Chapter 19
Biodiversity and Ecology of Soil Fauna in Relation to Truffle

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19.1 Introduction

In the last few decades, numerous studies have attempted to discover the "secrets" of truffles. Since the 3rd International Conference on Truffle in Spoleto (2008), researchers have made considerable progress in advancing understanding of the biology and ecology of *Tuber* species and in improving the sustainable productivity of these valuable fungi (Águeda et al. 2014). The entire genome of *Tuber melanosporum* Vttad. has been sequenced (Martin et al. 2010), and those of other *Tuber* species are in progress (see Chap. 9).

Some authors have studied the particular pedological, chemical and physical characteristics developed by some *Tuber* species in the brûlé, the area around the host plant where the germination and the growth of other plants are inhibited (Callot 1999; Ricard 2003; Granetti et al. 2005; Mello et al. 2013; García-Montero et al. 2014); others have explained the production and development mechanisms in this area (Sourzat 2004; Granetti et al. 2005; Streiblová et al. 2012). The substances produced by *Tuber* mycelium, which are well known and widely studied, adversely affect seed germination and the growth of young trees inside the brûlé (Plattner and Hall 1995). An interesting aspect that makes the truffles an engaging yet difficult case of study at the same time is their particular dispersal system. A truffle cannot release its spores, trapped as they are in their underground realm, and it needs an alternative dispersal system via animals. When an animal eats truffle, most of the flesh is digested, but the spores pass through unharmed and are defecated on the ground, where they can germinate if the conditions are right (Trappe and Claridge 2010).

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We can assume that truffles emerged between 100 and 200 millions of years ago (Jeandroz et al. 2008; Bonito et al. 2013). As truffles retreated underground, mutations eventually led to the formation of aromatic compounds attractive to animals (Trappe and Claridge 2010). Many animals are known to be "truffle eaters": small mammals such as mice, squirrels and rabbits, big mammals like wild boars in the Northern Hemisphere (see Chaps. 21 and 22) and rat-kangaroos, armadillos and meerkats in the Southern Hemisphere. Molluscs are attracted to truffles, too, and insects may feed on truffles or lay eggs in them so that their larvae have a ready food source when they hatch (Trappe and Claridge 2010). Spore dispersal by animals can promote the fungal colonization of new habitats. Moreover, as highlighted by Bonito et al. (2013), spore deposition via animal mycophagy may be a more targeted dispersal mechanism than wind or water dispersal, because animals could enrich spores with nutrients (e.g. calcium, magnesium and potassium) and deposit their faecal pellets loaded with spores near the roots of suitable host trees. Indeed, the authors pointed out that truffle fruit bodies usually have durable, thick-walled spores that can withstand and possibly benefit from passing through the digestive tract of animals. These selected traits across a diversity of truffle lineages suggest that the transition from epigeous to hypogeous fruiting is driven by strong selection for traits that promote animal dispersal.

There is undoubtedly much more information still to be discovered. There are only a few studies on the interaction between truffles and animals (with the exception of mammals) or on the relationship between truffles and soil fauna. As we said above, truffles "live" in the soil and complete their whole life cycle within it. It would be really interesting to establish whether soil animals affect truffle, and if so, how, and conversely whether truffles affect soil fauna, by means of different soil chemical characteristics that allelopathic compounds make in the brûlé. In this chapter, we are going to discuss the various aspects of the relationship between truffles and soil fauna.

19.2   Role of Soil Fauna

The living component of the soil should be considered as the motor that drives soil functioning. Within it, invertebrates have been shown to influence almost every level of the decomposition cascade (Wolters 2000), and the ecosystem services provided by soil fauna are one of the most powerful arguments for the conservation of edaphic biodiversity. Soil fauna perform many different and very important functions within and for the soil. Invertebrates affect soil processes both directly and indirectly. Direct effects result from the incorporation and redistribution of various materials, while indirect effects result from soil invertebrates shaping the microbial community by both constructive (e.g. transport of fungal spores) and destructive means (e.g. selective reduction of viability; Shaw 1992). In addition, edaphic animals influence soil processes by altering distal factors controlling

microbial performance through particulation, channelling and alteration of nutrient availability (Wolters 2000).

Although some soil animals are carnivorous, the most widespread ecosystematic activity of soil meso- and macrofauna is the "processing" and "mixing" of organic detritus in soil. Processing includes not only simple comminution of organic debris into smaller fragments but also various degrees of decomposition performed by enzymes and the gut microorganisms that feed on organic material (Killham 1994). Many organisms, such as isopods, myriapods, earthworms, springtails, a wide range of mites, larvae and adults of some insects, feed on vegetable and animals debris. This mechanical degradation facilitates the action of microorganisms and accelerates the degradation processes.

The results of food web analyses indicate that microfauna (organisms smaller than 100 μm) and, to a lesser extent, mesofauna (animals between 100 μm and 2 mm in size) have a particularly strong impact on C and N fluxes due to their rapid turnover rates and the consumption of microorganisms with low C/N ratios, while macrofauna (animals larger than 2 mm) make a less direct contribution to community metabolism because of longer generation times and the consumption of materials with high C/N ratios (Anderson 1995).

Another very important function of soil organisms is their burrowing activity, which causes direct and indirect chemical, physical and biological changes. Above all, earthworm action produces a remarkable effect not only on soil structure but also on its chemical composition, because the organic matter ingested is returned in a form easily usable by plants. They dig and eat soil, creating tunnels, channels and holes to live in. Horizontal and vertical burrowing by soil animals shifts organic material along the soil profile. Bioturbation significantly facilitates interactions with stabilizing inorganic fractions (Wolters 2000). Earthworms consume a large amount of mineral substances that are mixed with the organic matter and expelled in the form of casts (Fig. 19.1a), which are rich in nitrogen and other nutrients such as calcium, magnesium and potassium. They also contain a vast quantity of undigested bacteria, which proliferate easily in the soil, contributing to the humification and mineralization of organic matter. Casts are not expelled in the same environment. This could allow the widespread dispersal of hypogeous fungi spores far from their source of origin. This is another very important function of soil organisms, in particular for hypogeous fungi. Indeed, the hyphae of mycorrhizal fungi could make up a significant proportion of the total microbial biomass in some soils and can become one of the most important sources of food for fungus-grazing animals such as springtails (Menta et al. 2013). For example, through their faeces, springtails can spread still viable fungal spores to areas as far away as several metres from their point of origin. At the same time, fauna feeding on microorganisms can control specific plant pathogens. Root herbivory influences individual plant performance and higher-level processes both directly and indirectly (Brussaard 1998): directly by selectively feeding on seeds and seedlings, thereby preventing the establishment or abundance of certain plant species, and indirectly by interfering with the carbon and nutrient acquisition and the allocation of plants in interaction with above-ground herbivores. The action of some organisms, such as
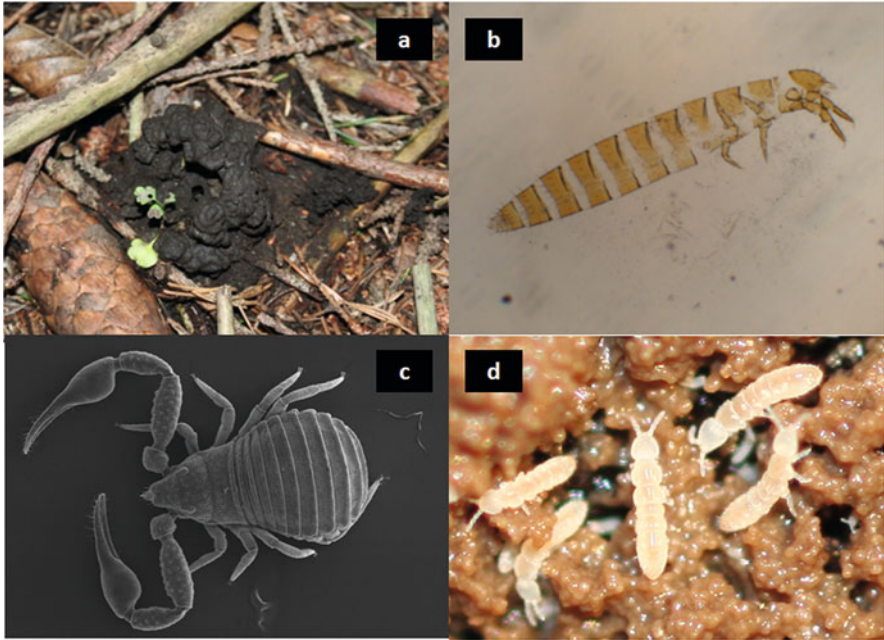
Fig. 19.1 Earthworm cast (**a**) (photo by C. Menta); *Acerentomon italicum*, Protura (photo by L. Galli) (**b**); *Geogarypus minor*, Pseudoscorpionida (SEM, photo by M. Zinni); (**c**) *Folsomia candida*, Collembola (photo by C. Menta) (**d**)

protozoa, nematodes, rotifers, some springtails and mites, which feed on bacteria, actinomycetes and fungi (both hyphae and spores), is very important for density regulation and microorganism diffusion.

Soil fauna, especially molluscs and earthworms, also have an impact on soil, thanks to their cutaneous mucus secretions, which cement the soil, making it more stable. These secretions, together with the animal's faeces and body, influence the concentration of most of the nutrients in the soil, reducing the litter's C/N ratio and promoting breakdown. In addition, the ingestion of large amounts of mineral soil is particularly well documented by macro-soil engineers (Lavelle et al. 1998).

19.3   Relationships Between Soil Fauna and Truffles

An interesting environment present in the soil is the rhizosphere. The term rhizosphere, in its broadest sense, refers to the portion of soil surrounding roots in which the organisms are influenced by their presence; its extension varies greatly, but it is generally considered to be the cylinder of soil used by the root hairs and in which they emit exudates (Killham 1994). Protozoa and nematodes are the main consumers of microorganisms developing near living and dead roots and in hotspots in

the soil matrix; rhizosphere/non-rhizosphere soil ratios are in the range 1.3–3.5 for protozoa numbers and 3–70 for nematode numbers (Brussaard 1998). The interaction between soil animals and plant roots can take a variety of forms that lead to benefits for or repress the growth of the plants and often involve interactions with the microbial populations of the soil. This relationship becomes more complex when it involves mycorrhizas. In this sense, the rhizosphere also becomes the soil portion where mycorrhizas and organisms interact. For example, at different stages of their lifecycle, truffles in particular release specific volatiles in order to interact with particular organisms (Splivallo et al. 2011). Secondary metabolites produced by fungi are one of the largest classes of natural products. Such compounds may not play a fundamental biochemical role in the normal growth or development of fungal cells, but they clearly play an ecological role. Secondary metabolism is important in many fungal processes, including stimulation or inhibition of organisms by allelochemicals and regulation of symbiotic and protective interactions with microbes and other interacting roots (Angelini et al. 2010). In truffles, these compounds are responsible for the formation of the brûlé, which is characterized by scarce plant cover due to the phytotoxic activity of the fungus (Splivallo 2008).

In general, the abundance and diversity of soil animals are greatest in soils with little or no disturbance, such as those of permanent grassland (Menta et al. 2011a) and natural woodland (Menta et al. 2013), where they play a vital role in nutrient cycling (Killham 1994). However, the particular conditions generated inside the brûlé by truffles' aromatic compounds could affect soil fauna in many different ways, both directly and indirectly. The brûlé is in fact characterized by lower levels of organic matter, sometimes higher pH values and lower retention capacity (Menta et al. 2014). Many of these factors could adversely affect organisms, which tend to avoid this environment, or could lead to a shift in the soil community, encouraging the presence of stress-resistant organisms. It has been demonstrated, for example, that the main factors driving Collembola distribution are vegetation, microflora, soil structure and soil moisture (Menta 2008).

Above all, the lack of vegetation cover could lead to soil moisture deficit. Soil moisture affects soil organisms because water is essential for life and for enzyme activities and metabolism and because soil moisture affects soil temperature and soil aeration. Furthermore, under wet conditions, oxygen does not diffuse through the soil as readily, so the levels available to organisms may become depleted, leading to anaerobic conditions (FAO 2015). In soils with sparse vegetation cover, such as the truffle brûlé, the high frequency of dry conditions on the surface causes nematodes to be more common at depths of 5–10 cm (Menta 2008). Diplura prefer soil with a high stable moisture content. Isopods, which avoid dry conditions, may also escape from the brûlé areas. Water stress also influences the size and activity of soil animal communities for two reasons, a reduction in water-filled pores and the thickness of soil water films (which controls soil aeration and the mobility of some animals) and a reduction in the free energy of the water, making water uptake increasingly difficult (Killham 1994). Furthermore, it has long been known that the production of earthworm casts, an excellent indicator of earthworm activity, is directly related to rainfall and soil moisture status (Killham 1994).

Burrowing species, such as *Lumbricus terrestris*, take refuge deep in damp soil, whereas species that live on the surface, such as *Allolobophora caliginosa* (*Nicodrilus caliginosus*) and *Eisenia rosea*, are declining in population (Menta 2008) due to soil moisture depletion.

Inside the truffle brûlé, the organic matter to be demolished comes in much smaller quantities compared to other ecosystems. This could lead to a different soil community structure, with a small presence of detritivores, and consequently predators, and possibly an increase in herbivores or organisms that feed on fungi.

Many works have documented the intimate relationship between soil fauna and organic matter. The amount and depth of organic matter on the forest floor, for instance, influences the distribution of springtails and acari Oribatida (Hasegawa 2001). Many soil invertebrates, such as symphylans, proturans, diplopods and earthworms, and many detritivores are more abundant in soils rich in organic matter. Similarly, pH could influence soil organisms because different species are active at different pH ranges. In a study conducted in ecologically analogous sites in oak-hickory forests, which are characterized by different amounts of acidic deposition, Kuperman (1996) found a positive correlation between pH and the abundance of different soil macroinvertebrates such as earthworms, gastropods, termites, carabids, staphylinids, cockroaches and dipteran larvae. Esher et al. (1993) reported huge effects of mild acid treatments on populations of earthworms. Several experiments have shown that many earthworms have particular limits in terms of tolerance to soil acidity and that they tend to avoid unfavourable pH levels. In laboratory experiments with *Eisenia foetida*, 100 % mortality was observed at pH < 5 or pH > 9 (Kaplan et al. 1980). Edwards and Lofty (1975) found that the numbers of Chilopoda and Symphyla were much greater between pH 5.0 and 6.0 than at higher or lower levels and none of these animals were present at a pH below 4.0. Wireworms and other insects were more numerous in plots with a pH between 4.0 and 7.0, i.e. very acid or alkaline soils did not support large numbers of these arthropods in their study (Kuperman 1996).

Kuperman (1996) performed a linear regression analysis to determine which parameter, pH or the amount of surface organic matter accumulation could affect soil macroinvertebrate community most. The regression analysis showed a significant relationship between soil pH and the total number of decomposers in study sites along the deposition gradient. Approximately 87 % of the variation in numbers of decomposers was explained by the soil pH. Furthermore, the relationship between the abundance of the macroinvertebrate decomposer community and the amount of surface organic matter accumulation along the deposition gradient was also highly significant. Approximately 71 % of the variation in the amount of surface organic matter accumulation was explained by the abundance of decomposers. The results of this study also show that the observed patterns of decreasing abundance of decomposers, increasing organic matter content and decreasing soil pH along the deposition gradient seem to be related.

The brûlé is also characterized by lower organic carbon content. It has been demonstrated, indeed, that organic carbon in the brûlé decreases by about 52 % (Bragato 1997). This parameter could significantly affect the soil fauna community as well. Kuperman (1996) found a significant negative correlation between this parameter in A_1 horizon and the numbers of Lumbricidae, Carabidae, Gastropoda and Staphylinidae. According to studies in a wide range of ecosystems, soil invertebrates mediate about 15 % of the C and 30 % of the N turnover (Anderson 1995).

19.4 Soil Microarthropod Biodiversity in the *Tuber* Brûlé

According to the phylogenetic hypothesis that hypogeous fungi, like truffles, evolved with an active system of spore dispersal, spore discharge must be by animal dispersal. Some animals have evolved a capacity for feeding on truffle-fruiting bodies, and in so doing, they have become active agents of spore dispersal (Pacioni et al. 1991). These animals have been dubbed "hydnophagous" (Pacioni et al. 1989), from the Greek *hydnon*, truffle, and *phagous*, eating, and this category includes species belonging to various taxonomic groups. Not just truffles but all mycorrhizal plants in the world are likely to have at least one (often many) species of insect herbivores that attack them (Koricheva et al. 2009). In the case of the truffle, the diet of certain animals, such as mammals (rodents, deer, boar), birds and slugs, includes these hypogeous fruiting bodies, which sometimes account for their entire diet: a case in point is provided by several species or genera of arthropods, mainly Coleoptera and Diptera. Various authors have described mechanisms explaining the impact of soil microarthropods on fungal communities. Hanlon and Anderson (1979), for instance, indicated that microarthropod feeding activities can exert a strong differential effect on fungal and bacterial populations, and some reviews on arbuscular mycorrhizae and soil fauna interactions suggest that Collembola have the potential to restrict mycorrhizal functioning in the field (Fitter and Sanders 1992; Fitter and Garbaye 1994). One of the most specialized fungivores that attack truffles is the beetle *Leiodes cinnamomea* (Coleoptera: Staphylinoidea, Leiodidae). It is univoltine, with a European distribution. It is known to feed on several species of truffle (*Tuber* spp.) and completes its lifecycle in or near the fungal fruiting body (Arzone 1970; Newton 1984). Hochberg et al. (2003) showed that adults of the beetle *L. cinnamomea*, though inflicting substantial damage to the fruiting bodies of the black truffle in the larval stage, are not attracted to ripe truffle odours. Some individuals, however, showed persistent attraction when tested repeatedly, showing that the odours can be perceived by the truffle beetles. Coleoptera are the most widely recorded, but there is also a large amount of data on Catopidae, Cryptophagidae, Leiodidae, Micropeplidae,
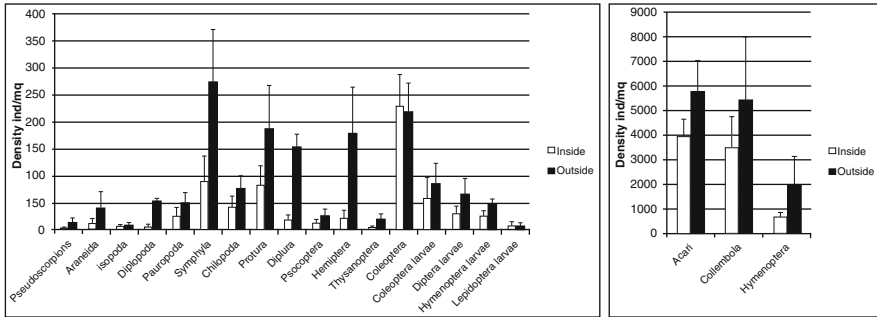
Fig. 19.2 Microarthropod community inside and outside the brûlé (based on data published by Menta et al. 2014)

Nitidulidae, Ptiliidae, Staphylinidae and Scarabaeidae. Some insects (Diptera and Coleoptera) have also been reported as fauna nutritionally related to the carpophores (Pacioni et al. 1989). The most notable insects are the "truffle flies", eight species of *Suillia* (Heleomyzidae) (Janvier 1963; Pacioni et al. 1989; Bratek et al. 1992; Callot 1999; García-Montero et al. 2004).

Besides the works mentioned above, there are only a few studies on the relationship between soil fauna and truffle biology (Queralt et al. 2014). Menta et al. (2014) tried to highlight differences among the microarthropod communities associated with the *Tuber aestivum* Vittad. brûlé and the area outside the brûlé. This research took into account three different areas, two in Italy (North and South) and one in central Spain (Guadalajara province). The authors did not observe a univocal trend, but almost all microarthropod groups were more abundant outside the brûlé (Fig. 19.2). These groups were Acari, Hymenoptera, Diplopoda, Symphyla, Pauropoda, Protura (Fig. 19.1b), Diplura, Hemiptera, Pseudoscorpionida (Fig. 19.1c) and Araneida. This trend suggests that these groups could find an unfavourable environment inside the brûlé, probably due to several factors, including the lower content of organic matter. This tendency was not followed by Coleoptera, or by Lepidoptera larvae, which probably find better conditions in the brûlé in terms of food resources and chemico-physical conditions. Menta et al. (2011b) and Tarasconi et al. (2011) reported interactions between microarthropods and *T. melanosporum* showing lower densities of mites and ants inside the brûlé. Within the collembolan group, Menta et al. (2014) showed that the families Hypogastruridae, Sminthurididae and Isotomidae were more abundant outside the brûlé, while within the Isotomidae family, *Folsomia* genus showed higher abundance inside the brûlé. One study (Hodge 2000) pointed out the presence of spores and extraradical mycelium of arbuscular mycorrhizal hyphae in the gut contents of *Folsomia candida* (Fig. 19.1d). Queralt et al. (2014) focus instead on mite communities associated with the *T. melanosporum* brûlé. They found that oribatid mites dominated the community in terms of abundance and

species richness in wild and plantation soils. Most oribatid mites are mycophagous, and they could have a direct relationship with the black truffle cycle, interacting in the mycelium and spore dispersal. In some cases, they have been observed carrying spores attached to their bodies. The researchers also found a high-density population of the mites *Passalozetes ruderalis* Iberian endemism (Pérez-Íñigo 1993) and *Arthrodamaeus reticulatus* (Pérez-Íñigo 1997) in truffle areas and assumed that they could be potential truffle-related species. Soil fauna could have a positive impact on truffle development not only in terms of spore dispersal. Earthworms and ants, for example, as "ecosystem engineers" due to their important contribution to soil porosity, breakdown of organic matter and incorporation of organic matter into the soil, could have a positive effect on the truffle, altering the physical characteristics of the soil. The list of truffle-associated organisms most often includes, besides earthworms, nematodes and protozoa. Callot (1999), Ricard (2003) and Pargney et al. (2010) indicated that earthworms are often found around the truffle carpophores in the soil burns. These soils usually have low levels of organic matter, and earthworms therefore search near the carpophores for organic matter contained in the bacterial populations and droppings of microarthropods and macrofauna (García-Montero et al. 2013). These authors pointed out that earthworms benefit *T. melanosporum* development. Lulli et al. (1999) and Castrignano et al. (2000) indicated that this truffle requires considerable soil porosity, mainly originated by earthworms and ants. García-Montero et al. (2010) indicated that earthworm casts can have a great impact on the soil in the *T. melanosporum* brûlé. On the other hand, Callot (1999) found that Nematoda and Protozoa maintain the relationship between microbial activity and the truffle, while Acari and Collembola, besides regulating this relationship, also help to disseminate spores. Lastly, large animals, in addition to helping in the previously mentioned functions, also affect soil structure (Queralt et al. 2014).

19.5 Conclusions

Studies of the relationship between truffles and soil fauna are scanty, and they often concern particular species of truffle, such as *T. melanosporum* and *T. aestivum*. It would be important to analyse not only the effects of animals on truffles, in terms of dispersal of ingested spores, for example, but also the direct or indirect effects of truffles on animals. The truffle volatiles and the reduced plant cover present in the brûlé may both have a detrimental effect on some species. A further challenge will be to clarify whether *Tuber* sp. is able to create a natural "microcosm", the brûlé, as part of a larger macrocosm, the soil around it, not only in terms of chemical-physical characteristics and plant cover but also in terms of soil animal biodiversity and functionality. Lastly, the authors have tried to give a simple representation of

Fig. 19.3 A schematic representation of soil fauna community inside and outside the *T. aestivum* brûlé (based on the literature data cited in the text and on unpublished data collected by the authors). The dimensional proportions of the animals are not respected. Abbreviations: *S*, Symphylan; *P*, Pauropoda; *D*, Diplopoda; *N*, Nematodes; *Ps*, Pseudoscorpion; *E*, Earthworm; *A*, Acari; *C*, Collembola; *L*, *Leiodes cinnamomea*; *S*, *Suillia* spp. All the drawings were made by the authors

the soil fauna community inside and outside the *T. aestivum* brûlé, based on the literature data cited in the text and on unpublished data collected by the authors themselves (Fig. 19.3).

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