Typically, centipedes constitute about 20% of the predaceous macroarthropods in temperate forests, but the percentage is lower in subarctic, boreal, and dry forests (Albert, 1979). Species diversity is lower for centipedes than for other predators such as spiders and staphylinid beetles.

25.4.2.3 Spiders

Spiders are the most numerous of the predaceous macroarthropods in ecosystems ranging from forest to grassland to agroecosystems. The taxonomy of soil- and litter-dwelling spiders remains unsettled, especially for the numerous species in the family Linyphiidae, which contains many small soil species. Spiders, which are strictly carnivorous, are generalist feeders that attack insects but also feed upon other invertebrates, including other spiders (Wise, 1993). Despite their numbers, there is no consensus on the abilities of spiders to control insect populations (Riechert and Lockly, 1984). Spiders do not reproduce rapidly enough to keep pace with exploding prey populations. Also, many species are territorial. In forest habitats, spiders may act as a stabilizing influence on populations of forest floor invertebrates by maintaining a continual predation pressure.

25.4.2.4 Beetles

In terms of numbers of species, beetles are the largest order of insects, being found in every habitat except the oceans (Richter, 1958; Thiele, 1977). In soil systems, beetles include species that are phytophagous, saprophagous, and predaceous. Carabid, tenebrionid, and staphylinid beetles are numerous predators in disturbed and undisturbed systems alike. Together with spiders, carabids are the typical ground-surface macroarthropod predators taken in pitfall traps in agroecosystems. Other active predators included the tiger beetles (Cicindelidae) whose larvae construct belowground retreats from which they capture prey. Phytophagous beetles include the Scarabaeidae (June beetles) whose larvae feed extensively on roots. Larvae of elaterid beetles (wireworms) are important root feeders in cropping systems and in forests. Although predaceous beetles are conspicuous, especially on the soil surface in agricultural fields, the phytophagous species are probably more important. The predaceous carabids may exert some control on caterpillars such as armyworms and similar species. Gypsy moth caterpillars, descending to the soil of the forest to pupate, may fall prey to carabid beetles in large numbers.

25.4.3 Sampling and Analysis

Macroarthropods are sampled in several ways. A good review of the general methodology used for sampling populations of soil macroinvertebrates is given in Edwards (1991). The most basic method involves delineation of an area a square meter or less followed by hand sorting organic horizons and digging to a set depth the mineral horizons of soil and collecting all macroarthropods encountered. Tullgren funnels are useful for extracting arthropods from bulk samples of soil and litter, and this technique relies on heat and light stimuli to drive organisms from the samples (Section 25.4.2.3 and Figure 25.7). It is also possible to collect subterranean macroarthropods by taking soil cores (10–15 cm diameter) and sieving them, either dry or with the use of a wet sieving apparatus. Another technique used to sample macroarthropods involves the separation of organisms from samples by taking advantage of their relatively low specific gravity and the hydrophobic properties of their cuticles. This generally involves some kind of flotation of organisms from samples in a high density liquid (usually salt or sugar solutions; Edwards, 1991).

When investigators are strictly interested in sampling the greatest number of species (i.e., sampling for diversity and not abundance or density), other sampling techniques are useful. For example, Snyder et al. (2006) found that targeted hand collecting of millipedes from sites selected a priori as being likely for encountering specimens (rather than randomly assigned spatially based approaches) produced the largest number of species in the shortest time. Another qualitative method in widespread use involves pitfall traps—cans set flush with the soil surface

FIGURE 25.7 Large Tulgreen funnels for extraction of macroarthopods from soil cores and litter.

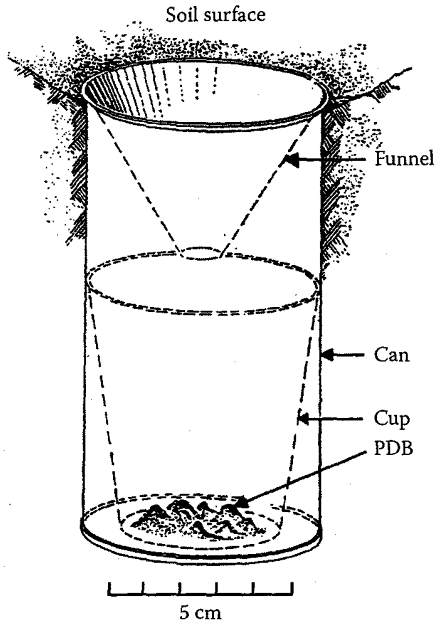

FIGURE 25.8 A pitfall trap for surface active macroarthropods. PDB = P-dichlorobenze preservative. (Reprinted from Reichle, D.E., and D.A. Crossley, Jr. 1965. Radiocesium dispersion in a cryptozoan food web. Health Phys. 11:1375–1384. With permission from Williams and Wilkins, Baltimore, MD.)

and containing a preservative (Figure 25.8). Pitfall traps are an inexpensive sampling technique, but are not entirely quantitative, since captures depend upon the mobility of animals as well as their density. In sampling programs designed for comparison of areas or seasons, pitfall traps are a preferred method (Bater, 1996). Each of these qualitative sampling methods can be rendered semiquantitative if care is taken to standardize the time that searching or trapping is conducted and comparisons may be made on the basis of equal effort collecting for a given habitat type or experimental manipulation.

Because ants and termites are social insects, population estimation for these insects requires special techniques. Species diversity of ants is readily sampled with baited pitfall traps (Romero and Jaffe, 1989), while subterranean termites are sampled using soil cores (Lee and Wood, 1971). Termite mounds may require complete destruction. A comparative sampling technique for desert termites uses rolls of toilet paper, which are placed on the soil surface and shielded from the sun with aluminum foil (Whitford et al., 1982).

Samples may be preserved in 70% alcohol prior to sorting. Although alcoholic storage is satisfactory for storage of specimens, most entomologists prefer that insects be pinned if possible. Different insect orders are pinned in different ways, and detailed instructions for pinning and labeling techniques are given in most entomology textbooks (Borror et al., 1992).

Sorting of adult macroarthropods into major taxa is straightforward. Reference to a general entomology textbook will allow the novice to make identifications to major hexapod taxa to family levels. More detailed sorting of other macroarthropod taxa such as spiders, diplopods, and chilopods may be done with the aid of literature guides (Dindal, 1990; Ubick et al., 2005). Additionally, because samples derived from subterranean sampling will usually include immature stages of Coleoptera, Lepidoptera, and Diptera (among others), special training is usually required for identifications, although a few groups are readily recognized. North American guides for the identification of immature insects including those found predominantly in soils are found in Peterson (1967) and Stehr (2005). Identifications of adult specimens to generic and species levels will also require services of a specialist in the taxonomy of the group. There is some promise in the development of molecular-based techniques for the identification of soil organisms, but to date these have been useful only for establishing the degree of genetic diversity in a sample, and not so useful for providing clues as to the identities of organisms (Wu et al., 2009). A DNA-based technique has been used to identify the gut contents of predatory beetles (Juen and Traugott, 2006), and in the future may prove useful for identification of bulk extracted organisms as well.

Once organisms have been collected and reliably identified, the data typically are reported in terms of presence/absence, relative abundance, or frequency of occurrence (e.g., from pitfall trapped collections), or when sampling is conducted in a spatially explicit way, in terms of density (individuals m^{-2}) or biomass (g ash-free dry mass m^{-2}). It is common for researchers to use abundance and identity data to calculate community measures such as indexes of diversity, evenness, similarity, or rank abundance. This kind of analysis is typically performed when sampling has been conducted in areas that have experienced different land uses or been subjected to experimental treatments that are expected to have influence on macroinvertebrate community structure (e.g., Decaëns et al., 2004; Callaham et al., 2006). Another useful and increasingly common technique for analyzing soil macroinvertebrate community structure is the use of multivariate statistical analyses to describe the dimensionality and variation in assemblages from different experimental treatments or habitats (e.g., Decaëns et al., 1998; Siira-Pietikäinen et al., 2003).

Because the net effect of macroarthropods on ecosystem functions such as decomposition or primary productivity are often dependent in some part on indirect effects through trophic interactions, ecologists are interested in food web structure and energy and nutrient flows through these webs. However, for subterranean linkages in food webs, observations have been difficult to make without fairly intensive disturbances to the system under scrutiny. Relatively recent developments in mass spectroscopy have improved this situation, and made it possible to process a large number of samples at reasonable cost for stable isotopic signatures of invertebrate tissues. This has greatly facilitated the determination of dietary relationships between individual taxa of belowground consumers (e.g., Callaham et al., 2000; Traugott et al., 2008; Seeber et al., 2009) as well as trophic relationships in soil food webs with better resolution than ever before (Halaj et al., 2005; Elfstrand et al., 2008), and this technology provides a fruitful avenue for future research on these organisms.

Finally, further recent advances in the soil food web and trophic interaction arena are due to molecular techniques that can achieve species-specific resolution for the analysis of gut contents (particularly useful in the analysis of gut contents of predators). These molecular approaches are of two basic types—those that utilize monoclonal antibodies and enzyme-linked immunosorbent assays (ELISA) to detect species (or group)-specific proteins from environmental samples (e.g., McKemey et al., 2006; Thomas et al., 2009), and those that utilize DNA-based assays where primers for suspected prey items are used to amplify the DNA of gut contents of predatory macroarthropods (Juen and Traugott, 2007; Kuusk et al., 2008). A good review of the methods for DNA-based approaches to assessing predator–prey interactions, along with a detailed discussion of challenges, is given in King et al. (2008). Both the DNA and ELISA techniques allow a level of resolution that is unprecedented in determining the diets of predators in soil food webs, and the ELISA technique has even been used to estimate densities of soil invertebrates (slugs) with reasonable accuracy at with greater speed than conventional estimation methods (McKemey et al., 2006). Fournier et al. (2008) conducted a comparative study to evaluate the relative sensitivities of ELISA and PCR techniques for detecting a specific prey item in the diets of 30 predator taxa, and found that after initial outlay of time and money for development of the antibody used in the assay, the ELISA technique was faster, more sensitive, and less expensive to process samples. Although these approaches promise major advances in future understanding of soil food webs, and have been used to good effect in aboveground contexts, they are in their infancy as applied to soil systems, and many of the methodological details are still under development (see King et al., 2008; von Berg et al., 2008). Thus, a great deal of work remains to be done in terms of methods development (e.g., production of appropriate primers and antibodies for detection of the full diversity of available food items in soil food webs), and this work must be accomplished before the potential of molecular techniques can be completely realized in soil ecological studies. Nevertheless, with continued growth in the number of investigators using these techniques, and with continued advances in molecular methodology, it is likely that the immense diversity and complexity of the soil biota will be understood with greater detail than had previously been possible.

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25.5 Enchytraeidae—Oligochaeta

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25.5.1 Introduction

The Enchytraeidae is a family of Oligochaetes that occur in terrestrial, littoral, and aquatic habitats. A total of some 600 species are now known worldwide, from the tropics to polar latitudes (Dash, 1990; Vaculik et al., 2004; Christensen and Dozsa-Farkas, 2006). Enchytraeids are mostly pale-colored and are anatomically similar to earthworms (only smaller). Their length ranges from 5 cm to less than 1 mm. Larger enchytraeids (up to 60 mm long) have been found in subarctic soils from the unglaciated portion of the northern Yukon (Canada) (Smith et al., 1990).

Of the Oligochaeta, earthworms (Lumbricidae) have been the subject of most studies. Enchytraeidae (also known as "potworms") have been studied less frequently although they are distributed throughout the world. The biology and ecology of enchytraeids have become somewhat better known during the