Chapter 6
Structure and ecology of soil macrofauna communities

KEY INDICATOR GROUPS AND THEIR ECOLOGY

The main groups of soil macrofauna in terms of their abundance and the importance of their activities in soil are: earthworms, termites, ants, Myriapoda, Diptera and Coleoptera (Lavelle and Spain, 2001).

Earthworms

Earthworms are terrestrial worms that burrow into and help to aerate soil. They often surface when the ground is cool or wet. They have a segmented body. The body may be divided into two parts: an anterior part with segments containing cephalic ganglions, reproductive organs, gizzards, calciferous glands and hearts; and a posterior part rearward of the hindgut comprising a series of rather similar segments (Figure 5).

Earthworms are invertebrates that may be present in very high densities. They are found in litter and soil in all except the coldest regions of the world. They feed on decaying litter and plant residues in soil. Earthworms are extremely important ecosystem engineers, and play a vital role in soil fertility. They are solitary and they are sampled most effectively by hand-sorting soil samples.

Earthworms have developed a range of adaptive strategies to live in soil. They can be divided into functional groups according to their feeding habits. They are classed into three main ecological types: epigeic, anecic and endogeic (Bouché, 1977; Lavelle, 1981; Lee, 1985). Those that are pigmented (presence of pigment in skin, generally more concentrated in the dorsal part) are divided into epigeic and anecic earthworms.

Epigeic earthworms (Figure 6) live within the litter layers, a changing environment, where they are subject to occasional drought, extreme temperatures and high predator densities. They are generally small (less than 15 cm long on average when adult), homogeneously pigmented (green, blue or reddish) and have rapid movements.

FIGURE 5
General view of an earthworm

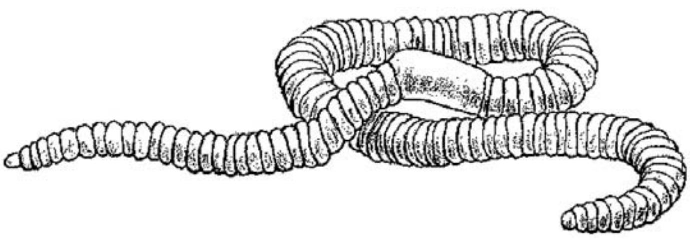


FIGURE 6
Epigeic earthworm

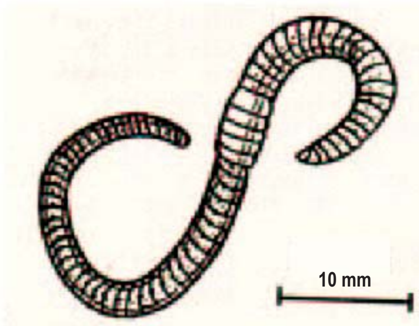


FIGURE 7
Anecic earthworm

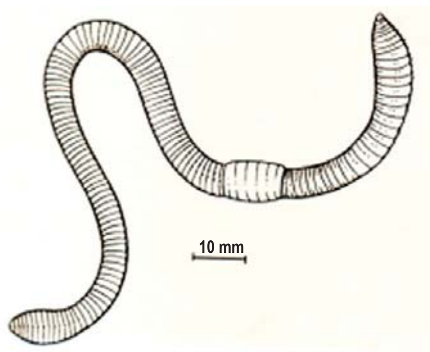
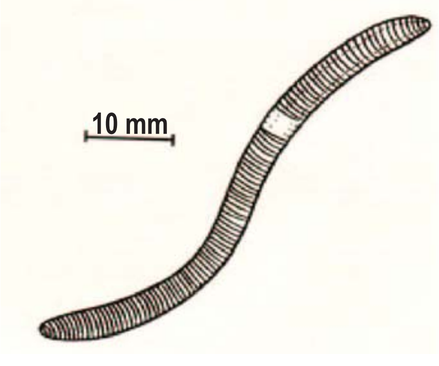


FIGURE 8
Endogeic earthworm



Anecic earthworms (Figure 7) feed on surface litter that they mix with soil. They spend most of their time in the soil. Anecic earthworms are large (more than 15 cm long when adult). They are pigmented dark green, blue, brown or reddish and the pigmentation is concentrated in the antero-dorsal part of the body. They dig subvertical galleries in the soil. The tail may be flat and enlarged in most common species.

The unpigmented earthworms (no pigment in skin, same colour on the dorsal and ventral parts, pink or slightly brown owing to the soil ingested) that live and feed in the soil are called **endogeic** earthworms (Figure 8).

The effects of earthworms in the soil differ according to the ecological category of the species involved. However, in many agricultural systems there may be only one type of earthworm.

As a result of their wide range of adaptations, earthworms have diverse functions in the soil (Plate 7). For example, epigeic earthworms are very efficient at making compost but have no impact on soil structure. Anecic earthworms strongly influence soil properties, they build a network of galleries near to the soil surface and deposit casts on the soil surface. Their activity enables the incorporation of large amounts of leaf litter into the soil. Endogeic earthworms are very important in soil structure because of their burrowing activities and their impact on soil aggregation (a concentration of fine soil particles) and SOM stabilization.

Earthworms generally exert beneficial effects on plant growth. However, negative or null effects may be induced in particular situations. The effect on grain yields is also proportional to the earthworm biomass (> 30 g fresh weight) (Brown *et al.*, 1999), although very high biomasses of a single species of earthworms (e.g. *Pontoscolex corethrurus*) may inhibit production under particular situations (see example above). Once the earthworms are established, a dynamic cropping system – involving crop rotations with long-cycle crops or perennials with good organic matter additions – contributes to securing lasting benefits from earthworm activities.

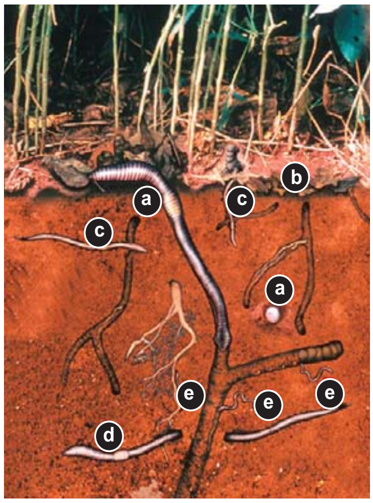


Plate 7
Functional diversity and significance of earthworms (adapted from I. Fabbri, UNESCO).

The following exercise, Exercise 5, increases awareness of the effects of earthworms in 'biotillage' – mixing and aerating soil through their burrowing activities.

EXERCISE 5: EARTHWORMS IN ACTION

Background

A terrarium is a closed ecosystem. Animals cycle the nutrients inside the container. The water, oxygen, and carbon dioxide are used, reused, and re-reused. However, energy in the form of sunlight does come from the outside.

As earthworms burrow through the soil, they consume large quantities of soil and fresh or partially decomposed organic matter from the soil surface. Earthworms deposit faecal material (casts) throughout and on top of the soil. As earthworms go upwards and downwards through the soil, they mix soil from the different soil layers with plant and animal debris from the soil surface. This mixing helps make nutrients more available for plant growth and increases water infiltration and air circulation in soil. Earthworm activity also helps roots to go deep into the soil.

Goal

To observe how earthworms dig in the soil and the effects they produce.

Time required

About 45 minutes to create the terrarium (also this can be prepared in advance).

The terrarium should be constructed knowing that results must be observed over several days.

Materials

Paper and pens.

For bottle ecosystem construction:

Two 2-litre clear plastic bottles, a knife, two pieces of mesh not very large (a mosquito net), string, some iron wire, and a lighter.

For the terrarium:

Gravel, fine sand, bedding material, dark potting soil, two pieces of tin foil or dark coloured paper, and two anecic and two endogeic earthworms.

Procedure

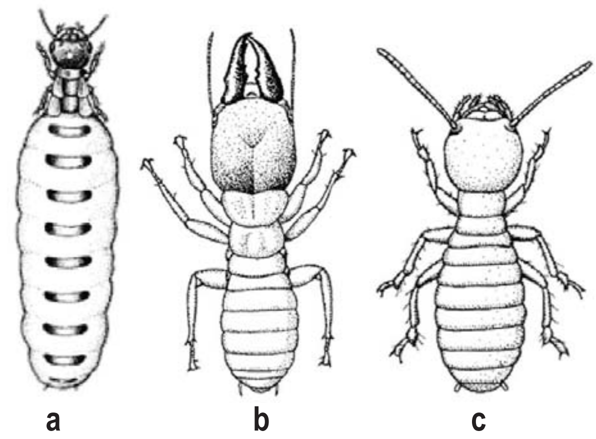
1. Construct two bottle ecosystems for the earthworms. For this:
   a. Rinse the bottles with water only and remove any labels.
   b. Cut the top 15 cm off each bottle.
   c. Make four to six drainage holes in the bottom of each bottle using the iron wire (which you heat with a lighter).
2. Add the following components to the bottom of each ecosystem in this order:
   a. Add some clean, washed gravel to the bottom of the bottle.
   b. Add a layer of moist bedding material.

c. Place a layer of dark potting soil on the moist bedding material.
d. Add a layer of moist sand.
e. Add another layer of dark potting soil (local soils with different colours can be used to realize this exercise).
f. Add a thin layer of organic matter (food). You can pick up some litter in the field or add some fresh vegetable leaves.
g. Add four earthworms on top of the organic matter (two anecic and two endogeic) in one of the bottle ecosystems. Leave the other as a control for your experiment.
h. Put the mesh on the surface of each bottle and fix it using a piece of string.
i. Draw a picture of your ecosystems.
j. Form the tin foil around the bottle ecosystem to limit the amount of light reaching the worms.
k. Place the ecosystems at room temperature or a bit cooler (15–22 °C). Do not place them in direct sunlight.
l. Check your bottle ecosystems every day. Make sure that you:
    i. moisten the soil (about 200 ml of water in each bottle);
    ii. add more moistened food to the top layer if necessary;
    iii. observe your ecosystems and record your observations;
    iv. draw a picture of your ecosystems.

Questions to discuss and points to analyse

1. What happens to the organic matter on the surface of the ecosystem with earthworms?
2. And without earthworms?
3. What do earthworms do with soil layers?
4. Do you see differences between the burrowing activities of the anecic and endogeic earthworms?
5. Why are earthworms considered to be decomposers?
6. Based on your observations, what do you think are the benefits of having earthworms in soils?

FIGURE 9
Main castes of termite colonies:
a) queen; b) soldier; c) worker



Termites

Termites are social insects. This means that they are organized, forming colonies where various castes (different individuals with different roles in the colony) with a set of morphological and physiological specializations coexist. The main castes are: the queen (the termite that forms the colony), the workers and the soldiers (Figure 9). They are abundant and considered a serious pest in dryland areas of Africa. It is important to note that some individuals of the society (reproductive ones) have wings, although they will always be found with the other wingless members of the society. (figure 9)

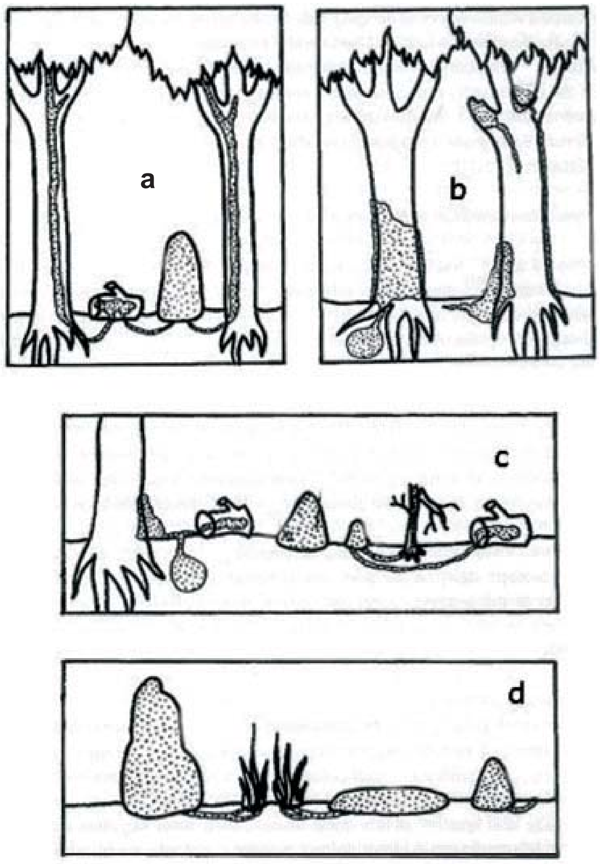
There are about 3 000 species of termites worldwide. Neither individual termites nor colonies normally travel long distances. This is because they are constrained to live within their territorial border or within their food materials. A number of species feed on living plants and some may become serious pests in agricultural systems where dead residues are scarce, e.g. in forest plantations (Wood, 1996). Most species feed on dead plant materials above or even below the soil surface. These materials include decaying material, e.g. dead foliage of vegetation, woody materials, including roots, seeds and even the faeces of higher animals (Lavelle and Spain, 2001). There are also soil–wood feeders and soil feeders, this means they ingest a high proportion of mineral material. Their nutrition derives mainly from well-decayed wood and partly-humified SOM. Another group of termites grows fungi in its nests (fungus-growing termites).

In general, termites may be separated into five broad groups according to the type of food they ingest (Josens, 1983; Eggleton *et al.*, 1996):

- Grass harvesters: these termites harvest the dead leaves of grasses, which may be stored in their nests; they belong to the families Hodotermitidae and Termitidae. A number of species in this category also collect litter: the tropical Australian species Drepanotermes rubriceps stores a wide range of materials in its low epigeal mounds including leaves of grasses, broad-leaved species and a diversity of seeds and small woody litter (Gay and Calaby, 1970).
- Surface litter feeders: termites that forage for leaf litter, live or dry standing grass stems and small woody items, usually cutting the material before consumption or portage to the nest system. They include some subterranean and mound-building Macrotermitinae as well as certain Nasutitermitinae that forage on the surface of the ground, and at least one lower termite, Hodotermes mossambicus, with a similar habit.

- Wood feeders: termites feeding on wood and excavating galleries in larger items of woody litter, which may become colony centres. This group also includes termites having arboreal, subterranean or epigeal nests but feeding elsewhere (Figure 10), and many Macrotermitinae cultivating fungus gardens. ("Wood" includes dead branches still attached to living trees and dead standing trees as well as fallen larger items which are fresh, or in any except the terminal stages of decay).
- Soil-wood feeders: termites feeding in highly decayed wood which has become friable and soil-like, or predominantly within soil under logs or soil plastered on the surface of rotting logs or mixed with rotting leaves. This group is synonymous with "intermediate feeders", sensu de Souza and Brown (1994), but not the same as the category "rotten-wood feeders" recognized by Collins (1989).

FIGURE 10
Selected termite nests in a tropical Australian savannah: (a) and (b) species associated with the exteriors of trees; (c) species attacking wood on the soil surface, dead shrubs and the bark of trees and soil-feeding species living in the mounds of other termites; and (d) nests of epigeal mound-building, grass-harvesting and litter-feeding species nests



Source: Lavelle and Spain (2001).

- Soil feeders (humivores): termites distributed in the soil profile, the organic litter layer and/or epigeal mounds, feeding deliberately on mineral soil, apparently with some degree of selection of silt and clay fractions. Although the ingested material is highly heterogeneous, there are higher proportions of SOM and silica, and lower proportions of recognizable plant tissue than in other groups (Sleaford et al., 1996).

The categories are not mutually exclusive and many species will feed upon at least two sources, especially under unfavourable conditions.

Termites are predominantly tropical in distribution. They may reach extremely high densities. Termites are important ecosystem engineers, and may have a similar role to earthworms in promoting soil fertility in tropical systems. They influence:

(i) soil porosity and texture through tunnelling, soil ingestion and transport and gallery construction; and (ii) nutrient cycling through the transport, shredding and digestion of organic matter.

Ants

Ants may occur in great numbers in soils and on their surfaces. Ants are effective predators, influencing herbivore populations and plant productivity. As with termites, ants modify soil chemical and physical properties by transporting food and soil materials during feeding and mound and gallery construction.

Because of their feeding habits, they are of less importance in regulating processes in the soil than termites or earthworms. In agricultural systems, the leaf-cutting ants of the genera *Atta*, *Acromyrmex* and *Trachymyrmex* are exceptions. They construct very large nests and their harvesting may lead to the incorporation of large amounts of organic matter and nutrients into the soil. In some locations, ants may have an important role in bioturbation (Levieux, 1976; Cowan *et al*., 1985; Lockaby and Adams, 1985) and add their effects to those of other groups of soil macrofauna.

In agriculture, although generally seen as pests, ants may protect crop herbivores such as honeydew-secreting *Homoptera* or act directly as herbivores themselves. Their beneficial role as effective predators should also be noted (Way and Khoo, 1992).

Where they are abundant, ants modify the physical structure of the soil (Figure 11 through the creation of systems of galleries and chambers. This activity influences soil porosity, aeration, infiltration and drainage and creates habitats for smaller organisms.

The activities of ants can also influence the soil chemistry by increasing the amounts of organic matter, P, K and N in the mounds (Petal, 1978; Carlson and Whitford, 1991). The physical changes and the elevated chemical status of many soil materials associated with mounds induce greater mineralization activity by decomposers (McGinley *et al*., 1994) and root and mycorrhizal growth.

FIGURE 11

A) Ants moving soil (from Nardi, 2003); B) a black ant transporting soil out of the nest

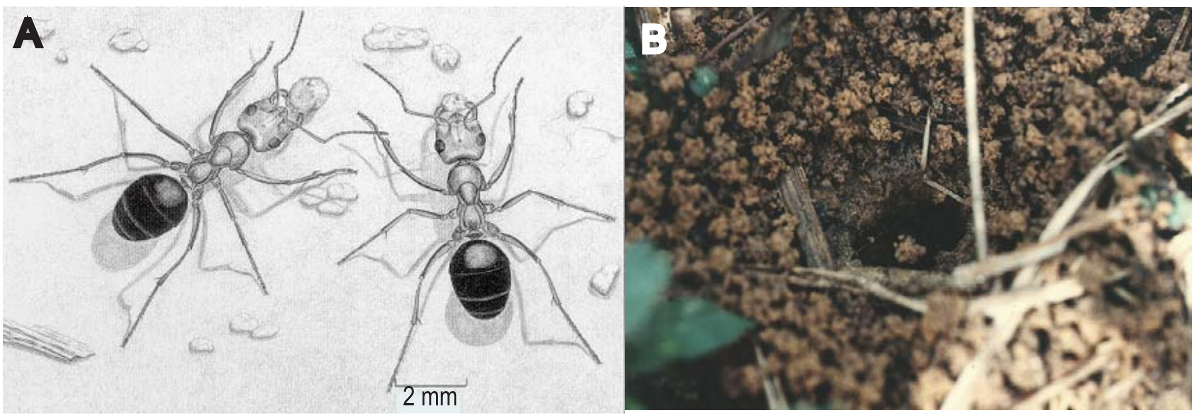


Plate 8
A millipede from Guadeloupe.

Other macrofauna such as woodlice, millipedes and some types of litter larvae, which act as litter transformers with an important shredding action on dead plant tissue, and their predators (centipedes, larger arachnids and some other insects) are also key functional groups that have an important influence on soil fertility.

Myriapoda

The group of Myriapoda comprises all soil invertebrates with more than seven pairs of legs. The largest myriapods are divided into two classes: Chilopoda (centipedes) and Diplopoda (millipedes).

Millipedes and centipedes are found on the soil surface, in the litter layers, under tree stumps and decaying logs where they can find food and humidity. Most have a limited ability to penetrate the soil. They move through it by displacing it in all directions.

Plate 9
A scolopendra (centipede).

Millipedes are generally large-bodied arthropods (Plate 8) that feed on plant debris (decomposed wood or leaf materials), leaving behind their numerous droppings that contribute to humus and soil formation. z

Centipedes are generally long, flattened, sometimes large-bodied animals (Plate 9) that actively hunt and eat other invertebrates (and occasionally small vertebrates) in the litter. However, some very small, unpigmented, blind centipede species (mostly *Geophilomorpha*) go down into the soil, following galleries and crevices to about 50 cm. They have large jaw-like structures (forcipules) with poison glands at their base (predators).

Fly larvae

Flies (Diptera) larvae are a very diverse group with an extremely wide range of food sources. They feed on decaying plant material but they tend to be internal feeders on dead plant and animal remains. Sometimes, they can become predominant in soils and may realize an important reduction in litter mass (Healey

FIGURE 12
Different types of Diptera larvae

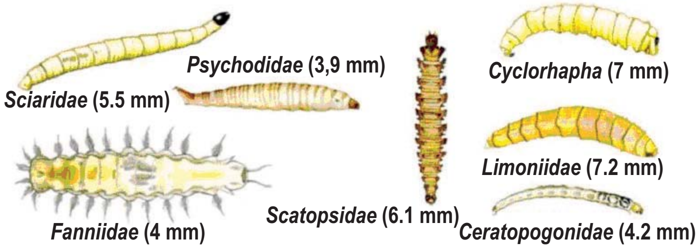
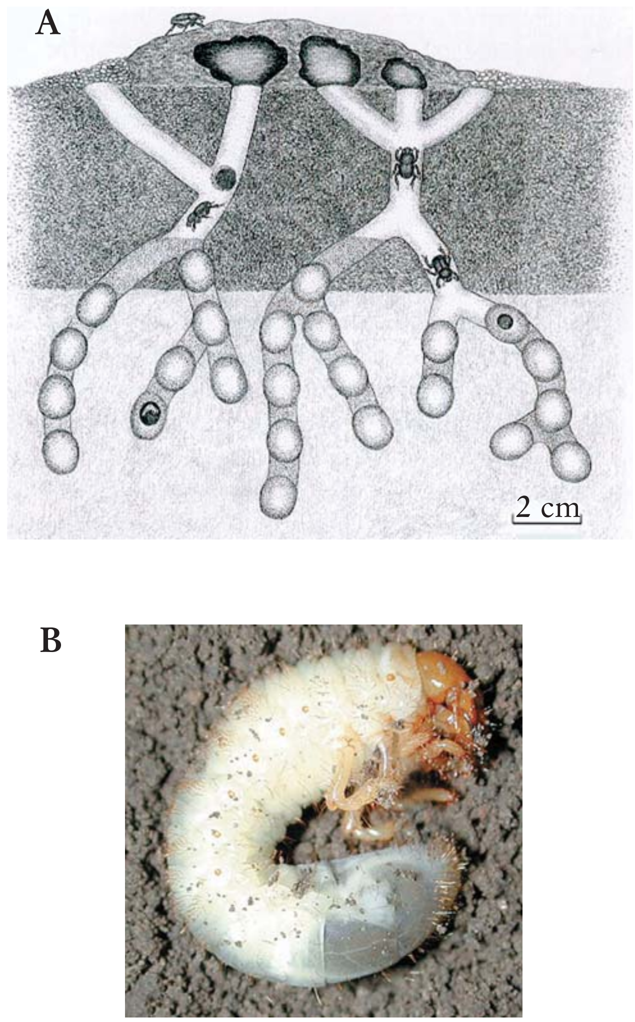


FIGURE 13
Activity of dung-beetles: A) subvertical galleries (from Nardi, 2003); B) white grub



and Russel-Smith, 1971; Deleporte, 1987). They live mostly in litter. They are probably most important in cold temperate soils, and can be very abundant in pastures (e.g. Tipulidae). Although often easy to confuse with Coleoptera larvae, they tend to be more slender, less grub-like, have smaller mouthparts, and move more actively in the soil (Figure 12).

Beetles

Beetles (Coleoptera) are the most diverse group of organisms in the world (with perhaps 3–5 million species). They differ widely in size (1–100 mm) and in the ecological roles they have in the soil and the litter. They have a similarly high diversity of feeding habits, and soil beetles can feed on fungi, plant roots, other invertebrates, buried wood, dung, corpses and other rotting organic matter. They have a wide range of feeding habits, being saprophagous, phytophagous or predators. Three groups are of great relevance in agricultural soils: (i) larvae from the family Scarabeidae (dung-beetles); and (ii) Curculionidae and (iii) Melolonthinae beetles, whose larvae (white grubs) may be abundant in grasslands and affect crop production by feeding on living roots (Villalobos and Lavelle, 1990).

Dung-beetles play a crucial role by burying dung in natural savannahs and grasslands used for cattle grazing in Africa (Brussaard and Hijdra, 1986). They dig subvertical galleries (like anecic earthworms) 10–15 mm wide down to 50–70 cm with a variable number of chambers that are further filled with large pellets of dung (Figure 13). The adult beetle lays one egg in each of these chambers and then the larva feeds on the pellet to complete its cycle (Lavelle and Spain, 2001). Their presence is generally indicated by small mounds a few centimetres high on the soil surface (Hurpin, 1962).

The following exercises, Exercises 6 and 7, enables participants to classify soil macrofauna, estimate their abundance and observe their effects on the soil, especially on soil structure, porosity and hence water infiltration (Figure 13).

EXERCISE 6: ESTIMATING SOIL MACROFAUNA ABUNDANCE AND ACTIVITIES IN SOIL

(Adapted from Source Anderson and Ingram (1993) and the IBOY report on soil macrofauna (**http://www.bondy.ird.fr/lest/iboy/workshop-report.pd**f) – Lavelle and Spain (2001))

Background

The category of soil macrofauna is defined as consisting of those soil invertebrates that are generally > 2 mm in diameter. Soil invertebrates can be classified according to their feeding habits and distribution in the soil profile as follows:

- Epigeic species, which live and feed on the soil surface. These invertebrates effect litter comminution and nutrient release. Mainly arthropods, e.g. ants, beetles, cockroaches, centipedes, millipedes, woodlice and orthopterans, together with gastropods and small, entirely pigmented earthworms (dark red, green or brown in colour). They are fast growing and move quickly.
- Anecic species, which remove litter from the soil surface through their feeding activities. Considerable amounts of soil, mineral elements and organic matter may be redistributed through these activities, accompanied by physical effects on soil structure and hydraulic properties. Earthworms (light or no pigmentation and slow movers) and non-soil-feeding termites are the main groups in this category, but it also includes some arachnids.
- Endogeic species, which live in the soil and feed on organic matter and dead roots, also ingesting large quantities of mineral material. The two main groups are earthworms (large, antero-dorsal pigmentation and very muscular, with a wedge-shaped tail) and soil-feeding termites.

Goal

By the end of the exercise, participants will know the standard characterization of soil macrofauna in different land-use systems and their relation to soil physical properties, as well as the significance related to the presence of beneficial or harmful groups of soil macrofauna in agricultural soils. The main groups of soil macrofauna are: ants, termites (humus feeders or wood-feeders), earthworms (epigeic, endogeic and anecic), dung-beetles, predator beetles, etc. The structures related to soil organisms and function are: earthworm casts on the surface and in the soil, termite structures, and ant hills (see exercise on biogenic structures).

Time required

Variable. Initial setup: 2 hours.

Materials

Machete (cutlass or parang), spade, plastic weave produce sacks for spreading on the ground, large diameter plastic or metal bowls (cuvettes), trowel, small plastic trays, fine forceps (or entomological forceps), fine paint brushes, sample vials in various sizes with secure alcohol-tight caps, Indian-ink pen (waterproof), stiff card for labels, notebook, large strong plastic bags (sealable), table and plastic chairs (for sorting), alcohol (70 percent), formaline (4 percent) if available for preservation of specimens (4-percent formalin is more suitable for earthworms), and a microscope.

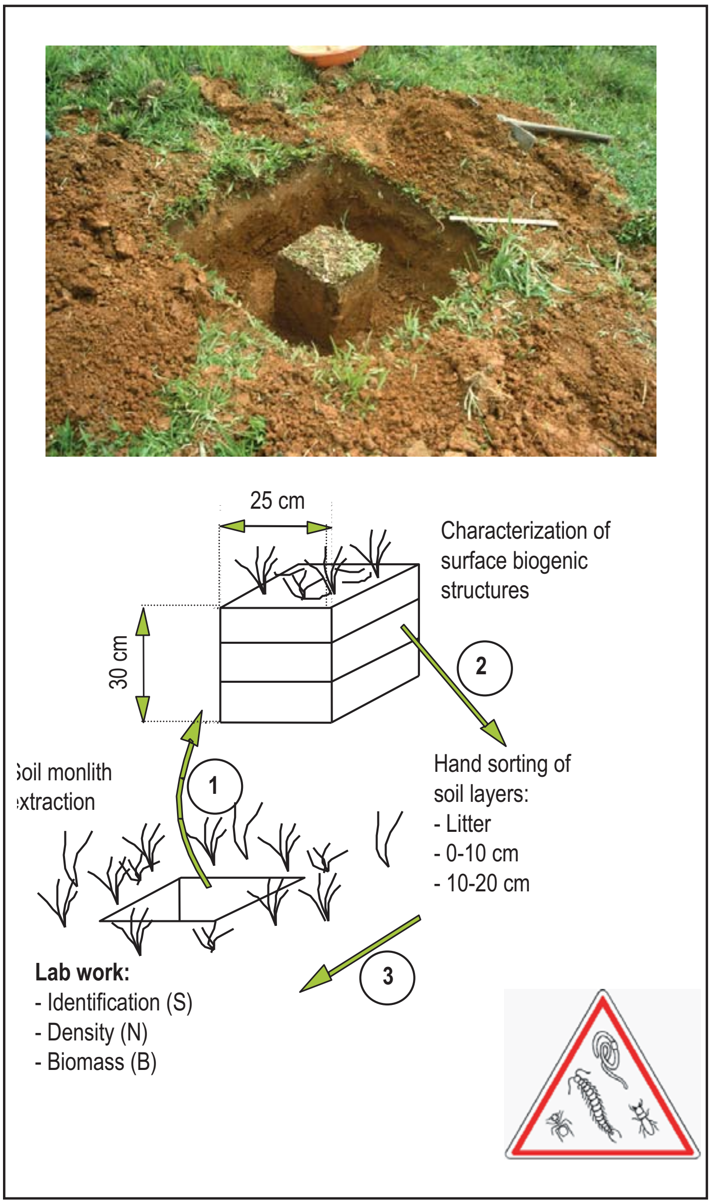
Procedure

The demonstration covers the preparations and material used to sample soil for the presence and abundance of soil macrofauna by performing the sampling methodology of the Tropical Soils Biology and Fertility Institute (TSBF method), which is the digging of soil blocks or monoliths of dimensions 25 cm long, 25 cm wide, and 30 cm deep.

A list of sites to sample showing a gradient in land-use intensification is elaborated by asking participants. Participants can be grouped to assess soil in three different land-use systems.

Steps:

1. Select sample area (land use, plot, etc.) and locate and mark the sampling points for monolith extraction (in the assessment of soil macrofauna communities, the sampling is generally conducted along a transect 40 x 5 m); these are equally spaced along the transect. The target number should be eight, although five will suffice as a minimum number).
2. Where present, remove litter from within a 25-cm square and hand-sort it at the site.
3. Isolate the monolith by cutting down with a spade a few centimetres outside the quadrat and then digging a 20-cm wide and 30-cm deep trench around it. (N.B. In a variant of the method, all invertebrates longer than 10 cm excavated from the trench are collected; these will be mainly large millipedes and earthworms with very low population densities but representing an important biomass. Their abundance and biomass can be calculated on the basis of 0.42-m2 samples, i.e. the width of the block plus two trench widths, squared.)
4. Divide the delimited monolith block into three layers: 0–10 cm, 10–20 cm and 20–30 cm. This can be done conveniently using a machete or parang held horizontally and grasped at both ends. Hand-sort each layer separately. If time is short or the light poor (sorting in closed canopy forest is usually difficult after about 3.30 pm), bag the soil and remove to a laboratory. Ants can be extracted by gently brushing small quantities (handfuls) of soil through a coarse (5 mm) sieve into a tray; the sieve retains the ants.
5. For each layer, the hand-sorted soil macroinvertebrates should be conserved in different containers filled with alcohol and marked using a piece of paper with the sample number and the layer noted on it; the paper is then put into the container.



Description of sampling protocol for the assessment of soil macrofauna in terrestrial ecosystems. Numbers correspond to chronological order and steps taken during sampling (adapted from Anderson and Ingram, 1993).

In the classroom:

1. Use the macrofauna key (see Annexe) to classify the animals from each container into the different main groups.
2. Count the number of individuals of each group present in each sample. Write down the results in a table (Table 3).
3. Recording the data. Make a table incorporating the group found in samples showing the sites where each occurred (e.g. Table 4). (Estimate abundance as number of individuals per square metre from each monolith; multiply the total of individuals of a raw by 16 as 1 m^2 is a 4 × 4 grid with squares of 25 × 25 cm). Calculate an arithmetical mean. Add up the total of individuals of each container belonging to the same sample.

Questions to discuss and points to emphasize

1. How can we assess soils for biological activity and how can soil macrofauna be estimated and its activities emphasized? Which types of animals are found mainly in litter? And in the soil? What are the main differences between these animals?
2. What forms of invertebrates (millipedes, isopods, molluscs, insects, insect larvae, and worms) live in the soils of agro-ecosystems and how do they relate to a “healthy” agricultural soil? Which land-use system had the highest diversity (greatest number of species)? Why?
3. How would you describe a pest problem related to the presence of macrofauna in the crop analysed? Are there any other symptoms (in the plants) that you could characterize as being associated with an attack by some groups of soil macrofauna, i.e. beetle larvae? How do you think these

results have been influenced by soil management practices in those areas? Consider factors such as amount and type of soil disturbance, organic matter inputs, presence of surface organic layer, etc.

4. Emphasize the main functions related to the activities developed by soil macrofauna: aeration, formation of channels where roots can penetrate, mixing and aggregation, soil compaction, porosity, increasing water infiltration, and burying of organic matter.
5. Emphasize the concepts of: soil quality / soil health; mineralization/ immobilization; autotrophic/heterotrophic food-webs; functional groups of soil biota; rhizosphere ecology; effect of land-use management on soils.
6. How do these findings relate to agricultural productivity and sustainability? Based on this information, would you alter any practices?

TABLE 3

List of macroinvertebrates found in each sample

Site	Ants	Termites	Earthworms	Woodlice	Snails	Spiders	Beetles, others	Number of groups Taxonomical richness
Forest 1 (litter)	325			28				
Forest 1 (0–10)	200			3				
Forest 1 (10–20)	3			0				
Forest 1 (20–30)	0			0				
Total Forest 1	528			31				
Forest 2 (litter)								
Forest 2 (0–10)								
Etc.								

TABLE 4

Woodlice density at four sites distributed across a land-use intensification gradient

Site	Total number of individuals (n = 5)	Total abundance of individuals (n = 5)	Arithmetical mean (ind./m²) (n = 5)
Primary forest	31	496	99.2
Secondary forest			
Grassland			
Crops			
Litter			
0–10			
10–20			
20–30			