Humusica 1, article 8: Terrestrial humus systems and forms – Biological activity and soil aggregates, space-time dynamics*

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ABSTRACT

Litter biodegradation is a process of life. Organisms feed, reproduce, die and decompose. Decomposition is essential, and it is never complete. In addition, the elements generated by this process become new bricks for building more complex structures in a dynamically evolving environment. In this article, we show some pictures of the main actors in litter biodegradation. We also try to associate living organisms to the soil aggregates they generate, furnishing photographs of organisms and aggregates visible in the field even with a naked eye. The transformation of dead bodies, organs or cells and droppings in the soil ecosystem is influenced by biotic and abiotic factors and hence it must be considered as a dynamic, never ending, local evolution. Instead of focusing on specific data, we have tried to present the involved phenomena to a non-specialised public (naturalists, students, teachers, etc.) through the use of graphical schemes, indicating arrows, photographs, and drawings. In the end, readers will be aware that things are not as simple as expected, that static models cannot give a precise image of a reality in constant evolution. The article can be inspected as a photo album, read as a comic strip or used as a dictionary. The authors aim to illustrate rather than to explain the relationships between humus systems, climate and biodiversity.

* Singing while reading? Cantare (Bepi De Marzi) – Coro femminile (female voices) "Plinius": https://www.youtube.com/watch?v=wnOqjJ5rpiIIli, ilè, ilò (Bepi De Marzi) – Coro maschile (male voices) "I Crodaioli": https://www.youtube.com/watch?v=2JD1q5aWeJk&index=105&list=PLgq5EK55CawXon9PyIVQXTOcjpHmkUpFh.

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1. Introduction

Soil organisms are crucial to soil formation, litter decomposition, nutrient cycling, biological control and for providing support for plant growth. All these processes are dynamic and in continuous evolution, the rates they occur change dramatically with different actors and environmental factors. Therefore, in this article, humus system dynamics is described with the help of diagrams and pictures with the aim to illustrate the relationships between humus systems, climate, and soil biodiversity even to a non-specialised public (naturalists, students, teachers, etc.). In the first section, we consider the main groups of soil organisms involved, their defecating and burrowing activities, fungal/bacterial components, and soil structures; in the second section, we describe litter biodegradation and horizon formation; in the third part, historical, biological, and environmental backgrounds give a final overview of the soil system at different scales.

Looking through this showcase of pictures and drawings would help in understanding the great complexity of soil and its functional role in soil organic matter transformation. However, it cannot solve the huge problem of classifying soil organisms, a very difficult issue shared among many specialists. Many identification guides are available for a first raw identification of some commonly collected animals, among them Paulian (1971), Coineau et al. (1997), Olsen and Sunesen (2004), Bellmann (2006), Leraut (2008), Dierl and Ring (2009), Chinery (2012), Olsen et al. (2012), Carter and Hargreaves (2015), Dijkstra and Lewington (2015), Kerney and Cameron (2015). A general assignment to main groups is generally sufficient for most ecological research, biodiversity surveys, and teaching purposes, training courses (many examples in Humusica 3). More detailed and demanding scientific surveys, such as Bouché (1972), Benckiser (1997), Lieutier et al. (2004), Singh (2007) require the contribution of specialists for every taxonomic group, since the collection technique has to be adapted to each type of animals (e.g. wet versus dry extraction) and must take into account sample size and environmental factors that limit their activity.

Before showing some photographs of the main groups of soil organisms, we would like to draw the attention of potential readers to two pictures of soil food networks: the first one (Fig. 1a) attributed to Dindal (1990) and the second (Fig. 1b) produced by an unknown author. In the first figure soil animals and microorganisms are simply organized in several “levels of consumers” (grey bubbles) linked by energy flows (arrows) to plant remains through the decomposition process. In contrast, a much more precise network of relationships among three levels of consumers (all enclosed in one rectangle) is showed on Figure 1b. Each group of soil organisms is connected to external compartments, such as soil humus, plant debris, mineral nutrients, plants-algae-lichens-bacteria, respired CO_2, and heat energy losses. The arrows also link CO_2 and solar energy to plants-algae-lichens-bacteria (primary producers). Here, soil humus is considered as a specific, particular soil, which receives inputs (thick arrow) from the large box of consumers but also nourishes (thin arrows) bacteria and fungi. In Humusica 3, recent findings on food soil webs are described (see contributions by Geisen, Bonkowski, Fusaro, Squartini and Paoletti). For example, it can be seen how changes in land use can strongly influence the organisation of this network and how the direct channel from roots, via root-feeding nematodes and omni-carnivorous nematodes is connected to higher trophic levels (Morriën, 2016). This is also represented in Fig. 1b (thick arrow linking the box enclosing plants, algae, lichens and bacteria as well as that of nematodes).

Both representations of the soil food web give a good idea of a functional soil. Soil is a living world even more complex than the one we can see around us with our own eyes. Many large animals living in the soil can be extracted by hand-sorting soil samples. For a functional, albeit not exhaustive, classification (school and university trainings, ecological research, studies on environmental impacts, etc.) we recommend using dry Berlese funnels (invented in 1880!) in which animals are forced to escape from the source of light and heat above and they are collected in a container filled with a preserving solution (Fig. 2a). An old version can be found at https://upload.wikimedia.org/wikipedia/commons/3/3b/Berlese.png, while a more modern version is represented here, http://svalbardinsects.net/assets/images/UNISextractor-(1).jpg. In the case of legless organisms, a derived wet technique (Fig. 2b) invented by O'Connor in 1955 (O'Connor, 1955, 1962) is preferred since these animals need a continuous water film to swim through the soil.

More curious readers will find more detailed and complete information on soil biology methods in various books which have been published on the subject, such as Killham (1994), Lavelle and Spain (2001), Gobat et al. (2004), Coleman et al. (2004), Abbott and Murphy (2007), Karlovsky (2008), Nautiyal and Dion (2008), Bardgett (2008), Whalen and Sampedro (2010), Dixon and Tilston (2010), Cardon and Whitbeck (2011), Lukac and Godbold (2011), Wall et al. (2012), Paul (2014), and Weil and Brady (2016).

2. Variety and activity of soil organisms and microorganisms: photo gallery

Even people not accustomed to the classification of soil organisms may recognize in Figure 3 many names of common soil dwellers. Thanks to recent molecular studies, the arrangement of past and present organisms in an evolutionary tree of life has experienced a rapid development over the last 15 years (e.g. the Tree of Life Project, the achievement of which is available at http://tolweb.org/tree/).

Soil organisms include unicellular microscopic organisms such as prokaryota (i.e. without a membrane-bound nucleus) which includes archaea, bacteria, and protists together with multicellular organisms such as fungi (micro- and macrofungi, including mycorrhizal fungi), and animals. Soil animals are usually broadly classified into four groups according to their body width: (i) microfauna (less than 0.1 mm) which includes tardigrades (water bears), rotifers (wheel animals), and nematodes (round worms); (ii) mesofauna (0.1–2 mm) including enchytraeids (potworms), Acari (mites), wingless hexapods [collembolans (springtails) proturans, diplurans], pseudoscorpions or false scorpions; (iii) macrofauna (2–20 mm) such as spiders, slugs, snails, woodlice, millipedes, centipedes, earthworms, ants, termites, and other big insects, and megafauna (greater than 20 mm) that includes several species of amphibians, reptiles, and mammals whose main activity is burrowing the soil (Orgiazzi et al., 2016; see also Fig. 3). Soil organisms also include plant roots, whose exudates attract a variety of organisms, which either feed directly on these secretions or graze on the microorganisms feeding on them, as well as soil lichens colonising a huge range of soils (Orgiazzi et al., 2016).

Although estimates of some species numbers are available for most groups of soil organisms, they are still preliminary and much lower than the projected number of undescribed species. For

example, the number of described soil-dwelling fungal species is estimated to be at least 74,000, while their projected number is over 1.5 million (Hawksworth, 2001). Similarly, the quoted number of described nematode species ranges between 26,000 and 40,000, but is thought to be above one million (Lambshead, 2004; Lambshead and Boucher, 2003) and in the case of mites, perhaps only as few as 3 to 5% of the total number of species are presently described (Hawksworth and Mound, 1991; Walter and Proctor, 1999).

3. Soil biodiversity, abundance, and distribution in the soils is modulated by abiotic and biotic factors

Small-size invertebrates exhibiting a short cycle of development and usually concentrated in the litter layers are exposed to abrupt changes in temperature and moisture (Briones et al., 1997; Zenkova et al., 2011). This leads to important seasonal variations of soil communities, both in species composition and abundance, as well as to vertical stratification when cold/hot or waterlogged/dry spells create unfavourable conditions to their activities at the surface (Fig. 4). For example, in a study of soil invertebrate communities along an altitudinal gradient Zenkova et al. (2011) found that soils become impoverished in autumn across all altitudinal zones and that certain groups of macrofauna (earthworms, gastropods, and some insects) disappeared completely from the litter layer in mid-September. Similarly, Solida et al. (2015) found that moister, more continental and relatively undisturbed woodlands with a closed canopy and high humus quality sustained a more complex microarthropod community, whereas more disturbed and xeric Mediterranean woodlands showed lower values of all investigated biodiversity parameters due to water limitation. Indeed, several studies have highlighted the strong influence of microclimate on oribatid (Irmler, 2004) and collembolan communities (Lindberg and Bengtsson, 2005; Makkonen et al., 2011; Petersen, 2011; Salmon et al., 2006). Drought periods also represent an important limitation factor for enchytraeid populations, which tend to be smaller during summer, with negative implications for decomposition rates (Nurminen, 1967).

Another study on the response of oribatid mites to secondary succession indicated that most species were able to tolerate large changes in abiotic conditions and humus forms and responded primarily to pore volume, making them more susceptible to space limitation than to the chemical characteristics of the habitat (Nielsen et al., 2008). Indeed, investigations on the impact of rainforest deforestation and replacement by pastures on soil structure (Vera et al., 2007) showed a marked decrease in soil porosity, from 80% in undisturbed systems to 65% in pasture soils and a concomitant change in soil fauna activity. Similarly, changes in soil pH through liming and nitrogen amendments decrease numbers of oribatid mites and Collembola in short- or medium-terms (e.g. De Goede and Dekker, 1993; Fisk et al., 2006; Hågvar, 1984; Hågvar and Amundsen, 1981; Kopeszki, 1993; Persson, 1988), but induced a long-term stimulation of lumbricid populations (Deleporte and Tillier, 1999; Graefe and Beylich, 2003; Hirth et al., 2009).

Besides abiotic conditions, also biotic factors can have a strong influence on the composition and structure of soil communities (Fig. 4). Species interactions can be positive, negative or neutral. These could occur between individuals of the same species belonging to the same or different

populations (e.g. competition for food or space), between different species (e.g. predation, antagonisms) or between above- and below-ground communities (e.g. plants attracting or detracting certain soil biota in the rhizosphere). Very few studies have investigated competition within soil communities (Bardgett, 2002; Decaëns, 2010), despite it is suspected to be an important mechanism structuring species assemblages at local scale (Christiansen et al., 1992; Hågvar, 1990; Hodge et al., 2000; Postma-Blaauw et al., 2005; Theenhaus et al., 1999; Winkler and Kampichler, 2000).

Examples of positive interactions between species include the observed synergy between millipedes, woodlice, and earthworms during litter comminution and humus formation (David, 1987; Zimmer et al., 2005). In addition, it is well known that certain big-size animals create micro-habitats in the form of biogenic structures (e.g. casts, burrows, nests, and middens) for other soil organisms and, for this reason, are called “ecosystem engineers” sensu Jones et al. (1994). Similarly, facilitation processes, such as those provided by wood-boring beetles, allow other invertebrates to colonise fallen trees and hence to find shelter, food, and places for egg laying (Zhuo et al., 2006).

Predation and competition for space and resources are the most commonly reported negative interactions occurring among soil biota, but also habitat disturbances due to, for example, burrowing and mixing by earthworms (Migge-Kleaian et al., 2006). In many other cases, biotic interactions can be simultaneously positive and negative. For example, the outcome of a laboratory experiment, in which earthworms were involved, included negative interactions such as a reduction in population numbers of collembolans, but also positive effects such as an increase in the diversity and evenness of this mesofaunal community (Mudrák et al., 2012). However, positive and/or negative effects are often transient and hence, only one of them determines the overall response in the long-term (Migge-Kleaian et al., 2006).

At local scale, the outcome of these biotic relationships is determined by prevailing environmental conditions (Fig. 4). Decreases in enchytraeid numbers are usually associated to competition with earthworms (Räty, 2004 Räty and Huhta, 2003). However, Didden et al. (1997) found that both groups can perfectly coexist in the same soil depending on temperature and moisture levels and concluded that they occupy different niches. Therefore, by exhibiting better adaptations to specific conditions, certain species can exploit certain habitats more successfully than others. In agreement with this, Hågvar (1990) suggested that acid-tolerant oribatid species living commonly in dysmoder forest soils are not attracted by acidity, but rather compete better with acid-intolerant species when (and only when) soils are acid. From this, it has been suggested that competition with resident species strongly determines the colonisation rate of dispersing species (Shigesada and Kawasaki, 1997) and hence influences C retention in soils (Huang et al., 2015).

At habitat scale, the strong influence of environmental filters (such as local microclimate, spatial heterogeneity and soil characteristics) in shaping soil biota distributions, together with their low dispersal abilities has resulted in the overall consensus that aggregated or patchy distributions are inherent to soil organisms (Berg, 2012). The nested distribution of soil fauna at the scale of centimetres to meters, both horizontally and along the soil profile, is arranged in a predictable way (Ettema and Wardle, 2002), and has led to well documented spatial patterns of species assemblages in relation to morphological characters, feeding habits, enzymatic capabilities and burrowing activities (reviewed by Briones, 2014).

4. Soil organisms, droppings and soil aggregates

Wallwork (1970) considered seven groups of animals correlated with humus systems: Acari (mites), Collembola (springtails), Myriapoda (centipedes and millipedes), Isopoda (woodlice), Annelida (referring to earthworms only), Isoptera (termites) and Insecta (insect larvae). Bernier and Gillet (2012) concluded that most soil fauna taxa are involved in several humus forms by exhibiting a different vertical stratification. However, for the purpose of this article, which is the classification of humus systems and its understanding for sustainable agricultural and forest management, soil organisms playing an active role in the formation and maintenance of soil horizons (Hole, 1981) have been classified into five groups:

- Those generating a soil biomacrostructure, i.e. a biomacrostructured A horizon (Code: maA, described in Humusica 1, article 4) = Aneciendovermic-macroarthropodic A horizon: large endogeic and anecic earthworms in temperate and humid tropical forests and grasslands, large macroarthropods in warm dry climates (e.g. insects in Mediterranean maquis and subdesertic areas, millipedes in tropical evergreen forests and termites in dry tropical savannas);
- Those generating a soil biomesostructure, i.e. a biomesostructured A horizon (Code: meA, described in Humusica 1, article 4) = Endoepivermic-mesoarthropodic A horizon: epigeic and small endogeic earthworms, large enchytraeids, and small macroarthropods (woodlice, small insects, even in larval stages);
- Those generating a soil biomicrostructure, i.e. biomicrostructured A horizon (Code: miA) = Enchy-microarthropdic A horizon: enchytraeids, microarthropods (very small insects even in larval stages, mites, collembolans);
- Those invisible to the naked eye: nematodes, protozoa, microbes (fungi, bacteria and micro-algae), living in the soil and/or at the inside of plants and animals;
- Predatory animals (spiders, pseudoscorpions, centipedes, but also predatory soil-dwelling nematodes at micro-scale) have a poor effect on soil structure, to the exception of those which create cavities such as traps and subterranean nests. Their food is low in fibres, rich in nitrogenous compounds and the largest part of the ingested prey is assimilated. The excrements of these predatory animals are rather liquid or occupy a small volume, and thus do not participate directly to the transformation and/or accumulation of organic matter.

Humusica 1, article 4, §3 (Biological features of biostructured A horizons) includes a key for identifying soil animal faeces that allow associating soil aggregates and those groups of animals involved in soil genesis and transformation. In the following pages, a gallery of pictures illustrates the most common groups that soil observers may encounter across Europe (earthworms, enchytraeids, and arthropods). Some photographs show the faeces of these animals, too.

4.1. Epigeic, anecic, and endogeic earthworms (Lumbricidae)

Epigeic, anecic, and endogeic earthworms are relatively easy to distinguish in the field thanks to the following characters (Bouché, 1977):

- Epigeic earthworms are uniformly dorsally pigmented (Figs. 5 a and 21) and they live essentially in the organic horizons (OL, OF, and OH). Their casts (Figs. 5b and c) are organic and made of unrecognizable litter residues which have been finely ground by their muscular gizzard (Fig. 5c), generating biomeso-soil organic aggregates;
- Anecic earthworms are darkly pigmented in the fore part of their dorsal area (Fig. 6a). Young (Fig. 6b) or diapausing (Fig. 6c) individuals are lighter in colour. Anecic earthworms move vertically in the soil and feed and cast at the surface. They are the most important soil engineers generating biomacro-soil aggregates (Figs. 6a and c–f).
- Endogeic earthworms are lightly pigmented or colourless or green (Fig. 7a). They live in the organic-mineral layers of the soil, just under organic layers but not in them. They burrow horizontally and excrete organic-mineral droppings forming biomeso- or biomacrosoil aggregates according to their size. In Figure 7b, the A horizon in which an endogeic earthworm has been found, has been classified through soil sieving into three aggregate sizes, from left to right ≤1 mm, between 1 and 4 mm, and > 4 mm.

4.2. Enchytraeids, soil-dwelling nematodes, molluscs, and macro-, meso-, and microarthropods

For the purpose of this manual, all these animals are presented together because they structure the soil in similar aggregates, the dimensions of which depend of animal body form and size. Enchytraeids are small white or transparent worms varying in length from a few millimetres to a few centimetres (Figs. 8 and 9a–c). They usually concentrate near the surface of Moder, whereas they are restricted to middle depth in Mor and are mainly present in the lower depth of Mull (Bernier and Gillet, 2012).

In Figure 9c, a magnified picture of enchytraeid faecal material shows that minute faeces (0.1 mm) of these microannelids form larger fluffy masses. On the same figure, it is possible to see a beech leaf partially eaten (skeletonized) by enchytraeids, which ingested the tender parts of the limb and left the network of fine veins.

Besides enchytraeids, a vast array of different soil organisms can colonise soil profiles. Long-established grassland may have nematode populations as great as two hundred billion per hectare (Zunke and Perry, 1997). Nematodes are a highly abundant and diversified group of animals, belonging to microfauna, and can be classified into bacterial-,fungal-, plant-feeding, predaceous and omnivorous trophic groups (Yeates and Coleman, 1982; Orgiazzi et al., 2016). They look like small, transparent non metameric enchytraeids. Beautiful images can be seen at http://soilbugs.massey.ac.nz/gallery/nematodes.html. Like bacteria and fungi, but also for many very small soil animals such as micro-arthropods, it is very difficult to estimate by the naked eye the influence of nematodes in the formation of a soil structure. By feeding on fungi and bacteria, nematodes ingest a high number of microbial cells (Ingham et al., 1985), which could have an indirect effect on soil aggregate stability. Furthermore, it has been estimated that they convert up to 10% of

available N into other products (body tissue and excreta), that can be easily used by other decomposers (Nielsen, 1949).

Because many groups of soil organisms tend to concentrate their feeding and casting activities in certain horizons, they can determine the physical structure of the soil they work. Thus, numerous molluscs (snails, slugs) may also be found in the organic horizon of the soil (Fig. 10). Arthropods (Figs. 11a–d) are an immense group of animals, very active in the soil during different stages of their life cycle (larvae, nymphs, adults). Many larval stages of flying insects (flies, beetles) are living seasonally in the soil (Figs. 12a–c). Chelicerata (spiders, pseudoscorpions, mites), Myriapoda (centipedes, millipedes), Crustacea (woodlice, landhoppers), Hexapoda (insects, collembolans) are some of the main groups of soil-dwelling arthropods (Figs. 13 a–f, 14 a–c and 15a–d). Litter is transformed in the soil by all these animals (Fig. 16a–e).

They ensure the biotransformation of any dead plant material, influencing the cycle of vital elements, providing the plants with assimilable nutrients and building the necessary soil structures that retain mineral elements and water for plant uptake. Here are some more pictures illustrating this important process of soil formation (Fig. 17a–f) and the location of observable structures in the three parts of the pedon (Humipedon, Copedon, and Lithopedon, Fig. 18).

5. Microbiome: fungi and bacteria

It is a well-known fact that bacteria and fungi dominate different environments, with the former group regulating biodegradation processes in neutral and base-rich soils and the latter one in the rather acid and base-poor soils (Wardle et al., 2004). However, both groups of microorganisms are present in every humipedon. It is certain that they are the core of soil functioning: the soil is (completely) dominated by the two microbial groups, bacteria and fungi. However, they are invisible to the naked eye and so numerous and variable that most of our understanding focuses on the functioning of a perceptible system, i.e. only through the presence and activity of much larger organisms which are visible at our scale of perception, like plant roots and macrofauna. Except for well-known dinitrogen-fixing microbial communities, evidenced through symbiotic root nodules visible on some groups of plants (Fabaceae, *Alnus*, *Hippophae*), the action of microorganisms in the soil can be evidenced only through the use of more complex techniques such as respirometers, molecular markers, isotope labelling, etc.

5.1. Biodegrading fungi

Fungi are powerful biodegrading heterotrophic organisms worldwide. They acquire their nutrients by secreting enzymes, which are able to degrade recalcitrant plant metabolites such as celluloses, lignins and tannins. Their enzymes hydrolyse the target compound and the fungus secondarily takes up the resulting low-molecular compounds (Leonowicz et al., 2001). The fungal

body is made of a micro-tube (hypha) that penetrates the soil (or wood or any other living or dead plant tissue) as a three-dimensional net (the fungal mycelium). Hyphal length may reach several kilometres in a square meter of soil (Berg et al., 1998). These organisms show a great diversity and can invade any type of habitat using different strategies of reproduction and growth (Figs. 19a and b). For the purposes of this manual, we distinguish three groups of fungi according to their ability to degrade lignin, celluloses, and hemicelluloses, the main components of plant cell walls:

- White rots: Basidiomycetes producing enzymes (e.g. manganese peroxidase) are able to degrade lignin (some white rots even decompose lignin faster than cellulose) and other phenolic compounds such as tannins. Manganese is also involved in the regulation of other ligninolytic enzymes (laccases, Mn peroxodase);
- Brown rots: Ascomycetes and Basidiomycetes able to attack celluloses and hemicelluloses and partially lignin at some distance from their cell wall through their extracellular enzymes. Brown rot fungi are very important for biotechnological applications since they have enzymes which are very useful for degrading man-made aromatic hydrocarbons;
- Soft rots: Ascomycetes and Deuteromycetes (imperfect fungi, commonly known as “moulds”, without any known “perfect” sexual form, mostly belonging to Ascomycetes) able to digest celluloses and hemicelluloses, but not lignin, by forming small cavities in plant cell walls through which they grow. They can attack the median layers (pectin), exposing secondary and tertiary walls (cellulose then lignin as an infill) to the attack of other microorganisms.

For more information on white-, brown-, and soft-rot activities, many pictures can be found at https://en.wikipedia.org/wiki/Wooddecay_fungus.

5.2. Mycorrhizas

The symbiotic association between fungi and plant roots increases plant nutrient and water acquisition and protects the host plants from pathogens and parasites such as parasitic fungi and nematodes (Read, 2002). In return, fungi obtain sugars and the associated chemical energy from the plant. This particular symbiosis is called mycorrhiza and manifests itself at the level of plant root systems as different structures (for a beautiful synthesis, related to roots evolution and functioning in living and extinct plants, refer to Brundrett, 2002):

- Ectomycorrhizae (ECM), in which the hyphal mantle encloses the root tips and the Hartig net (i.e. the hyphal network between cortical cells) surrounds the plant roots, within the root cortex (Fig. 20); ECM fungi encompass more than 6,000 species, primarily of basidiomycetes with some ascomycetes and zygomycetes, but their diversity is poorly known in tropical and southern regions (Molina et al., 1992; Castellano and Bougher, 1994). The rapid diversification of these fungi continues to this day. ECM fungi produce enzymes that can digest plant cell walls at lower levels than saprophytic fungi can do (Bending and Read, 1997; Kohzu et al., 1999). Mostly present in Moder and Amphi systems;
- Endomycorrhizae (VAM), in which the fungus penetrates the cortical cells and fills the spaces between the epidermis and the cortical root cells. The association produces two types of

structures, arbuscular mycorrhiza (AM) and vesicular arbuscular mycorrhiza (VAM). Collecting AM and VAM, today VAM fungi are placed in the zygomycetous order Glomales, in the genera *Glomus*, *Acaulospora*, *Scutellospora*, *Gigaspora*, *Paraglomus* and *Archaeospora* (Morton and Redecker, 2001). These fungi are incapable of growth without plants. Mostly present in Mull systems;

- Mycorrhizae of Ericaceae, Epacridaceae and Orchidaceae. *Hymenoscyphus*-like fungi associate with the Ericales and bryophytes throughout the world. Less dependent of plants than VAM or ECM fungi (Chambers et al., 1999; Read et al., 2000), they are able to acquire organic nutrients in acidic soils (Smith and Read, 1997). Orchids have mycorrhizal associations with soil fungi believed to be essential for seed germination and to assist the growth of adult plants (Rasmussen, 1995; Currah et al., 1997) The benefits provided by orchids to their mycorrhizal fungi are not clear. Mostly present in Mor and Tangel systems.

5.3. Bacteria

Bacterial cells may amount to billions in a single gram of soil (Fig. 21a), typically many tens of millions of bacterial cells in a common gram of soil and millions in a millilitre of fresh water (Schloss and Handelsman, 2006).

We know that microorganisms are strongly involved in the process of general evolution (Mazzoleni et al., 2015a, b; Mazzoleni et al., 2015a, b; Cartenì et al., 2016). Until recently it was thought that bacteria were present everywhere in the world. However, Fierer and Jackson (2006) showed that acidic soils of tropical forests (i.e. ecosystems which exhibit the highest plant and animal biodiversity) had fewer bacterial species than neutral soils of deserts, and a recent study conducted across 80 dryland sites from all continents except Antarctica (Maestre et al., 2015) assessed that the abundance of soil bacteria and fungi was reduced as aridity increased. By adding nitrogen and phosphorus to 25 grassland sites across the globe, Leff et al. (2015) discovered that the relative species richness of mycorrhizal fungi, methanogenic archaea and oligotrophic bacteria decreased while that of faster-growing, copiotrophic bacterial taxa increased.

Soil samples from A horizons were analysed for humic substances and in parallel Amplified Ribosomal DNA Restriction Analysis (ARDRA) community profiles were determined (Carletti et al., 2009). It was found that in base-poor soils, such as those found in Alpine mountain forest ecosystems, bacteria were less active and contained a lower number of functional groups than in base-rich soils. In these base-rich soils, bacterial communities were more uniform and universal than in base-poor soils, where taxa consisted of more specialised communities (Fig. 22). A similar pattern has been evidenced by Fierer et al. (2012) using metagenomic sequencing to compare composition and functional attributes of 16 soil microbial communities collected from cold deserts, hot deserts, forests, grasslands, and tundra. Communities from plant-free cold desert soils had the lowest levels of functional diversity and the lowest levels of phylogenetic and taxonomic diversity. Using settled dust samples from ca. 1200 locations in USA, Barberán et al. (2015) confirmed the observations by Ranjard et al. (2013) showing that airborne microbial communities, like terrestrial plants and animals, exhibit non-random geographic patterns, explained by climate and soil variation.

Metagenomics supports the validity of the present classification of humus systems, which is based on the idea that specific groups of “biodegraders” (soil fauna and microorganisms) characterize the biological response of a given soil to a given environment.

6. Litter quality and biodegradation processes

A model of litter transformation is proposed in Humusica 1, article 2. B. Berg supplies a recent and in-depth information in an article in Humusica 3. In order to introduce the reader to a more dynamic comprehension of soil functioning, the importance of litter chemical composition during the process of litter degradation is showed in Figures 22a and b.

In litter, the contents of chemical components differ between deciduous and coniferous tree foliage (Berg and McClaugherty, 2014). Thus, litter degradation rates can differ even under similar climatic conditions. Conifer needles are generally richer in lignin than deciduous tree leaves (with the exception of sclerophyll leaves which share many properties with conifer needles) and are associated with Mor or Tangel “systems of biodegradation”. Rapid attack and biodegradation are possible in broad-leaved forests and generates a Mull humipedon while Moder and Amphi play intermediate roles in mixed coniferous-broadleaf litter substrates.

During an international meeting soil specialists were asked to summarize their field experience. The three graphs depicted on Figure 23 show the position of five black points representing the central reference of each main terrestrial humus system, expressing, even in an approximate fashion, the relationships between humus systems and forest biome productivity and climate (temperature and precipitation regimes). On Figure 24, hypothetical humus systems from boreal to tropical forests are placed along a global trend of increasing litter production, and compared with some observed humus systems in the Italian Alps. Most interesting conclusions are reported in the figure captions.

7. Analysis of humus system scales and dynamics (historical, biological, and environmental backgrounds)

Very few studies have tried to link specific organisms to the formation of a particular horizon across different humus forms and at different geographical scales, i.e. from local scales (e.g. spatial soil heterogeneity at any given soil type) to landscape (e.g. different ecosystems) and global scales (e.g. different biomes). Indeed, recent studies have highlighted the need for developing new theoretical models to better explain patterns of belowground community organisation and to use this information for understanding their impact on aboveground community dynamics and ecosystem functioning (Wardle et al., 2004; Bardgett, 2008; Bardgett and Van der Putten, 2014).

7.1. Humus system dynamics at large time and space scales

Soil formation is a dynamic process with several players driving different processes at different stages. The first step involves weathering of the parent material (rocks, minerals) through climatic, biological, chemical and physical processes into smaller fragments, finer textured materials and new chemical compounds (e.g. Orgiazzi et al., 2016). Microbial activities and biological crusts (lichens, algae, mosses and cyanobacteria) are the main responsible agents of the initial weathering of bedrocks, but in later stages this process is speeded up by other biological agents which exert physical pressure on the parent material (e.g., plant roots) or produce organic acids that dissolve minerals (e.g., microorganisms). Burrowing animals, such as earthworms, can also enhance the process by exposing rock fragments to the surface or via gut processes (Carpenter et al., 2007; Liu et al., 2011). Surface dwellers such as epigeic earthworms and enchytraeids are assumed to be the first biota to develop at the expense of organic matter accumulation and to drive the initial steps of soil structuring, via chemical changes of the ingested soil during gut transit and casting. Then, if soil texture is favourable, bioturbation activities of deep burrowers, i.e. anecic and endogeic earthworms, improve the physical structure and nutrient content of the soil and from this, the formation of mull humus (Frouz et al., 2008; Lavelle et al., 2004). Later on, soil biota add organic matter to the top layers of the incipient soil through the breakdown of senescent plant material (litter and roots).

Wallwork (1970) considered that although certain soil organisms are always active in every main humus system, their relative importance changes according to the humus system: mites and springtails dominate in Mor, mites, springtails and insect larvae dominate in Moder, millipedes and woodlice dominate in Mull-like Moder and earthworms (and/or termites) dominate in Mull. Summarizing Wallwork's thought, humus systems can be split into two main categories on biological bases: 1) Mull-like Moder and Mull, mainly inhabited by earthworms and bacteria and with organic-mineral complexes in the neutral or slightly alkaline A horizon; 2) Mor and Moder, mainly inhabited by mites, springtails, and fungi, and without organic-mineral complexes in the acid A horizon.

Wallwork's scheme has been contradicted by Ponge (1999, 2003) and Graefe (2005), which demonstrated the existence of a gradient of increasing soil biodiversity with increasing humification of soil organic matter, from Mor to Moder and then to Mull (see also Fig. 25). For example, open ecosystems such as meadows, pastures and agricultural fields often contain Mull specialists, i.e. bigger-sized invertebrates such as earthworms, ants, millipedes, termites, etc., whereas Moder soils, typically encountered in closed ecosystems such as forests, are inhabited by acid-tolerant groups, such as enchytraeids, mites, and collembolans (Ponge et al., 2003; Auclerc et al., 2009). These results also confirm previous observations in which a shift in humus type due to a change in land-use was accompanied by alterations in soil collembolan communities (Ponge, 1993). Similarly, the diversity of oribatid mite communities have also been seen to increase with increasing humus content of the soils, from dunes to forests via bog ecosystems (Murvanidze et al., 2011).

Changes in soil pH through liming and nitrogenous amendments are also known to influence humus shift from Moder to Mull (Picard et al., 1993; Theenhaus and Schaefer, 1995) and in turn, have an important effect on soil fauna communities (Fig. 25). Several studies have shown that liming and nitrogenous amendments decrease numbers of Oribatid mites and Collembola in the short or medium term (e.g. De Goede and Dekker, 1993; Fisk et al., 2006; Hågvar, 1984; Hågvar and Amundsen, 1981; Kopeszki, 1993; Persson, 1988) but stimulate lumbricid populations in the long term (Deleporte and Tillier, 1999; Graefe and Beylich, 2003; Hirth et al., 2009). In the case of the

ecological classification of earthworms proposed by Bouché (1977), for those endogeic worms living in the tropics, Lavelle (1983) made a distinction between 'polyhumic', 'mesohumic' and 'oligohumic' worms to account for differences in relation to the amount of organic matter ingested. Relationships between soil pH and earthworm life forms are well-known (Sømmer et al., 2002; Römbke et al., 2005). The largest ecological range for ecological factors is assigned to epigeic earthworms, which live in organic layers, move only seasonally deeper in the mineral soil (in some Amphi humus forms) and can also tolerate lower pH values ($pH_{water} < 5$). In contrast, many endogeic and anecic species avoid acid topsoils, preferring sub-alkaline, neutral or slightly acid conditions ($pH_{water} \geq 5$).

Similarly, it is well-known that fungi are more tolerant than bacteria to low pH values in the topsoil (Matthies et al., 1997). Therefore, acid Mor/Moder topsoils are dominated by fungi and characterized by slow litter biotransformation and subsequent accumulation of not or imperfectly humified organic residues. On the contrary, Mull topsoils are dominated by bacteria, which can rapidly mineralize the organic substrates, leading to fast disappearance of litter and advanced humification of soil organic matter (Eskelinen et al., 2009; Van der Heijden et al., 2008).

However, a bipolar model of the natural fate of litter cannot be exhaustive. In sub-acid to sub-alkaline soils, fungi are known to rapidly transform stable phenolic components of litter (lignin, tannins) into soluble organic compounds (Toutain, 1981), which can move downwards and be integrated into the underlying organic-mineral horizons. In any case, bacteria (Scotti et al., 2008) and fungi (Ponge, 2003) are genetically and functionally different according to the humus system (Gobat et al., 2003, 2004).

The concept of "twin humus" was originally developed by Hartmann (1944, 1952, 1970) and thereafter elaborated by Brêthes et al. (1995) as a particular Mull form in the French classification system with the name of Amphimull. This system can be related to Wallwork's and Kubiena's Mull-like Moder and was published as a new reference called Amphi in Zanella et al. (2009). In this humus system, a zoogenic A horizon (derived from anecic and/or endogeic earthworms) and an OH horizon (from epigeic worms and/or arthropods and/or enchytraeids) are both present and probably reflect a dominant zoogenic litter turnover in periodically milder (warmer or moister) soil climate conditions. The Amphi humus system can be observed in many Alpine calcareous or base-rich siliceous areas (Hartmann, 1970; Zanella et al., 2001; Sartori et al., 2005; Galvan et al., 2008), where it becomes the dominant humus system in subalpine beech and spruce forests, but also in warmer areas where seasonal drought is a driving factor (here often called Xeromoder), on various geological substrates (Descheemaceker et al., 2009; Ponge et al., 2011; De Nicola et al., 2004). Recently, Graefe (2007) proposed using this humus system to better classify some atypical Moders relatively frequent in warm/dry forest areas in Germany.

Mull humus systems are typical of mild climates (Fig. 26) and nutrient-rich substrates (Zanella et al., 2001; Ponge, 2003; Zanella et al. 2011a, b). The strong influence of environmental factors on soil invertebrates is greater for those groups exhibiting short development cycles, usually concentrated in the litter layers (e.g. fly larvae, enchytraeids, epigeic earthworms). This leads to seasonal variation, both in species composition and abundance, as well as to downward migration when cold or dry seasons create unfavourable conditions for the animal's surface activities (Briones et al., 1997; Lindberg and Bengtsson, 2005; Salmon et al., 2006; Makkonen et al., 2011; Petersen,

2011; Zenkova et al., 2011; Solida et al., 2015), but also changes in their feeding strategies, with concomitant implications for humus formation.

For example, in the case of Mor systems at high latitudes, some collembolan species select substrates of higher quality than under more favourable microclimate conditions (Krab et al., 2010). Similarly, water limitation results in enchytraeid populations being smaller, with negative implications for decomposition rates (Nurminen, 1967). However, the ability of some species to migrate downwards to avoid adverse conditions at the surface can increase the mobilization of both labile and recalcitrant carbon pools (Briones et al., 1998, 2007, 2010).

In Amphi systems, when the climate becomes harsher (too cold or too dry), earthworm activity concentrates to the A horizon during unfavourable seasons. On the contrary, going towards a milder climate Amphi progressively gives rise to Mull, losing its OH horizon by the incorporation of holorganic droppings in the underlying A horizon (Sartori et al., 2004; Visintainer, 2008). This interesting shift has also been described by Bernier and Ponge (1994) and Bernier (1995) on siliceous substrates as a dynamic phenomenon associated with the forest cycle (Oldeman, 1990; Ulrich, 1987) mature and early succession stages are characterized by Amphi and Mull, respectively, while active growth phases are characterized by Moder (for a detailed description of these humus systems, Humusica 1, articles 4 and 5). This cyclic transformation of humus systems can be explained by the intervention of different groups of animals along the space/time dimension of the forest ecosystem, earthworms succeeding to arthropods at the end of a forest cycle (more details in caption of Figure 37). The driving force for these changes has been suspected to be responsible for changes in nutrient availability associated with tree growth phases and emigration/immigration waves of earthworms in a fine-grain heterogeneous forested landscape when selective cutting (as opposed to clear cutting) has been the dominant management method for centuries (Ponge et al., 1998).

Soil and vegetation co-evolved on our planet. The last 500 million years' process has been represented in Figure 27a, giving a few temporal references. Even if this picture has to be considered more as an artistic view than a real succession of historical facts, it helps understanding the time required for the formation of present-day ecosystems. A more precise time-window evolution is represented in Figure 27b, where a co-evolutionary sequence of the last 3000 years is reconstructed. This picture is based on today's soil-vegetation associations found around the Biological Station of Paimpont (France) on a base-poor substrate, from the youngest on a shallow soil, to the oldest on a deep forest soil.

The main humus systems typically present in Alpine forest ecosystems are shown in Figure 28a. The potential actors of litter biodegradation are depicted, assigning more relevance to soil biodiversity (Fig. 28b). Changes in thickness and composition of soil layers are related to vegetation and soil biodiversity. Even if all these facts are well-known and described scientifically, seeing all of them combined in a single picture provide a better understanding of the biological processes that ensure the formation and maintenance of natural environments.

7.2. Humus system dynamics at local and micro scales

From the same “multifactorial perspective” it is now possible to return to a smaller scale of observation and point out the general process of humipedon formation in the light of a potential interaction among soil actors of litter transformation and biodegradation. The process of litter transformation could be summarized in several steps that can be directly observed in the field by simple, recognizable diagnostic horizons in the humipedon (Fig. 29a). In particular, environmental frames, it is even possible to show specific ways of formation of different humipedons corresponding to the main humus systems (Fig. 29b).

In temperate climates, litter is transferred directly to the biomacrostructured A horizon of Mull systems. In contrast, in harsher climates and/or scarcer conditions for nutrient availability for the biological transformation of litter, a non-zoogenic OF horizon takes place in a Mor system. Moder, Amphi and Tangel are characterized by a more or less thick zoogenic OH horizon, humified organic matter being partially transferred to an underlying A organic-mineral horizon. Moder is a base-poor transition stage between Mull and Mor. Amphi is present in Mediterranean (periodically dry) and in mountain (periodically cold) climates, and Tangel in cold and very contrasted high mountain climate, on base-rich substrates.

Litter undergoes a progressive transformation and by observing a humipedon, from the top to the bottom, it is possible to obtain a dynamic representation of the process (Figs. 30a and b). Animal droppings have been counted at different layers of the humipedon during a student training course (P. Galvan, unpublished data), following a technique previously established by Bernier and Ponge (1994). From the left to the right side of the graph one can follow successive attacks by soil animals, expressed by signs of their defecating and/or burrowing activity.

Different animals succeed and thrive following their specific life cycles in response to substrate quality (Wall et al., 2008) and abiotic conditions (Klamer and Hedlund, 2004; Wall et al., 2008). Indeed, the decomposition of litter with low palatability often requires pre-conditioning (e.g., bleaching and softening) by white-rot fungi prior to faunal attack (Daniel et al., 1997; Hafidi et al., 1998). Fungal enzymes are capable to degrade plant polymers, which can solubilise phosphorous minerals (Tagger et al., 2008). Decomposition rate is initially controlled by litter quality and only thereafter, once litter becomes more palatable, soil fauna exerts a more prominent role in a second step of the decay process (Mori et al., 2009). This confirms previous evidence indicating that litter decomposition rates are more strongly related to which soil fauna groups are involved and the way they succeed each other (e.g., pre-conditioning of litter (softening) by bacteria and fungi and thereafter penetration by microfauna and mesofauna) than to the chemical nature of the litter (Ponge, 1991). Furthermore, macrofauna digestion, excretion and enrichment activities increase microbial attack. Thus, animal faecal pellets provide an additional nutritional substrate for microorganisms (Tagger et al., 2008). Macroelements such as Ca, Mg, and Fe also play important roles in litter decomposition and previous studies have demonstrated that millipedes, centipedes, and earthworms incorporate these elements in their bodies leading to accelerated mineralisation (Song et al., 2008). Recently, it has been shown that earthworms are also capable of neutralizing plant polyphenols that otherwise strongly decrease decomposition rates of fresh plant litter (Liebeke et al., 2015). In addition, living organisms also critically contribute to the leaching of organic and mineral solutes and their relocation in deeper horizons.

On the other hand, historical climatic conditions determine the abundance or dominance of specific faunal groups in a certain area. For example, if anecic earthworms are abundant in a particular soil, they will rapidly bury fresh fallen litter, and other litter-consuming organisms that live in deeper layers will simply consume this organic matter inside the network of subterranean earthworm galleries and thus will not form any OF or OH horizons. The system is in equilibrium as a Mull system. On the contrary, if pedoclimatic conditions are not favourable to these large earthworms (cold acid or warm dry soils), arthropods and/or enchytraeids will find a high amount of unburied litter and will transform it in OF and OH horizons which may stay several years in the upper part of the humipedon.

The kinetics of soil organic matter transformation from litter input to the final emission of CO_2 into the atmosphere, and to the formation of a nitrogen pool for plant uptake is usually described by a system of first-order linear differential equations with varying coefficients. The role of soil organisms in these soil organic matter models is typically assumed to be in the form of a foodweb, where microorganisms are the primary decomposers, microfauna are first-order predators by grazing on microbes, mesofauna are transformers of the litter-organic layer interface and macrofauna are litter fragmenters, soil mixers, and responsible for aggregate formation (e.g., De Ruiter et al., 1998; Holtkamp et al., 2011; Osler and Sommerkorn, 2007; Schröter et al., 2004).

Thanks to specific studies considering soil temperature, photosynthesis, and respiration (data in Rodeghiero, 2003; Rodeghiero and Cescatti, 2005; Rodeghiero et al., 2010) it is possible to better understand the dynamics of soil organic matter (Figs. 31a–c). Soil temperature and water availability have to be considered jointly to understand the presence of a given type of humipedon in a given site (data in Rodeghiero, 2003, Figs. 32a and b).

The series of humus systems defined by diagnostic horizons and involving different actors of litter biodegradation is set along an ecological base-richness gradient from lowland (base-rich) to highland (base-poor) in an Alpine frame (Fig. 33). The distribution of humus systems along this ecological gradient is linear, but Amphi and Tangel may be seen as systems breaking the line from Mull to Mor in two points and developing new pathways. It is possible to imagine that when the original system adopts these new pathways, it becomes a two-niche system, dividing the humus profile in two parts: the organic-mineral one at the deeper layers, dominated by anecic and endogeic earthworms, and the organic one at the topsoil, dominated by arthropods and enchytraeids. If the natural frame becomes large and variable enough, all types of humus systems are possible and assembled in the studied territory like mosaic pieces. Even in small locations (a few hectares) in temperate regions, three humus systems are often present (Mull, Moder, and Amphi), while at high elevation (> 2000 m in the Alps) Mor and Tangel are very common.

7.3. How and in which humus systems is organic matter stored in the soil?

Figure 34a clearly illustrates that soil organic matter has a different status according to different humus systems. In a Mull system, organic matter is strongly linked to mineral particles, because of bioturbation caused by anecic and endogeic earthworms. In humus systems without these two categories of earthworms organic matter consists of more or less altered (ingested or fragmented) plant residues (leaves or needles, twigs, bark). This form of organic matter might only

react slowly in the case of a rapid warming events because organic molecules become chemically more stable when covalently linked to minerals (Balesdent et al., 1998, 2000, 2005; Virto et al., 2010), and are less accessible to bacteria and fungi and not at all to larger animals or roots. The quantity of organic matter fixed in clay aggregates is much more important in Mull systems than in all other humus systems (De Nicola et al., 2004). On the other hand, a similar amount of organic carbon can be measured in different humus systems (Sartori et al., 2004; Garlato et al., 2009a, b; Bonifacio et al., 2011; Ascher et al., 2012; Andreetta et al., 2011). Humus systems and organic carbon contents are relatively independent. The physical structures in which carbon is stored may differ according to regions (Fig. 34b) and this certainly can strongly influence soil carbon dynamics.

7.4. Above-ground control on humus systems: the forest cycle

Despite the current debate on the direction of the relationships between above-ground vegetation and below-ground communities (reviewed in Ponge, 2013), plants can exert competition pressure on soil animal and microbial communities directly by competing for the same resources or indirectly by changing humus forms (Fig. 4). For example, the antagonistic interaction observed between epigeic worms and enchytraeids in Norway spruce ecosystems was interpreted as the result of competition for nutrients between trees and soil organisms, favouring the less nutrient-demanding faunal groups (here enchytraeids) when tree growth is at its highest rate (Galvan et al., 2008). Similarly, the lower abundance of collembolans in two subalpine spruce forests has been linked to a denser root system of spruce trees, making it a better competitor for water acquisition (Salmon et al., 2008).

In addition, forest dynamics is accompanied by important changes at the level of the humipedon. Humus forms cover the forest floor of natural or semi-natural forests as pieces of a mosaic corresponding to phases of the forest cycle (Bernier and Ponge, 1994; Bernier, 1995, 1997). Their distribution is also well-correlated to other ecological factors like climate and parent material (Slompo, 2004) and chemical changes in the soil (Pizzeghello et al., 2006; Salmon et al., 2006; Galvan et al., 2008; Cason et al., 2008). Indeed, later successional stages can be linked to changes in the quality and the horizontal and vertical distribution of food resources (Hedde et al., 2007; Salmon et al., 2006). On each point of the forest floor, the ratio between holorganic and organic-mineral humic components changes over time (Figs. 35a–d). According to space-for-time substitution studies (chronosequences), the thicker litter layer developed during the pole stage of the forest cycle provides a more favourable microclimate (acidic, cool and moist conditions) for litter-dwelling species having a holorganic diet. The nutrient condition of the soil improves with stand maturation, nutrients being mainly retranslocated within the sapwood of mature trees, while the soil stock of nitrogen, phosphorus, magnesium, potassium, and calcium has been depleted during the preceding pole phase (Andrews et al., 1999). This creates a more favourable environment for organisms exhibiting survival strategies to drier environments and preferring sub-neutral conditions, such as anecic and endogeic earthworm populations that live in organic-mineral layers and mix holorganic residues and/or droppings with mineral fine grains (anecic species) or ingest already mixed organic matter (endogeic species). This biological improvement is followed by an important incorporation of organic horizons in the newly built organic-mineral layers with a concomitant shift of the humus

system towards Amphi then Mull, the latter being associated with the regeneration phase (i.e. the establishment of a new cohort of trees). The process stops when the population of actively growing trees increase their uptake of the necessary mineral elements from the soil, thus impoverishing the topsoil and competing with the decomposer community, possibly through mycorrhizal networks (Averill et al., 2014). The humus form switches again, this time to Moder (Dysmoder) or Mor, the organic-mineral horizon becoming poorer in bases and deprived of anecic and endogeic earthworms. Such a natural cycle, allowing the forest ecosystem to be renewed over centuries if not millennia at the climax stage, can be observed only if refuges exist for temporarily collapsing soil-dwelling earthworm populations, allowing recolonization when conditions become favourable again (Bernier and Ponge, 1994). Foresters could mimic the natural process of forest regeneration by establishing uneven-aged forest stands, with small management units of no more than a few acres. For example, in a mountain spruce forest over siliceous parent material in the Alps, the high elevation interferes with faunal vitality since low temperatures restrict the duration of favourable seasons (Bernier, 1997) and as a result, the sequence of humus forms throughout a complete forest cycle revolves around a central Mull under 950 m, Amphi at 1550 m, and Moder at 1800 m (Fig. 36).

Finally, we illustrate two examples in which artificial plantations of conifers have been established in temperate forest stands that were previously occupied by broadleaved trees (Figs. 38a and b). It can be seen that conifer development locked up the process of litter degradation, leading to the freshly accumulated organic matter not being incorporated in the underlying old organic-mineral horizons.

8. A few links to biological indicators of soil quality

A simple methodology for estimating the strength of soil structure:

http://aocsols.free.fr/fichiers%20programmes/guide%20profil%20sol%20CA%20tarn%202008.pdf

A biological indicator of soil quality based on the composition of macro-invertebrate communities:

http://www.ademe.fr/sites/default/files/assets/documents/indice-biologique-qualite-sols-ibqs-2011.pdf

An indicator of biological quality of agricultural soils based on a restricted array of selected biota in Ponge et al. (2013).

A biological soil quality indicator (BSQ) based on scoring microarthropod abundance in permanent grasslands in Gardi et al. (2002).

Some among many reviews related to biological soil quality indicators: Benckiser and Schnell (2006), Cenci (2006), Benckiser (1997), Bonanomi et al. (2014), Chaussod (1996), Doran and Zeiss (2000), EuropeanCommission (2012), Fletcher et al. (2011), Dighton and Krumins (2014), Artz et al.

(2010), Lal (2015), Martinez-Salgado et al. (2010), Pankhurst et al. (1997), Pulleman et al. (2012) and Porre et al. (2016).

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Figure captions

Fig. 1. a) Soil food web represented by Daniel D. Dindal (available at http://lbartman.com/worksheet/food-chain-activity-for-high-school.php); b) Soil food web, unknown author (available at http://3jc9u229pdq31afjhhp0b1lf.wpengine.netdna-cdn.com/files/2013/08/soil_food_web.jpg).

Fig. 2. The two most common devices used for a preliminary survey of soil animals. a) standard dry Berlese funnel extraction; b) wet O'Connor funnel extraction. The use of these extraction methods is sufficient for many basic research and teaching purposes. Nematodes can also be extracted using wet extraction in the dark (no light). More demanding and specific tools are necessary for a more extensive survey of soil pedofauna. In particular, earthworms cannot be extracted with these devices and combinations of hand-sorting and chemical extraction are performed in the field.

Fig. 3. A simplified tree of life for soil organisms. It allows an easy allocation of main groups of actors to litter biodegradation and soil transformation processes. Three branches are distributed at the first level (https://en.wikipedia.org/wiki/Kingdom(biology) of classification: Archaea (extremophile bacterial organisms), Bacteria and Eucaryota (or Eukaryotes, all others). Eucaryota can be divided into Protists (unicellular Eucaryotes), Fungi (not photosynthetic, heterotrophic, often with chitin in cell walls), Plantae (cellulose in cell walls, chlorophylls a and b and plastids bound by only two membranes and capable of storing starch) and Animalia (heterotrophic, motile, with embryos passing through a blastula stage). Animalia contains the five main groups of animals that one can find in the soil: Annelida (segmented worms), Nematoda (roughly approximated definition: non segmented worms), Mollusca (soft invertebrates with or without shell), Arthropoda (segmented animals with exoskeleton and 6 or 8 or more legs), and Chordata (animals with dorsal rod).

Fig. 4. Relationships between environmental filters (MAT = mean annual temperature; MAP = mean annual precipitation), biotic performance filters (best adaptation to prevailing conditions through natural selection, dispersal abilities and population density regulation) and soil processes along temporal and spatial (horizontal and vertical) scales. Colour figures in the web version of the article.

Fig. 5. Epigeic earthworms: a) Epigeic earthworm (*Lumbricus rubellus*) found in a beech-oak forest in Parisian region, in the OLn horizon of a Dysmull: the epigeic earthworm is of the size of a lens ocular; b) *Dendrobaena octaedra* with a few organic grains on its cuticle: two of these grains (size: 2 mm) correspond to its faeces, while others most probably correspond to enchytraeid faeces (size: 1/10 mm; c) enlargement of a faecal pellet of *Dendrobaena octaedra* (size: L = 3.9 mm, H = 2 mm); d) By the Station Biologique of Paimont (France), in a carpet of mosses and lichens, an unknown earthworm species that generated an OH horizon. This earthworm may belong to a hybrid epi-endogeic category, developing in the rocky acidic superficial soil of the region (Daniel Cluzeau personal communication). This means that the epigeic, anecic and endogeic categories of earthworms correspond to artificial groups that need to be better circumscribed considering the scale of the related ecological processes (Lavelle, 1983, 2012). Colour figures in the web version of the article.

Fig. 6. Anecic earthworm: a) Anecic earthworm (*Lumbricus terrestris*) in a meadow, among its freshly accumulated casts (the earthworm midden). Its reddish head is sinking in its vertical gallery from which soil is excavated; b) Earthworms collected in a grassland at the Station of Ecology of Fontainebleau (University Paris Diderot, France): mixed sample of endogeic (weakly and uniformly pigmented) and anecic (red-brown pigmented) earthworms; c) Earthworms in diapause are less pigmented. They protect themselves from seasonal drought and/or frost by building a little cavity deep in the soil, rolling their body into a ball and awaiting a better season for resuming their activity; d) enlargement (x 10) of an anecic organic-mineral aggregate; e) biomacrostructured anecic earthworm-made horizon; f) a single mamillated anecic earthworm faecal deposit (×10).

Fig. 7. Endogeic earthworms: a) Endogeic earthworm (*Allolobophora chlorotica*) found in the A horizon of a Moder evolving towards an Amphi, in an Alpine spruce-fir mixed forest; b) the A horizon (pH nearly 5) from which this animal has been extracted, is composed of aggregates of different sizes, respectively from left to right: ≤1 mm, between1 and 4 mm, and>4 mm.

Fig. 8. Enchytraeids. a) enchytraeids (small metameric micro-annelid worms); b) a small enchytraeid on a finger; c) a Petri dish containing a brown-red epigeic earthworm, a young anecic one with red forepart and light hind part (right), a large transparent enchytraeid (top) and here and there a few small enchytraeids (some just aside the large enchytraeid): dark spots present in the Petri dish are small pieces of litter and masses of enchytraeid faeces. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Fig. 9. Enchytraeids. a) in the OH horizon from an oak-beech forest in Parisian region; b) in the A horizon of an Alpine beech forest. In both photographs these animals are surrounded by an accumulation of their own faeces, building a biomicrostructure; c) Enchytraeids with their droppings and a beech leave eaten (skeletonized) by them (from Zanella et al., 2001). The yellow enchytraeid has been identified by U. Graefe as *Cognettia clarae*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Fig. 10. Snails (mollusks, Gastropoda), from left to right: *Trichia hispida*, *Discus rotundatum*, *Oxychilus alliarius*.

Fig. 11. a, b, c and d: examples of pedofauna collected by Université Pierre et Marie Curie (UPMC) students (Paris, France) from a Moder in a mixed beech-oak forest in Fontainebleau forest (France).

Fig. 12. Insect larvae. a) Coleoptera Elateridae (*Ampedus sp.*) in the OF horizon from an Alpine beech forest: surrounding dark-coloured aggregates do not correspond to the light-coloured faeces of this species which feeds on living roots; b) Coleoptera Erotylidae in the OF horizon from a Mediterranean holm oak (*Quercus ilex*) forest; c) Mecoptera Panorpidae (*Panorpa sp*.) in the OF horizon of a temperate oak-beech forest.

Fig. 13. How many animals can be found in a soil sample? a) The smallest animals reported on the photographs are mites (1 mm or less), with 4 pairs of legs. In the middle of the picture, just

below the large spider, there is a small entomobryid springtail; b) a lot of white enchytraeids, many oribatid mites, a large insect pupa and a long yellow geophilomorph centipede (predator of earthworms); c) Earthworm, centipede (top) and millipede (bottom) in a mass of detritus hiding small mites, springtails and ants; d) spiders of varying size; e) Can you find on this picture the two mites which have been magnified in (15a) (a Phthiracaridae on the left and a Mesostigmata on the right)?; f) Pedofauna from an Alpine spruce forest (altitude 1600 m). Counts performed by N. Bernier and L. Tarasconi at the National Museum of Natural History of Paris (photographs L. Tarasconi). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Fig. 14. Millipedes and woodlice: some species are able to roll themselves up into a ball when disturbed. a) the pill millipede *Glomeris connexa*, rolled up among its droppings; b) the woodlouse *Armadillidium vulgare* is also able to roll up in case of disturbance; c) the non-rolling woodlouse *Porcellio scaber*. These little crustaceans are very common in OL and OF horizons, in dead wood and under stones lying on the ground.

Fig. 15. Mites. a) a Phthiracaridae on the left and a Mesostigmata on the right; b) two oribatid mites, a Phthiracaridae on the left and three Ceratozetidae on the right; two watercolour plates of mites (by courtesy of N. Artuso) where it is easy to distinguish two groups of very common soil mites: c) Oribatida (Actinotrichida), with four front legs forward and two hind legs; d) Gamasida (Anactinotrichida), with two legs projected forwards, longer and different from the other six, or four in larval stage).

Fig. 16. Soil arthropods and their faeces. a) Top: a millipede (left) and enlargement of its droppings (right); bottom: a predatory mite (Mesostigmata, left) and droppings of phthiracarid mites (right) within a decaying spruce needle (photographs M. Tomasi and L. Frizzera); b) The millipede *Chordeuma sylvestre* among its droppings. This animal is very common in OL and OF horizons. Its faeces are organic and measure 2–4 mm on average, building a mesostructured; c) and d) Droppings of macroarthropods (millipedes) in the OH horizon of a Mediterranean Eumesoamphi; A biomesostructured arthropod-made A horizon in a holm oak Mediterranean forest. e) Vertical section of the horizon; f) The same horizon viewed from above.

Fig. 17. Organic arthropod-made horizons (×10). a) and b) zoOF horizon; c) zoOH horizon; d) transitional OH-miA horizon; A horizons: e) and f) biomicrostructured arthropod/enchytraeid-made horizons.

Fig. 18. Types of soil structure and their associated subpedons (adapted from FAO, 2006). Soil structure represents the arrangement of particles and pores in soils (Oades, 1993). Its main macroscopic features allow describing and identifying soil horizons in a soil profile. In a natural terrestrial Humipedon, soil structure is mainly biogenetic or under influence of soil fauna. The Lithopedon does not show any signs of soil aggregation and the Copedon is under the influence of biotic (faecal deposition, root exudation, microbial secretion) and abiotic (freeze/thaw, drying/rewetting) processes of soil aggregation. Authors of the figure: J. Juilleret, J.F. Ponge, A. Zanella.

Fig. 19. Biodegrading soil fungi. a) Five species of fungus biodegrading spruce needles. Fungal asexual structures are protruding from lines of stomata. These species can begin the attack even on living needle (classification and photographs by courtesy of L. Scattolin); b) Biodegrading soil fungi. Top: In the litter produced by broadleaved plants, the mycelium of biodegrading fungi show a typical fan appearance (here a white rot, as ascertained by the pale colour of bleached leaves rather than by the white colour of the mycelium). Bottom, mushroom pasta: some Farfalle "bow-tie pasta" left for three weeks in an empty and switched-off fridge. The substrate was fully utilized by fungi (most probably 2–3 Aspergilli species). The greenish colours come from conidia (spores) produced by the fungi cover the whole surface. Trillions of spores are present on these pictures. The same process may be observed in common plastic bins of home-made compost (Humusica 2, article 16, for details).

Fig. 20. Examples of plant-fungal relationships and spores. Orange carpophores of a wood-decay fungus (carpophore of *Laetiporus sp.*) on a tree trunk (*Tilia X europea*) black ectomycorrhizae on roots of lime trees (*Tilia tomentosa*) living in the soil under pavements in the centre of Paris; fungal asexual structures protruding from lines of stomata of a needle spruce. This species (*Ceuthospora pinastri* (Fr.) Hohnel.) can attack even living green needle (photograph and classification by courtesy of L. Scattolin); orange ectomycorrhizae of a symbiotic fungus on spruce (*Picea abies*) roots (from Zanella et al., 2001). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Fig. 21. Bacteria. Google images illustrating shapes of cells and colonies of these microorganisms living in countless numbers in soils and in the human microbiome.

Fig. 22. How bacteria inhabit forest soils (example in Carletti et al., 2009): in Alpine mountain forests, bacterial communities are sensitive to soil quality, being less numerous and more specialised in base-poor soils than in base-rich soils, climatic conditions being co-involved in the process.

Fig. 23. a) Changes in the amount of chemical components during the decomposition of Scots pine needles (simplified from Berg and McClaugherty, 2014): water soluble compounds are absorbed by microorganisms and other soil organisms or are leached out; hemicelluloses and cellulose are attacked by microorganisms via the production of exo- and endo-cellulases; the production of peroxidases allows the degradation of lignin and tannins, starting much later and at a lower rate because it requires sugars issued from previous degradation of cellulose and hemicelluloses to become available; lignin and nitrogen concentrations then increase in the remaining substrate; nitrogen is immobilized by lignin, becoming unavailable for other chemical reactions; finally, this substrate is transformed into a material that is strongly resistant to further biodegradation (heterocyclic ring polymerization proposed by Lindbeck and Young, 1965); b) Changes in lignin and nitrogen concentration according to climate and first-year mass loss (simplified from Berg and McClaugherty, 2014). The higher the annual actual evapotranspiration the more rapidly litter disappears. High evapotranspiration means warm conditions and good water supply (Mull system). Low evapotranspiration means dry continental or cold conditions (Mor or Tangel systems).

Fig. 24. Climate effects on production of carbon biomass. Carbon photosynthetic fixation (simplified from Lieth and Whittaker, 1975) has been related to average annual precipitation and air temperature (on the right). The main forest biomes have been placed on the left graph with

the aim to show their “climatic amplitude” for the same parameters. Under the temperature x-axis, a corresponding north latitude degrees’ scale has been indicated. Between the two graphs, some coloured rectangles display the net primary productivity of each of these biomes. On the graphs, five black points indicate the hypothetical “attractor factor” for five main humus systems: Mull with highest precipitation-temperature values for a maximum primary production, Mor and Tangel with lowest values for these two climatic variables, Moder and Amphi with intermediate values.

Fig. 25. Relationships between climate and litter production (left, simplified from Bray and Gorham, 1964; right, simplified from Rodeghiero, 2003). Black circles are humus systems (hypothetical on the left box, observed on the right box). The production of litter follows the same trends as primary production. In an equilibrated ecosystem, all the net primary production ends, sooner or later, in the soil in the form of leaf and root litter. On the graphical model, the amount of litter ranges from 0.1 to 0.6 kg of C m^{-2} yr^{-1}. The data refers to senescent foliage litter falling on the ground, not root litter (dead roots and root exudates) deposited belowground. When compared to the corresponding net primary productivity (NPP) there is an important mass of C which is stored belowground and a lower mass which is recycled or invested in plant growth (cyclic or linear). It seems that NPP stores 1/3 of total C aboveground, whereas 2/3 of C are stored belowground. These C fluxes can be hypothetically related to the five terrestrial humus systems, as shown on the picture.

Fig. 26. Relationships between environmental gradients and soil communities along four contrasting biomes. Data sources: C stocks from Trumper et al. (2009); N_2 fixation rates from Cleveland et al. (1999); mycorrhizal associations from Read and Perez-Moreno (2003); soil biota groups modified from Brussaard (2012).

Fig. 27. First attempt at an ecological framework for terrestrial humus systems. The gravity centres of the different humus systems have been positioned in the space of three main factors, temperature, annual rainfall and soil pH, known to influence litter biodegradation. The scheme aims to show the relative position of the main humus systems in a hypothetical three-dimensional space of potential development.

Fig. 28. a) Soil-vegetation co-evolution. Along the yellow line, vegetation evolved from mosses to ferns, then to conifers and broad-leaved plants, in a historical succession along the 500 million years of natural history of our planet. Soil profiles have been shown besides, considering analogous present-day environmental situations. The figure reminds us that the living soil has a history as long as that of Life in terrestrial ecosystems. Unit pictures were obtained from internet; b) Soil and vegetation, two sides of the ecosystem. 3000 years of common history on a base-poor (acid) substrate in France (forest of Paimpont, near Rennes, France). The series was studied during training courses in the frame of a teaching collaboration between the University Pierre-et-Marie-Curie (Paris, France) and the University of Padua (Italy). (For interpretation of the references to colours in this figure legend, the reader is referred to the web version of this article).

Fig. 29. Main humus systems in Alpine forest ecosystems (modified from Zanella, 2014). a) Diagnostic horizons of each main humus system are reported in correspondence with pictures representing main forest ecosystems; b) main groups of soil animals involved in the litter-

recycling process. Litter disappears rapidly if anecic and endogeic earthworms are dominant in the soil, as in broad-leaved temperate forests. Fungi dominate in cold high Alpine climate, generating a Mor humus system. Arthropods influence the humus system in periodically dry and/or not extremely acid ecosystems and generate Tangel, Moder or Amphi intergrade humus systems.

Fig. 30. a) Humus system formation according to four typical steps of litter transformation (OL, OF, OH and A horizons). The time of formation/disappearance of each horizon depends on environmental factors; b) Litter transformation and final humus systems. Numbers and succession of the different horizons are influenced by environmental conditions. Five different points of dynamic equilibrium (called humus interaction systems or humus systems) have been described in this guide for terrestrial ecosystems.

Fig. 31. Litter attack by soil organisms. a) Horizontal axis = depth of organic horizons in a Moder; vertical axis = % traces of animal activity (droppings, galleries, etc.). Traces of springtail and mite activity are numerous in the first top cm of the soil, then millipedes and enchytraeids dominate below 5 cm. Going deeper in the soil means going back in time. A general functional succession of biodegrading actors operates the recycling of litter; b) Each ecological frame corresponds to a particular succession of biodegrading actors regulated in time and space. We reported here five ecological attractors (front: Mor, Moder and Mull; background: Tangel and Amphi). At the level of Moder system, we pasted the preceding a), corresponding to attack waves of different Moder system's animals. In this perspective, a Mull humus system is a process of recycling in which the anecic and endogeic earthworms rapidly mask the activity of other biological actors of litter transformation and implementation in the soil.

Fig. 32. Changes in carbon flux, soil temperature and photosynthesis efficiency. Examples from the Italian side of central Alps: beech forest model, in Rodeghiero (2003); spruce forest, in Rodeghiero and Cescatti (2005). a) Soil respiration (flux of C) increases exponentially with soil temperature. Humus systems are represented as black circles on the graph. Mull (black dot 1) was investigated only in a beech forest; Moder (2) was common in mountain spruce forests of the studied region (red line); Amphi (3) is well-known in the studied region at the altitudinal level of sub-mountain (600–800 m) to mountain (800–1300 m) forests. The three humus systems show a differential response in terms of carbon fluxes controlled by water content and soil temperature. b) The flux of C from the soil depends on soil temperature: the lower the temperature, the higher the Q_{10} (temperature coefficient), i.e. the rate of increase of C flux when temperature is increased by 10 °C. Then, in a site with a low average annual temperature (example 5 °C in the graph), a sudden increase in temperature will rapidly generate a strong flux of carbon respired by the soil. This phenomenon can explain the presence of Mull at a relatively high altitude, even if the more common humus system at this altitude is Moder. Inversely, a low Q_{10} at lower elevation results in a slow response of soil microorganisms to changes in temperature and can explain the presence of undecomposed horizons like the OH of Amphi, instead of a usual Mull without OH horizon. c) Photosynthesis efficiency is higher in boreal forests. Here soil respiration, which is strongly dependent from temperature, shows a lower rate than in temperate and tropical forests (Saugier and Mooney, 2001); however, the decomposition process is also more sensitive to low

temperature than to photosynthesis and the balance between them results in a higher primary production and more litter input. This might explain the relatively high production of litter and soil organic horizons in high latitudes or in cold climates, generating Mor and Tangel humus forms (see Humusica1, article 2 for details). (For interpretation of the references to colours in this figure legend, the reader is referred to the web version of this article).

Fig. 33. Respiration in the soil along the year follows the curve of soil temperature if there is no water deficit (simplified from Rodeghiero, 2003: two years of data in continuum). a) Changes in C flux in relation to soil temperature and water content during one year (from J= January to D= December). Soil respiration (C flux) follows increases and decreases of temperature but is limited by water deficit during summer. This is the most probable explanation for the presence of an Amphi system (black circle). If this drier period of the year is long enough, soil respiration becomes arrested and organic horizons are formed in the upper part of the topsoil. b) Vertical axis: left, C flux from the soil, C content in annual fallen litter; right axis: soil temperature; horizontal axis: elevation. Little coloured circles correspond to vegetation and associated humus systems. Up to 1000 m elevation, soil C fluxes and temperatures change in parallel; from 1000 to 1800 m C flux from the soil increases though temperature decreases; temperature and litter mass show opposite trends and seem to be independent from the soil respiration flux. These responses can be explained by the amplitude of soil temperatures which is often restricted at high elevation, Q_{10} and consequently soil respiration being greater at high elevation (Rodeghiero, 2003).

Fig. 34. Humus forms associated with main living actors of biodegradation.

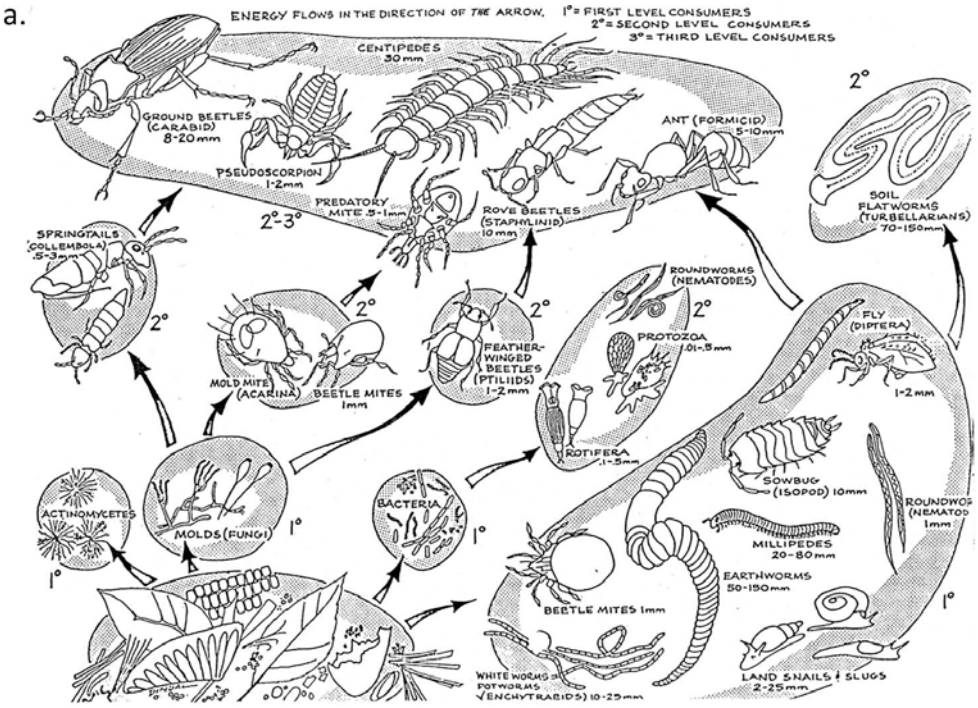
Fig. 35. a) Humus systems and the way organic matter is stored in the soil. Organic matter sequestered in clay aggregates is harder to degrade than organic matter as free residues; b) In Italian forests, the largest contents in organic carbon can be observed in different humipedons (first 30 cm of organic and organic-mineral soil horizons): Amphi in the western side of the Alp chain, Moder in central and eastern parts, and Mull in the Apennines. By comparing Figures 35a and b, it is possible to state that the organic carbon stored in C-rich terrestrial (not submerged) forest soils of the eastern part of the Alps is rather in the form of organic remains (Moder), while it is mostly in the form of organic-mineral aggregates in the Apennines (Mulls), and is shared in organic remains and organic-mineral aggregates in the western part of the Alps. Even if the content in organic carbon is equivalent (80–100 t/ha), its reaction (timing and dynamics) to global warming should differ (by the actors of biodegradation and the structures storing carbon) in these three types of humipedons.

Fig. 36. a) Aggradation (pole) phase of an Alpine spruce forest; b) Mor system (with a sharp and clear separation between organic and mineral layers). It characterises the base-poor topsoil of the aggradation sylvogenetic growth phase (sensu Oldeman, 1990); c) Innovation phase (sensu Oldeman, 1990) in the same Alpine spruce forest; d) Rhizo-Amphi humus system. It takes place in an open area (innovation phase) where the organic matter has accumulated on the surface during previous phases and was partially incorporated to the mineral layer by earthworms (see also Figure 37).

Fig. 37. Humus forms and forest mosaic during the sylvogenetic cycle in a mountain spruce forest at three elevations (950, 1550, 1800 m). From Bernier (1997), modified according to the present classification of humus forms. Mull system takes place (soil colonisation by anecic and endogeic earthworms) during the degradation, zero event and innovation phases (sensu Oldeman, 1990; Ulrich, 1987). However, tree growth (aggradation phase) "forces" the humipedon to evolve toward new humus systems, accordingly with given altitude gradients: Amphi (950 m), Moder (1550 m) or Mor (1800 m). The figure (modified from Bernier, 1997), shows observed changes in thickness of organic-mineral (red dashed line) and organic (black dashed line) humus horizons, along the different sylvogenetic phases, at three altitudinal levels. The humipedon cycle is related to the altitude: Mull (maA without OH horizon) and Amphi (maA or meA with OH horizon) systems at 950 m; Mull, Moder (miA and OH horizon) and Amphi at 1500 m; Amphi, Moder and Mor (never maA or meA, OH horizon and always nozOF horizon) at 1800 m. During the sylvogenetic cycle, the living soil evolves with the forest ecosystem. Soil changes may be detected at the level of the humipedon. (For interpretation of the references to colours in this figure legend, the reader is referred to the web version of this article).

Fig. 38. Two examples of locked-up processes of litter biodegradation. Organic matter and mineral soil do not get mixed by pedofauna and the two layers remain separated. This may happen when human intervention artificially modifies the plant composition of an ecosystem by planting conifers from a different area in a zone normally occupied by native broad-leaved trees. a) Norway spruce plantation in a previous beech forest (Central Alps); b) Radiata pine plantation in a holm-oak forest (Central Sardinia).

a.


ENERGY FLOWS IN THE DIRECTION OF THE ARROW. 1°= FIRST LEVEL CONSUMERS 2°= SECOND LEVEL CONSUMERS 3°= THIRD LEVEL CONSUMERS
CENTIPEDES 30 mm
GROUND BEETLES (CARABID) 8-20 mm
PSEUDOSCORPION 1-2mm
PREDATORY MITE .5-1mm
2°-3°
ROVE BEETLES (STAPHYLINID) 10 mm
ANT (FORMICID) 5-10mm
2°
SOIL FLATWORMS (TURBELLARIANS) 70-150mm
SPRINGTAILS (COLLEMBOLA) .5-3mm
2°
MOLD MITE (ACARINA)
BEETLE MITES 1mm
2°
FEATHER-WINGED BEETLES (PTILIIDS) 1-2mm
2°
ROUNDWORMS (NEMATODES)
2°
PROTOZOA .01-.5mm
ROTIFERA .1-.5mm
FLY (DIPTERA)
1-2mm
SOWBUG (ISOPOD) 10mm
MILLIPEDES 20-80mm
EARTHWORMS 50-150mm
ROUNDWORMS (NEMATODES) 1mm
1°
ACTINOMYCETES
MOLDS (FUNGI)
1°
BACTERIA
1°
1°
BEETLE MITES 1mm
WHITE WORMS OR POTWORMS (ENCHYTRAEIDS) 10-25mm
LAND SNAILS & SLUGS 2-25mm

b.

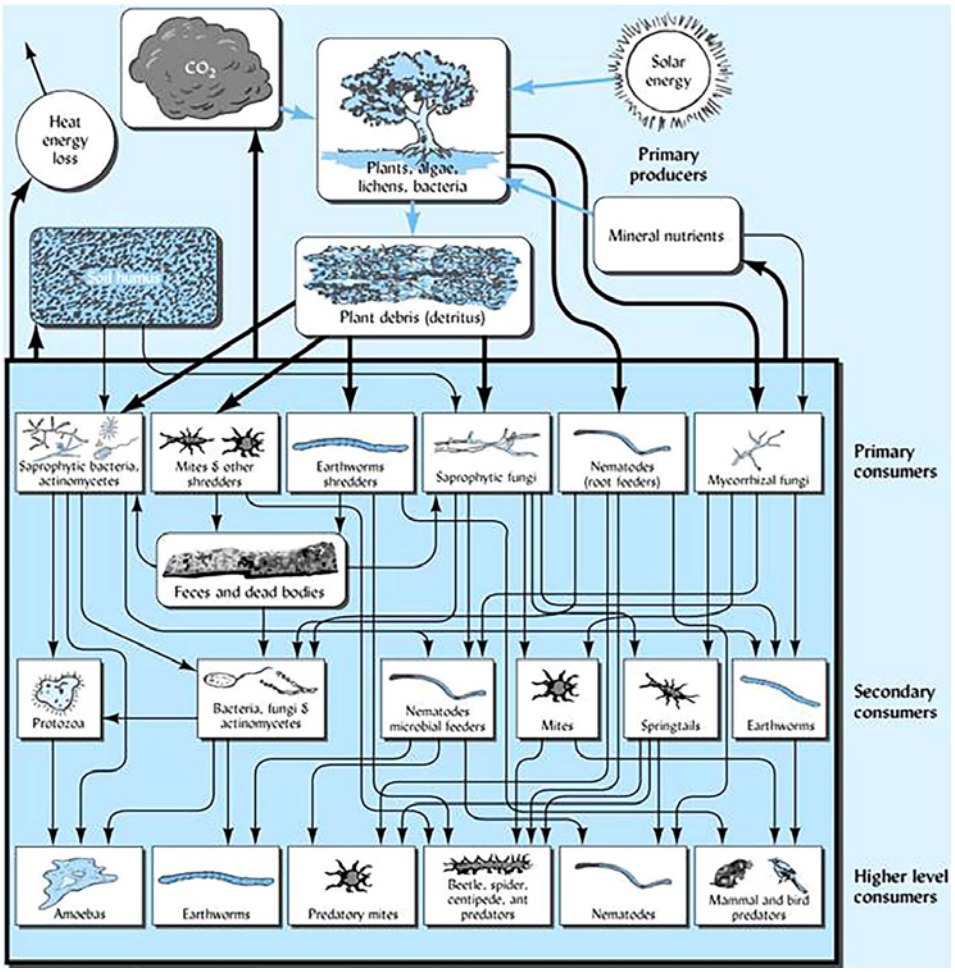

CO_2
Heat energy loss
Solar energy
Plants, algae, lichens, bacteria
Primary producers
Mineral nutrients
Plant debris (detritus)
Saprophytic bacteria, actinomycetes
Mites & other shredders
Earthworms shredders
Saprophytic fungi
Nematodes (root feeders)
Mycorrhizal fungi
Primary consumers
Feces and dead bodies
Protozoa
Bacteria, fungi & actinomycetes
Nematodes microbial feeders
Mites
Springtails
Earthworms
Secondary consumers
Amoebas
Earthworms
Predatory mites
Beetle, spider, centipede, ant predators
Nematodes
Mammal and bird predators
Higher level consumers

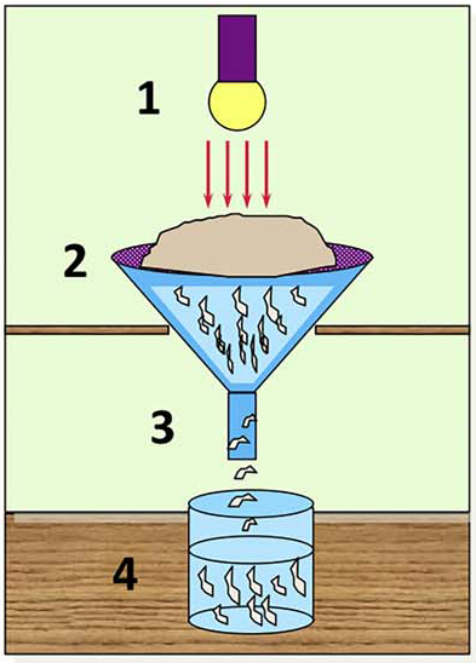
Fig. 1

a. # Berlese dry extraction

Berlese extractor diagram:

1. Heat (and light) source;
2. Funnel and metal mesh (≤ 4 mm) holding the fresh soil sample;
3. Animals moving away from the light and the heat and falling in the collecting container;
4. Collecting recipient filled with 70-90% ethanol to preserve the specimens.

Extraction duration: 72 h



b. # O'Connor wet extraction

Enchytraeids (with light) and nematodes (in the dark) extraction

1. Heat (and light) source;
2. A thinner metallic net (1 mm, holding fresh soil) is coupled with a plastic sock;
3. The plastic sock is restricted at its base with a nipper;
4. The soil sample is washed with water which drags enchytraeids and nematodes into the sock;
5. Slowly opening the nipper will free animals and water falling into the collector (6).

Extraction duration:
4h (enchytraeids); 24-36h (nematodes)

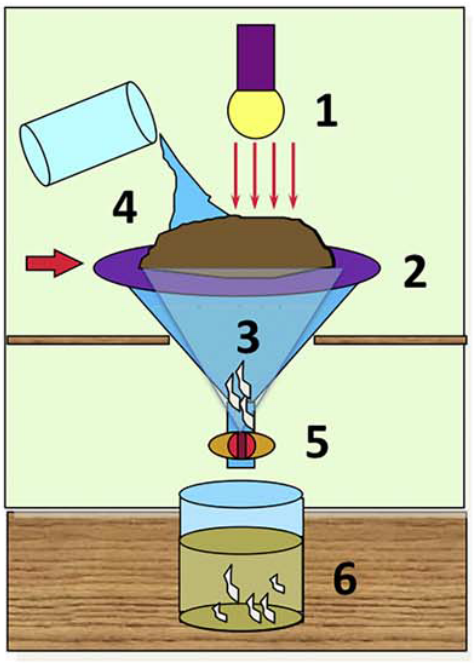


Fig. 2

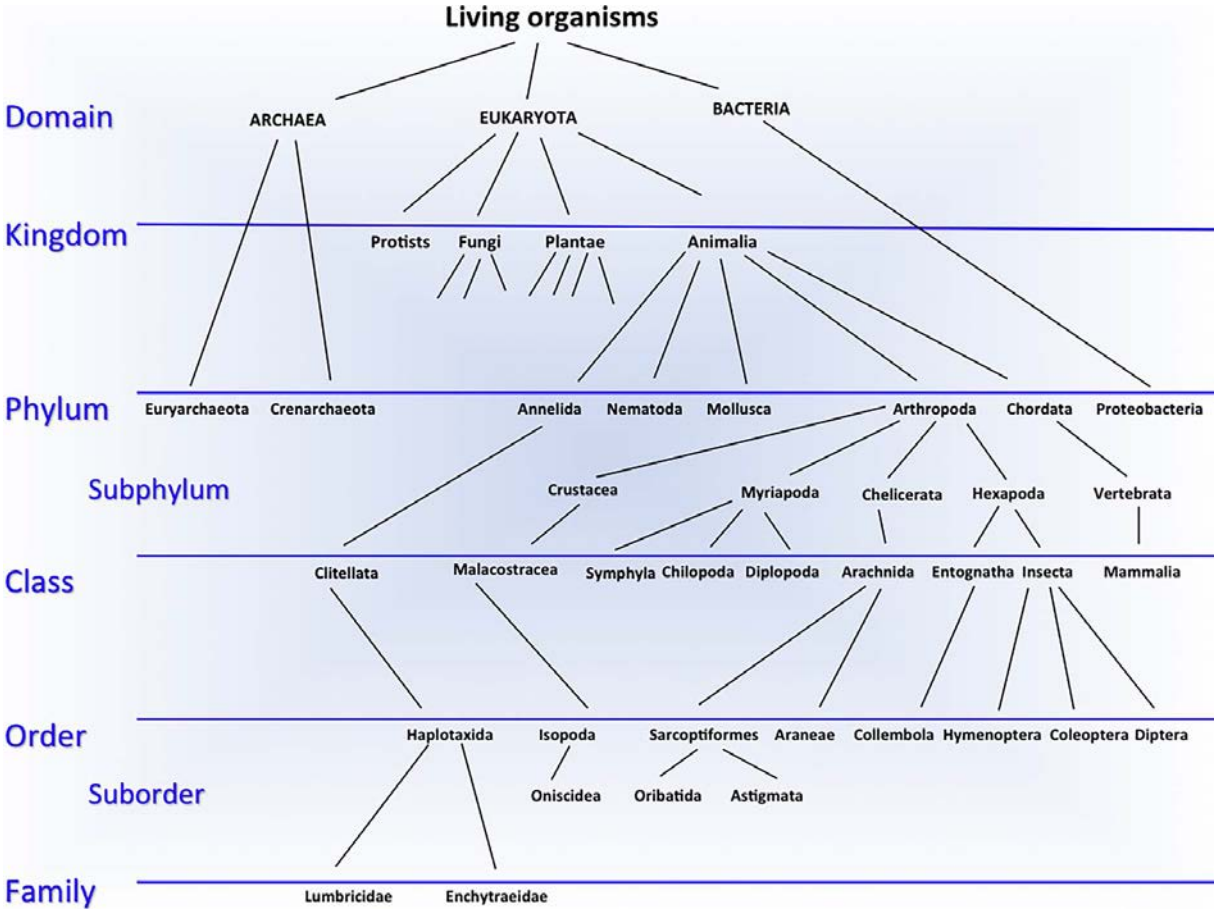

Living organisms
Domain
ARCHAEA
EUKARYOTA
BACTERIA
Kingdom
Protists
Fungi
Plantae
Animalia
Phylum
Euryarchaeota
Crenarchaeota
Annelida
Nematoda
Mollusca
Arthropoda
Chordata
Proteobacteria
Subphylum
Crustacea
Myriapoda
Chelicerata
Hexapoda
Vertebrata
Class
Clitellata
Malacostracea
Symphyla
Chilopoda
Diplopoda
Arachnida
Entognatha
Insecta
Mammalia
Order
Haplotaxida
Isopoda
Sarcoptiformes
Araneae
Collembola
Hymenoptera
Coleoptera
Diptera
Suborder
Oniscidea
Oribatida
Astigmata
Family
Lumbricidae
Enchytraeidae

Fig. 3

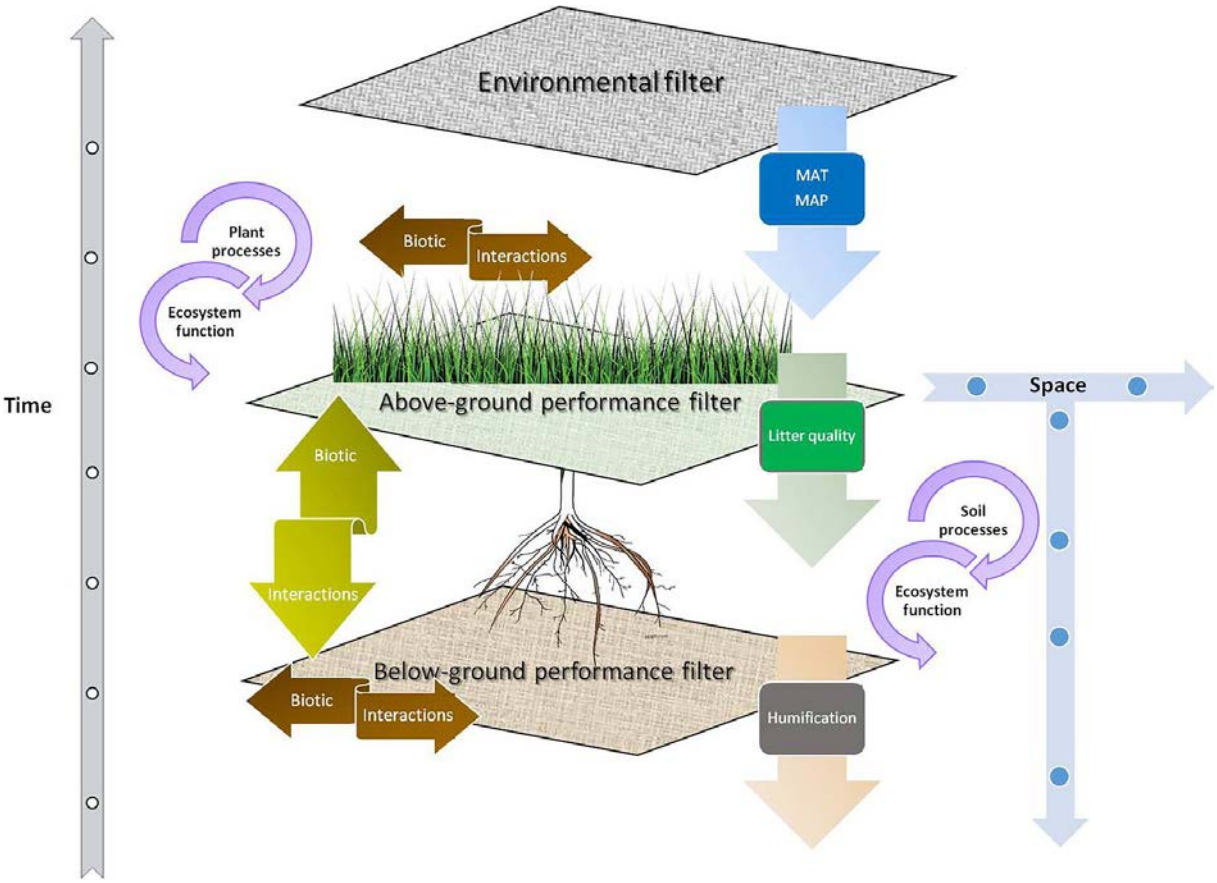

Environmental filter
MAT
MAP
Plant
processes
Ecosystem
function
Biotic
Interactions
Above-ground performance filter
Litter quality
Time
Space
Biotic
Interactions
Soil
processes
Ecosystem
function
Below-ground performance filter
Biotic
Interactions
Humification

Fig. 4



Fig. 5

a.



b.



c.



d.

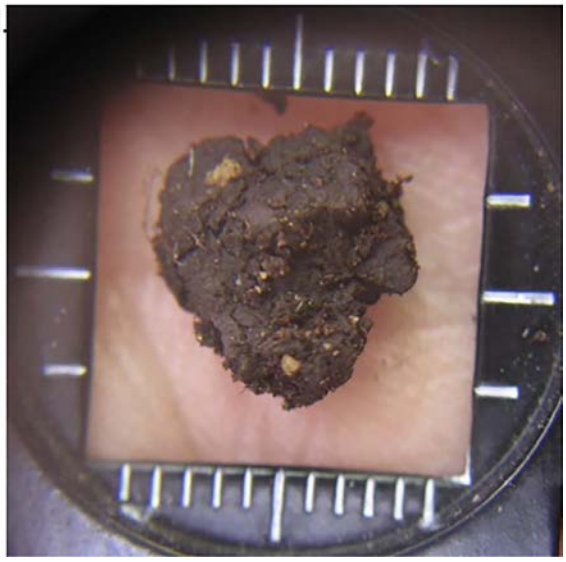
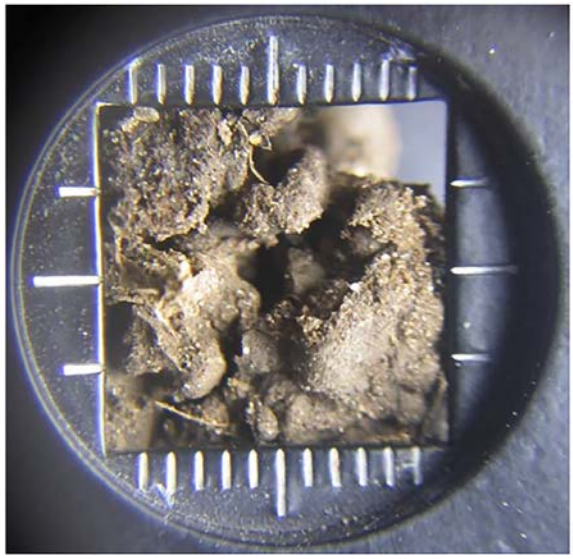




Fig. 6

e.



f.



Fig. 6 (continued)

a.



b.



Fig. 7

a.



b.



c.



Fig. 8



Fig. 9



Fig. 10

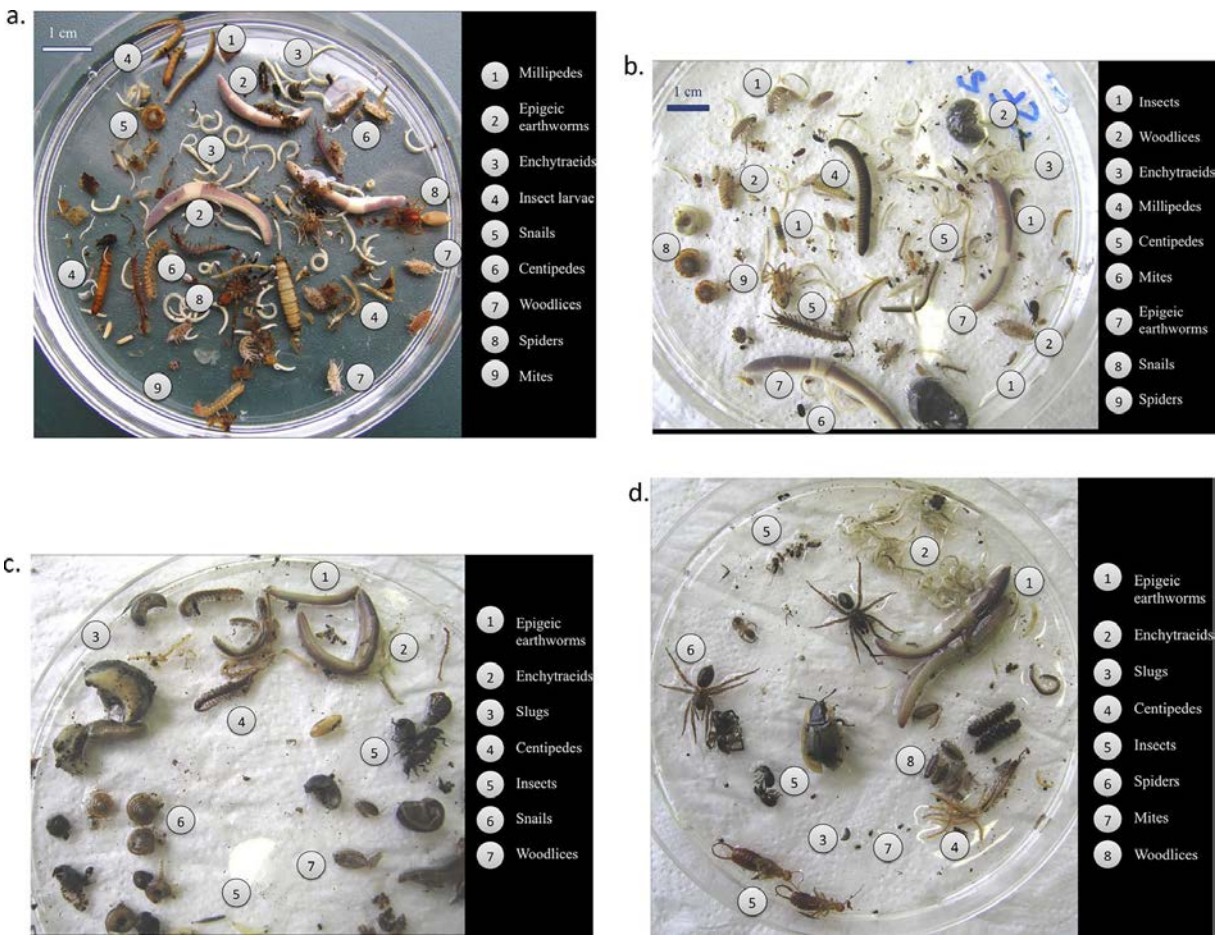

a.
1 cm
1 Millipedes
2 Epigeic earthworms
3 Enchytraeids
4 Insect larvae
5 Snails
6 Centipedes
7 Woodlices
8 Spiders
9 Mites
b.
1 cm
1 Insects
2 Woodlices
3 Enchytraeids
4 Millipedes
5 Centipedes
6 Mites
7 Epigeic earthworms
8 Snails
9 Spiders
c.
1 Epigeic earthworms
2 Enchytraeids
3 Slugs
4 Centipedes
5 Insects
6 Snails
7 Woodlices
d.
1 Epigeic earthworms
2 Enchytraeids
3 Slugs
4 Centipedes
5 Insects
6 Spiders
7 Mites
8 Woodlices

Fig. 11

a.



b.



c.



Fig. 12

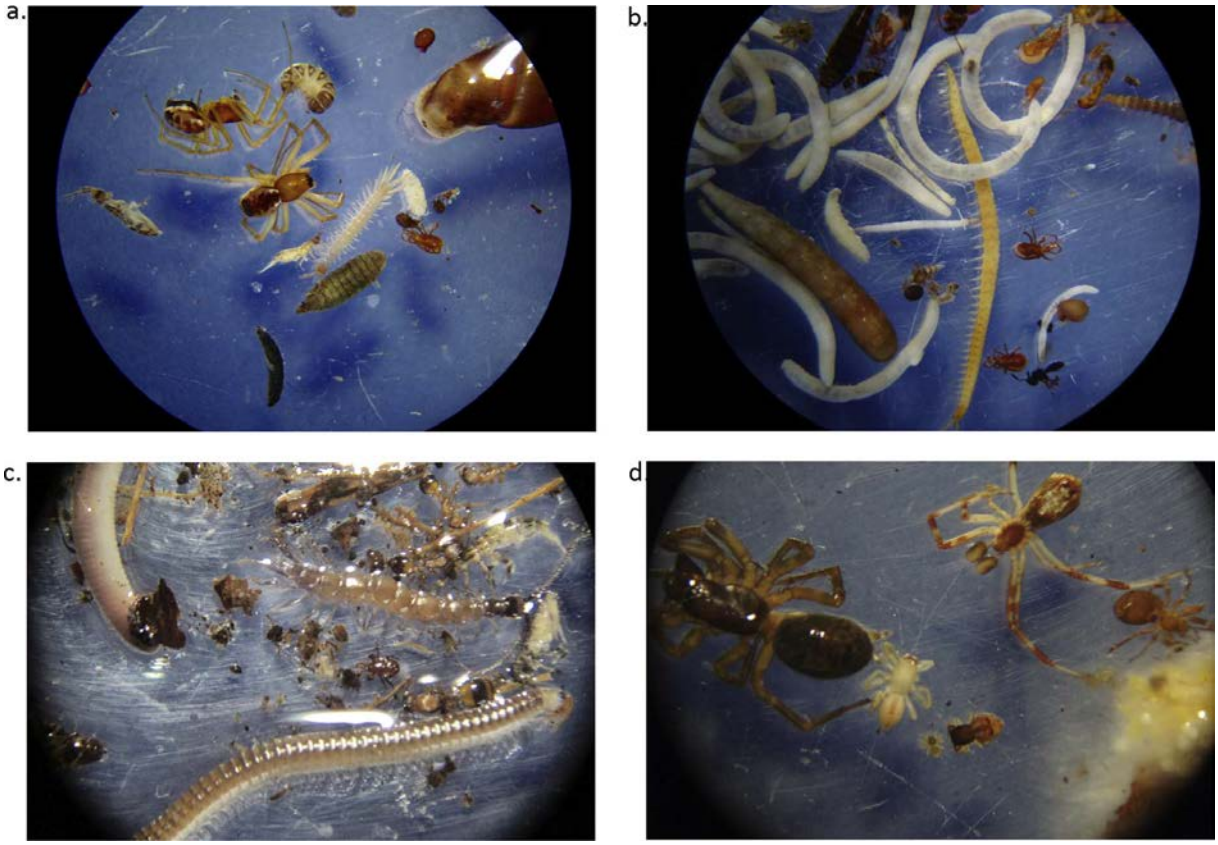


Fig. 13

e.



f.

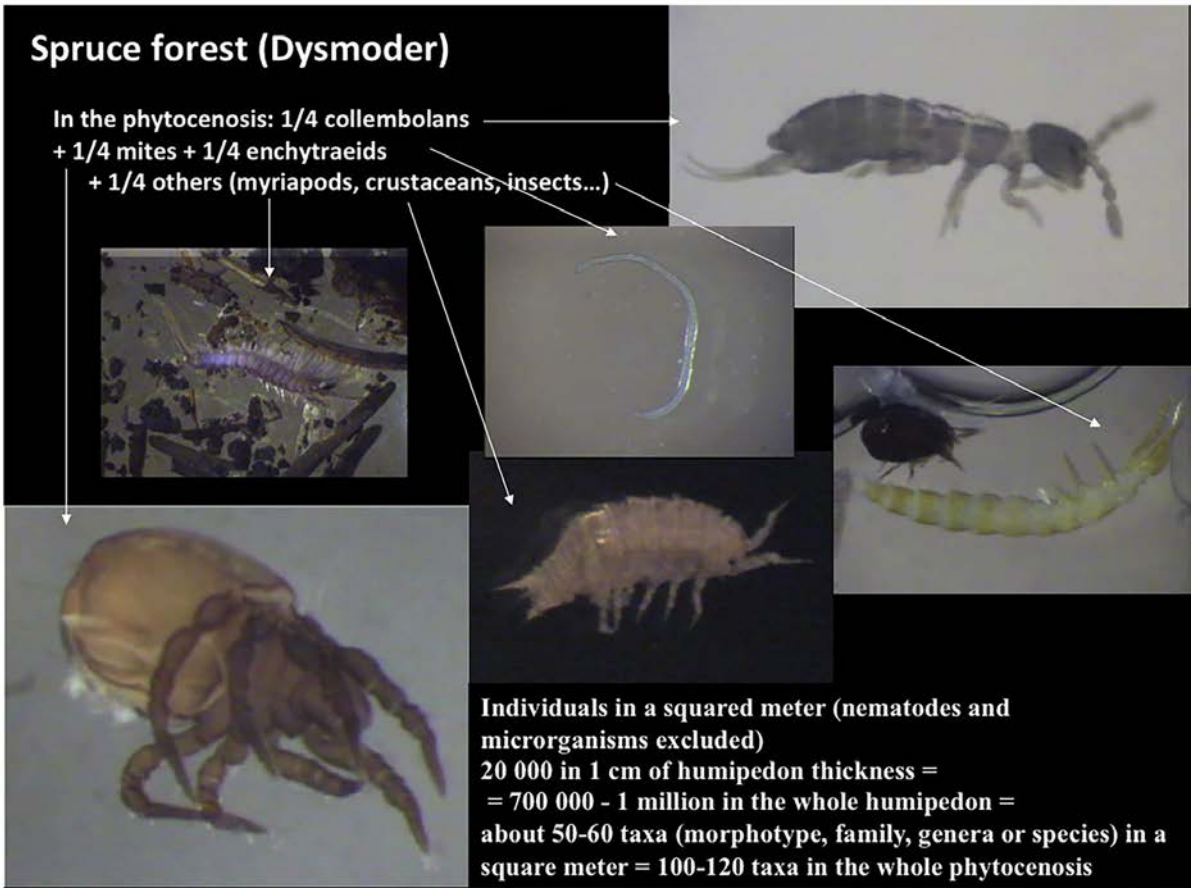


Fig. 13 (continued)

a.



b.



c.



Fig. 14

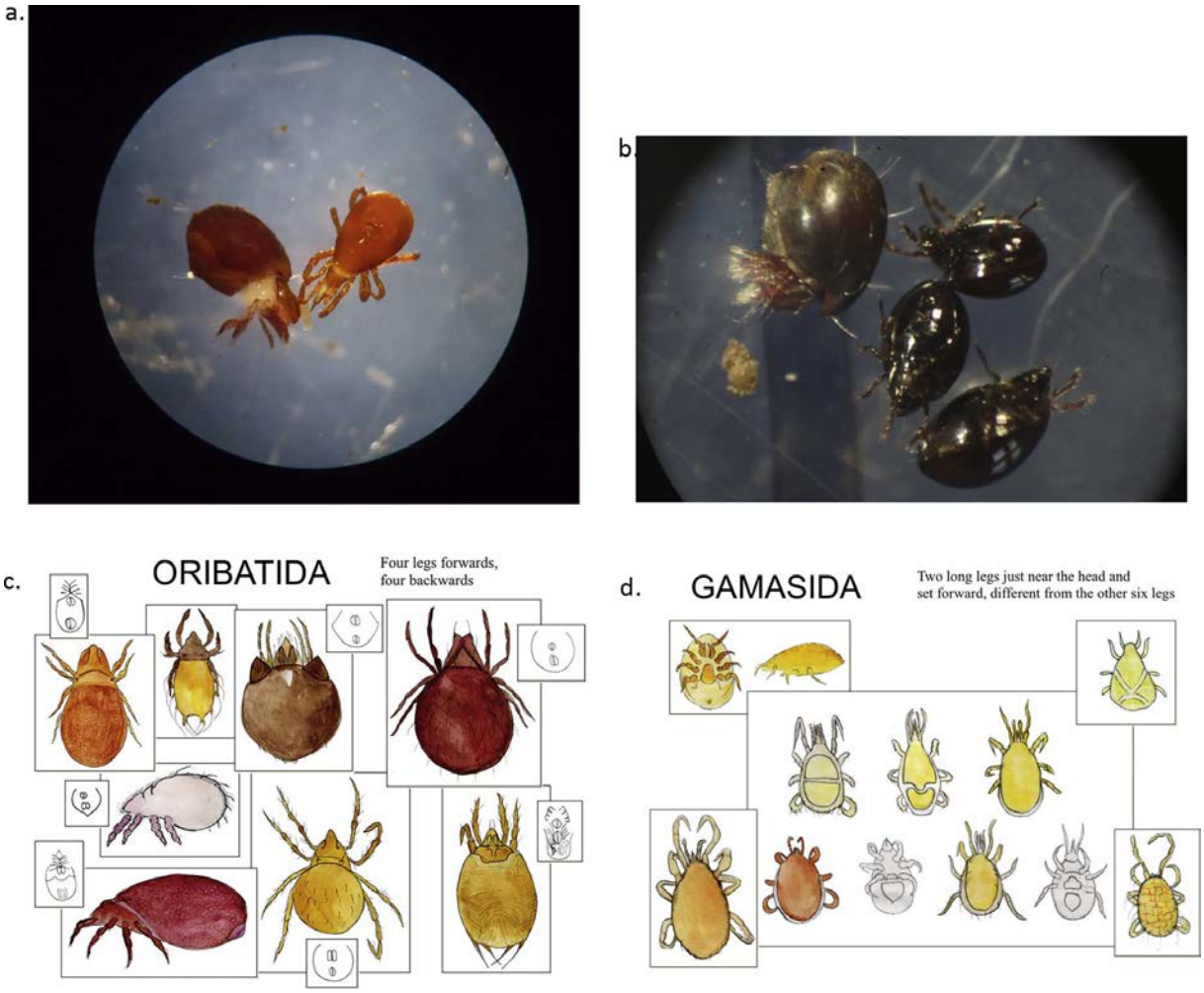

a.
b.
c.
ORIBATIDA
Four legs forwards, four backwards
d.
GAMASIDA
Two long legs just near the head and set forward, different from the other six legs

Fig. 15

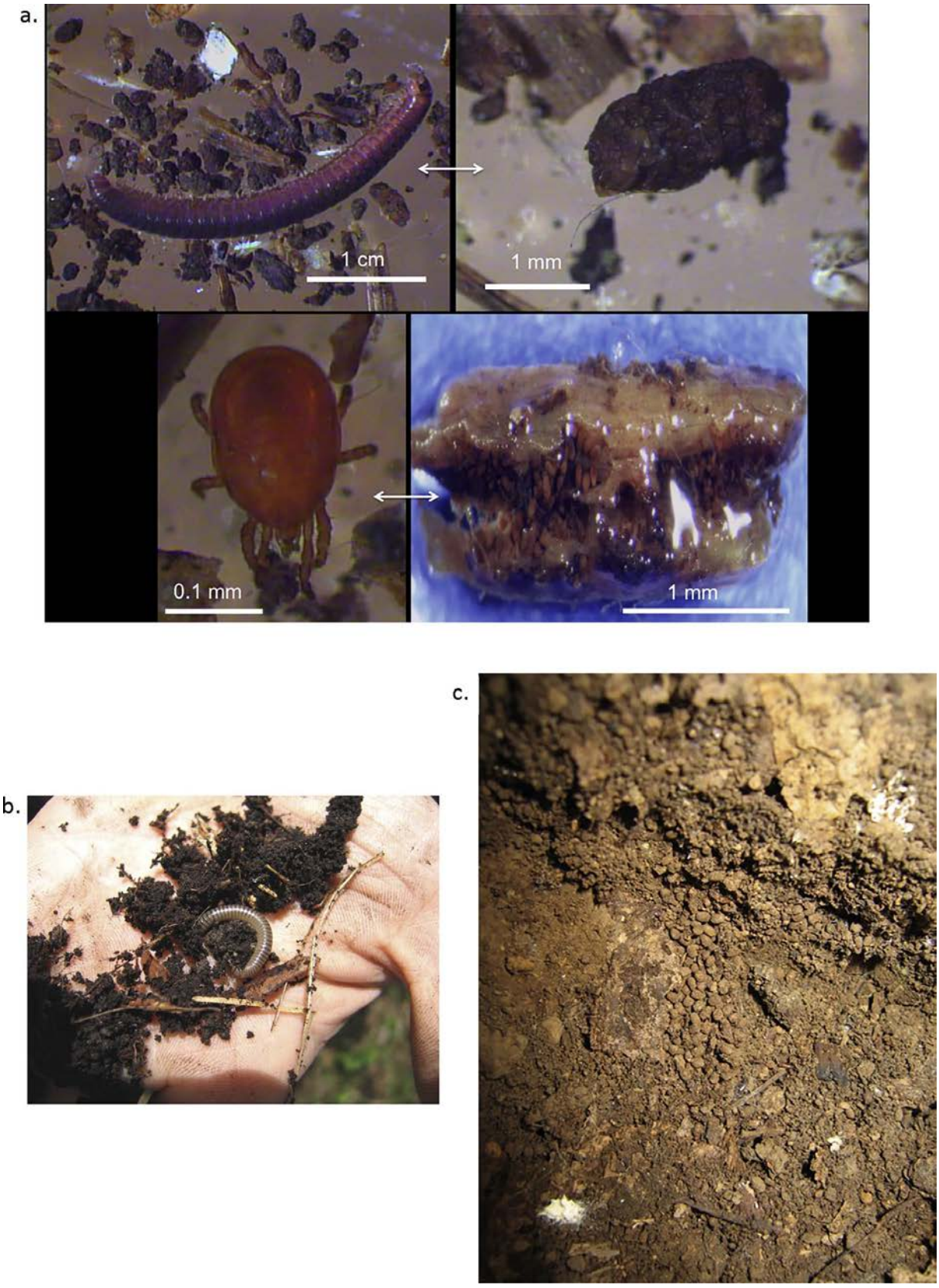


Fig. 16

d.



e.



f.



Fig. 16 (continued)

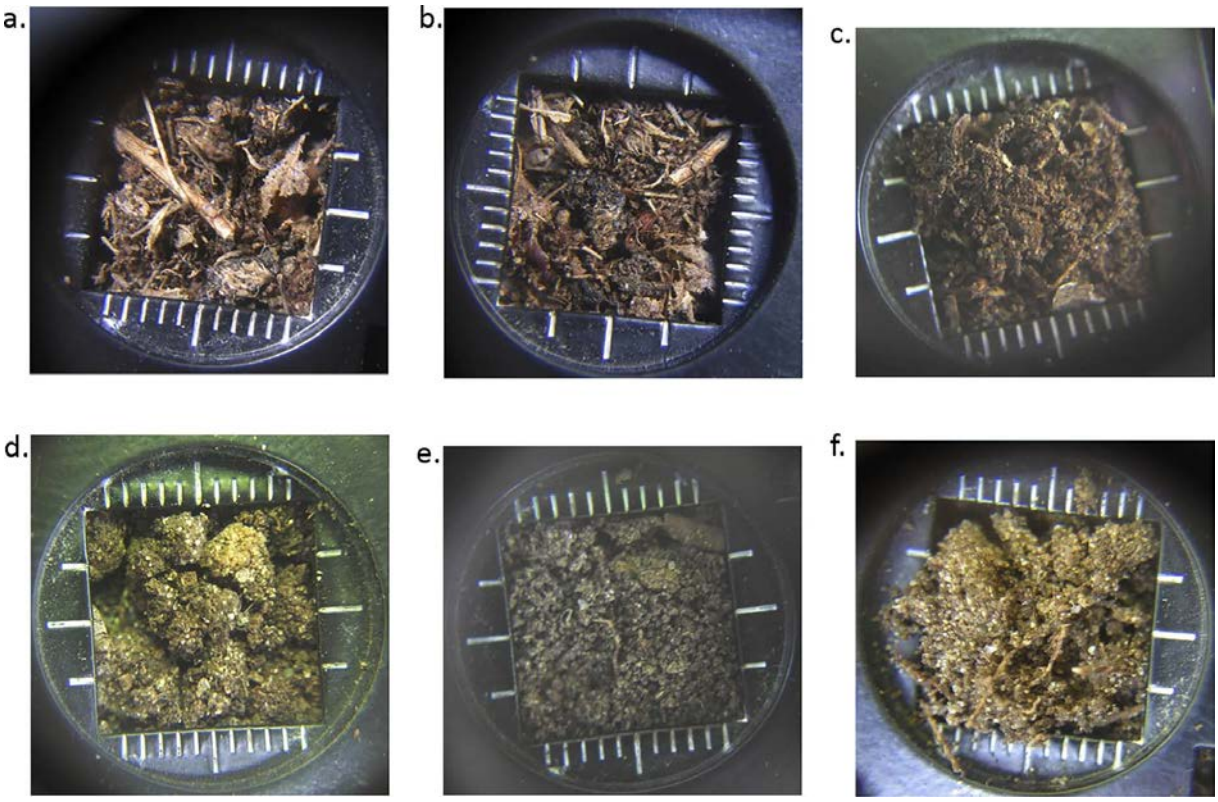


Fig. 17

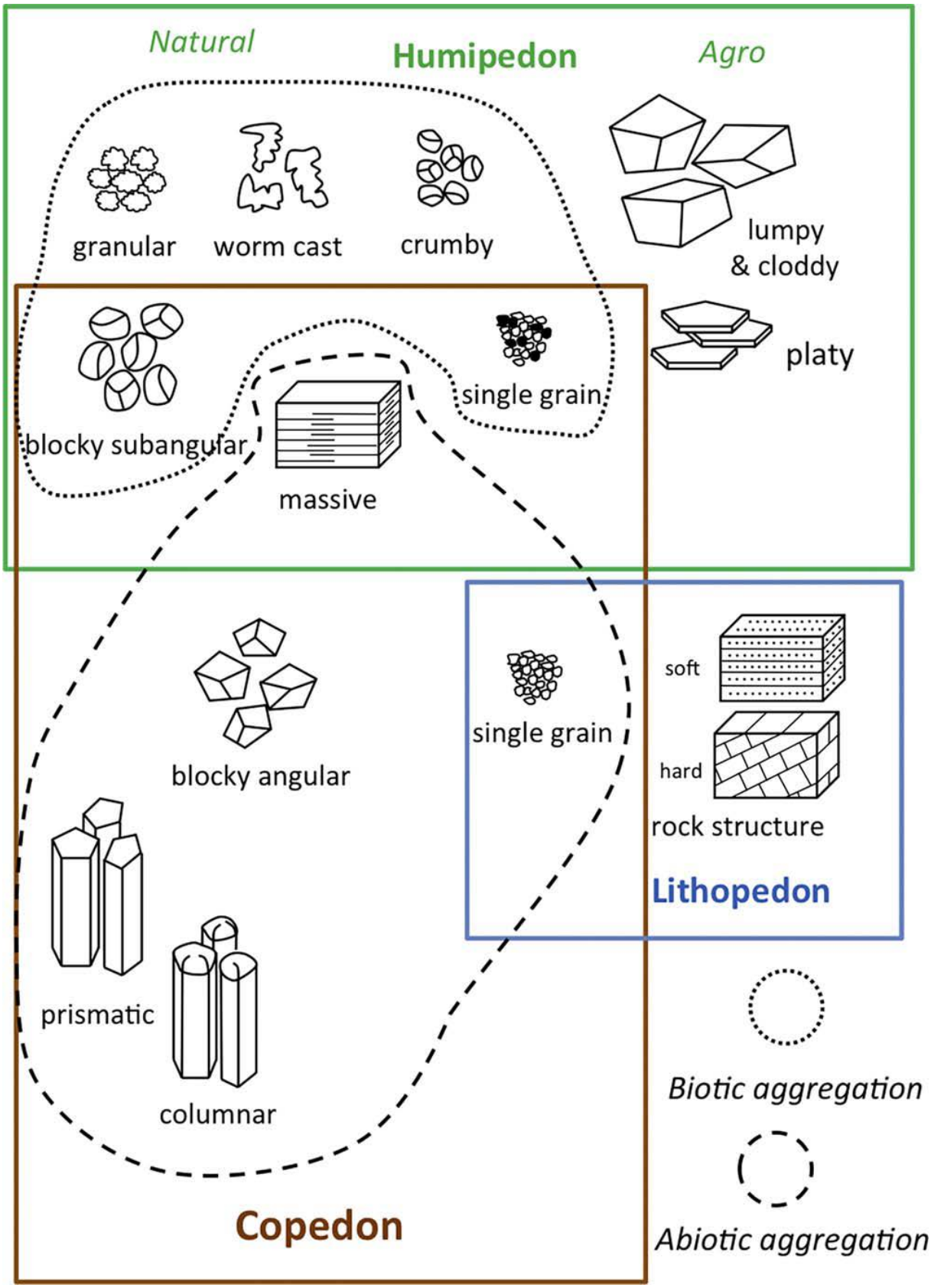

Natural
Humipedon
Agro
granular
worm cast
crumby
lumpy
& cloddy
platy
blocky subangular
single grain
massive
blocky angular
single grain
soft
hard
rock structure
Lithopedon
prismatic
columnar
Biotic aggregation
Abiotic aggregation
Copedon

Fig. 18

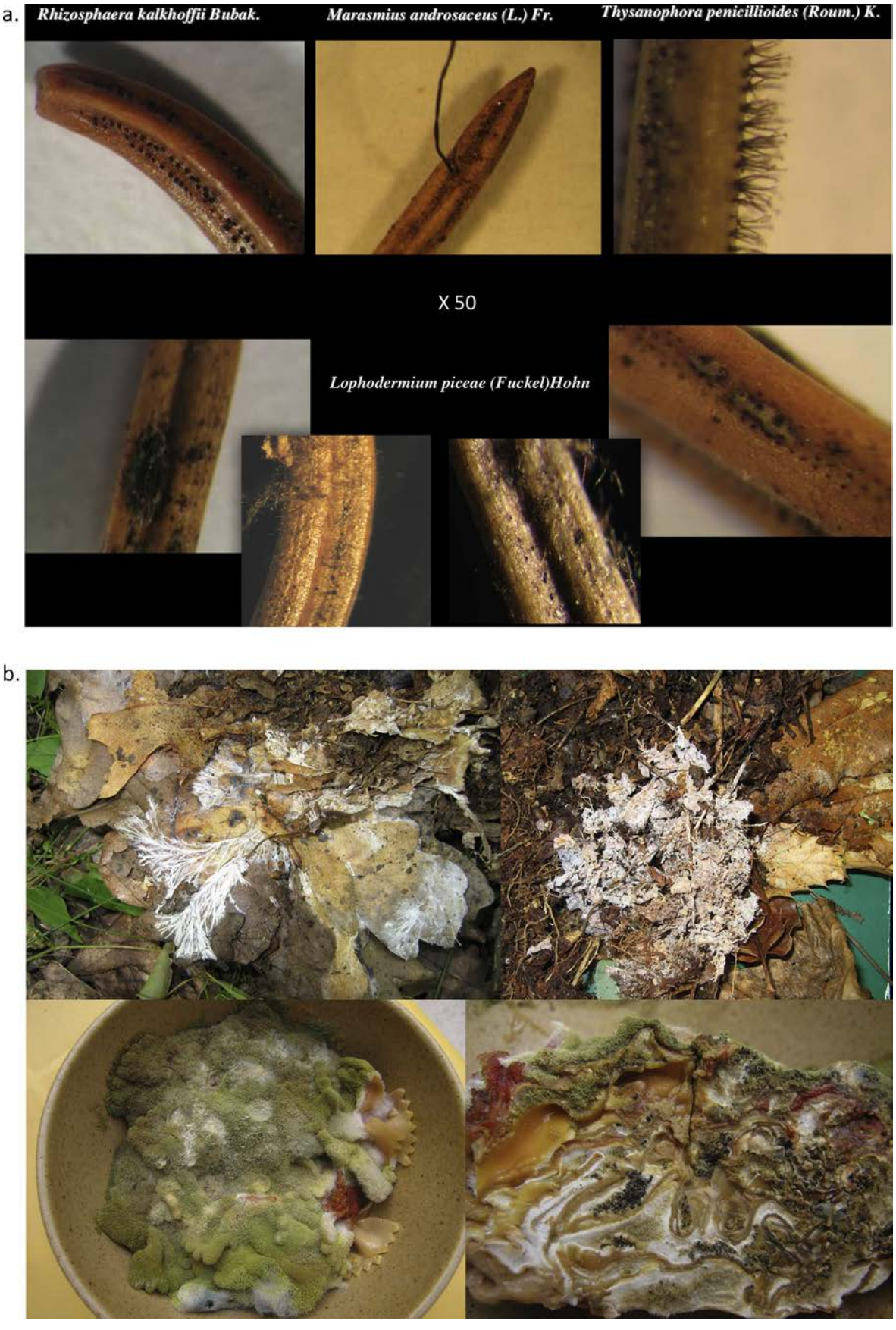

a.
Rhizosphaera kalkhoffii Bubak.
Marasmius androsaceus (L.) Fr.
Thysanophora penicillioides (Roum.) K.
X 50
Lophodermium piceae (Fuckel)Hohn
b.

Fig. 19



Fig. 20

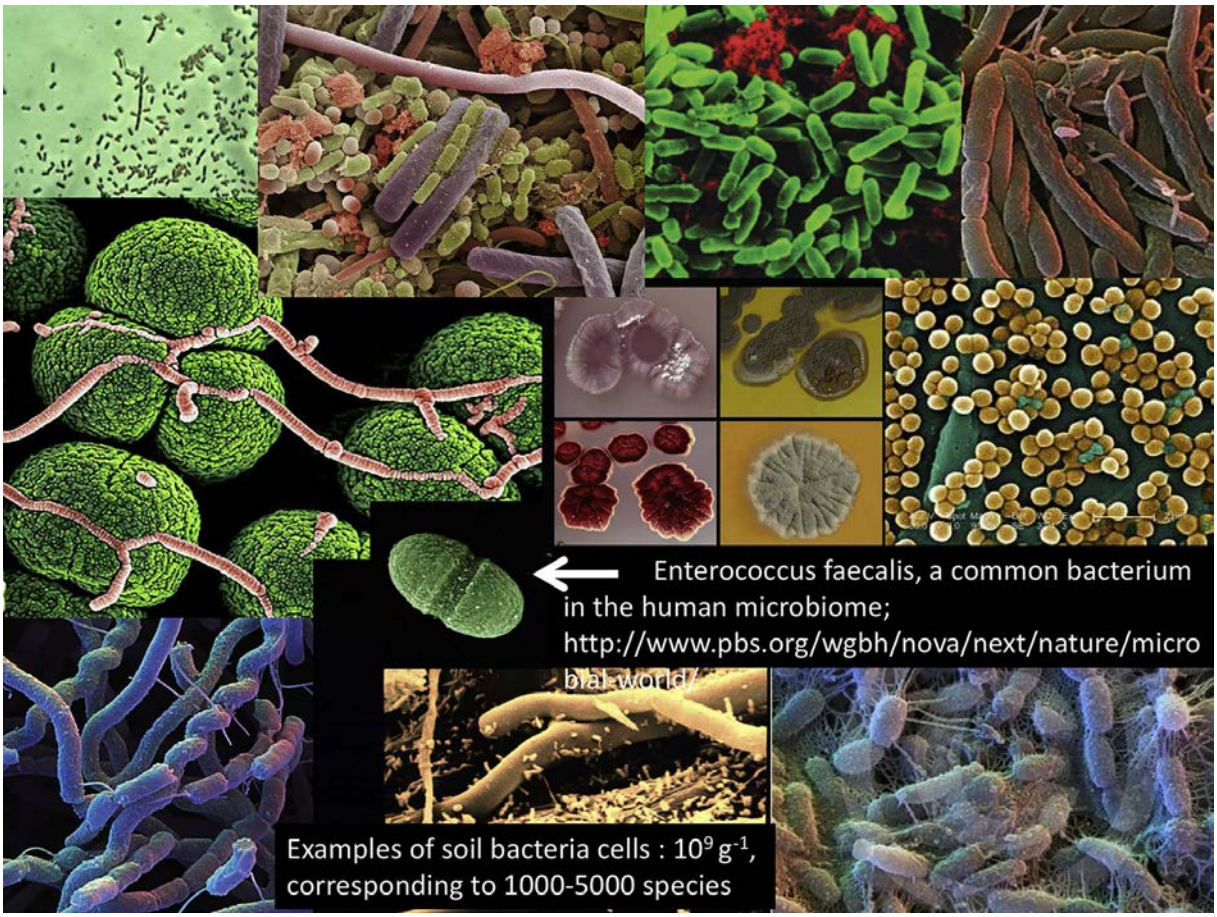

Enterococcus faecalis, a common bacterium in the human microbiome;
http://www.pbs.org/wgbh/nova/next/nature/microbial-world/
Examples of soil bacteria cells : 10^9 g^{-1}, corresponding to 1000-5000 species

Fig. 21

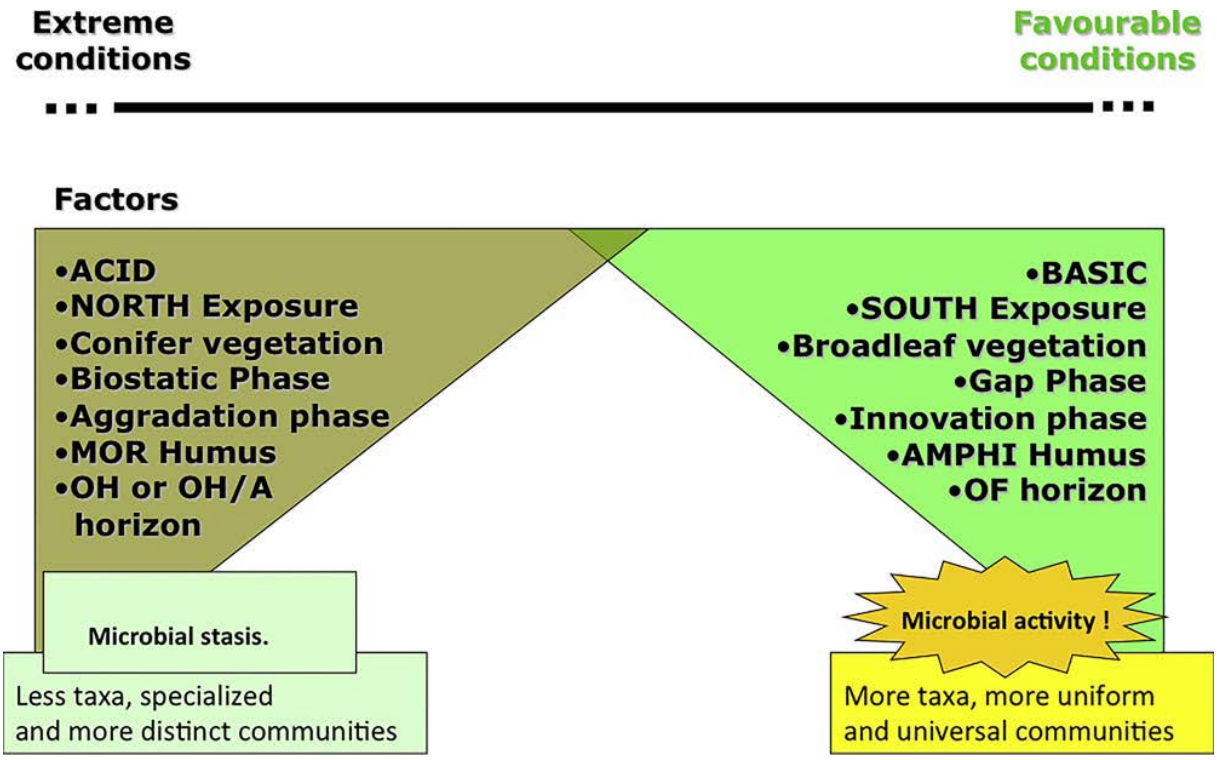

Extreme conditions
Favourable conditions
Factors
•ACID
•NORTH Exposure
•Conifer vegetation
•Biostatic Phase
•Aggradation phase
•MOR Humus
•OH or OH/A horizon
•BASIC
•SOUTH Exposure
•Broadleaf vegetation
•Gap Phase
•Innovation phase
•AMPHI Humus
•OF horizon
Microbial stasis.
Microbial activity !
Less taxa, specialized and more distinct communities
More taxa, more uniform and universal communities

Fig. 22

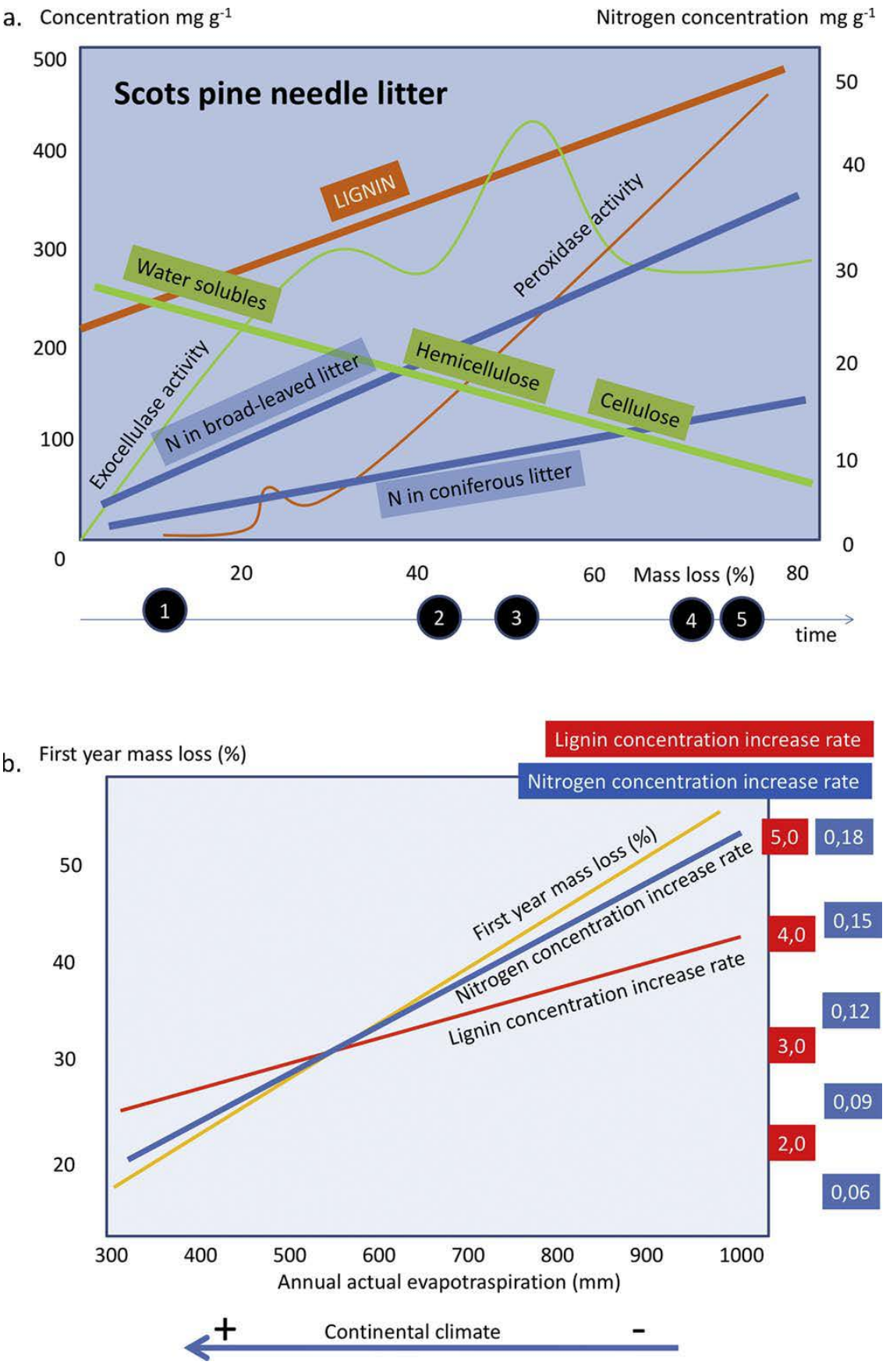

a.
Concentration mg g-1
Nitrogen concentration mg g-1
Scots pine needle litter
LIGNIN
Water solubles
Peroxidase activity
Exocellulase activity
N in broad-leaved litter
Hemicellulose
Cellulose
N in coniferous litter
Mass loss (%)
time
b.
First year mass loss (%)
Lignin concentration increase rate
Nitrogen concentration increase rate
First year mass loss (%)
Nitrogen concentration increase rate
Lignin concentration increase rate
Annual actual evapotraspiration (mm)
Continental climate

Fig. 23

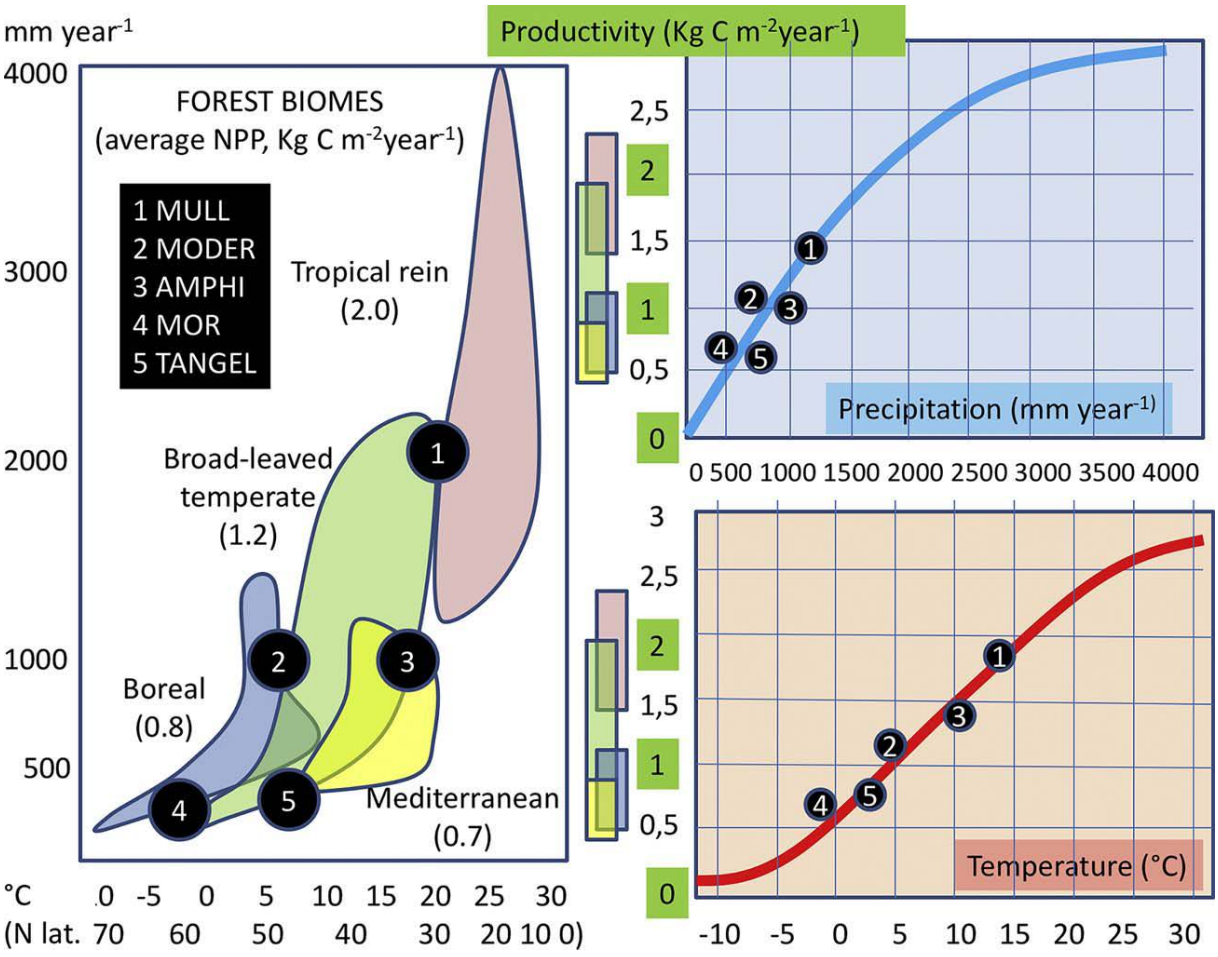
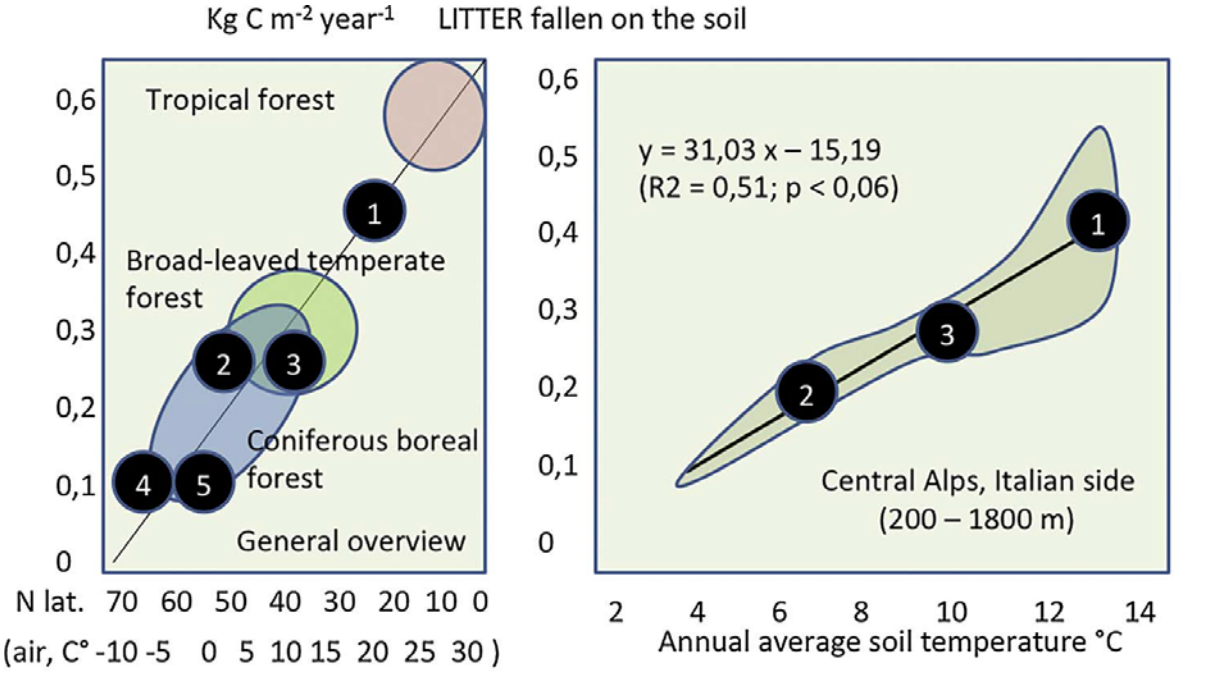

mm year-1
4000
3000
2000
1000
500
FOREST BIOMES
(average NPP, Kg C m-2year-1)
1 MULL
2 MODER
3 AMPHI
4 MOR
5 TANGEL
Tropical rein
(2.0)
Broad-leaved
temperate
(1.2)
Boreal
(0.8)
Mediterranean
(0.7)
°C 0 -5 0 5 10 15 20 25 30
(N lat. 70 60 50 40 30 20 10 0)
Productivity (Kg C m-2year-1)
2,5
2
1,5
1
0,5
0
Precipitation (mm year-1)
0 500 1000 1500 2000 2500 3000 3500 4000
3
2,5
2
1,5
1
0,5
0
Temperature (°C)
-10 -5 0 5 10 15 20 25 30

Fig. 24



1 MULL
2 MODER
3 AMPHI
4 MOR
5 TANGEL

Forest	NPP Kg C m^{-2} y^{-1}	On the soil litter Kg C m^{-2} y^{-1}	NPP – litter Kg C m^{-2} y^{-1}
tropical	2,0	0,6	1,4
broad-leaved	1,2	0,3	0,8
coniferous	0,8	0,2	0,6

Fig. 25

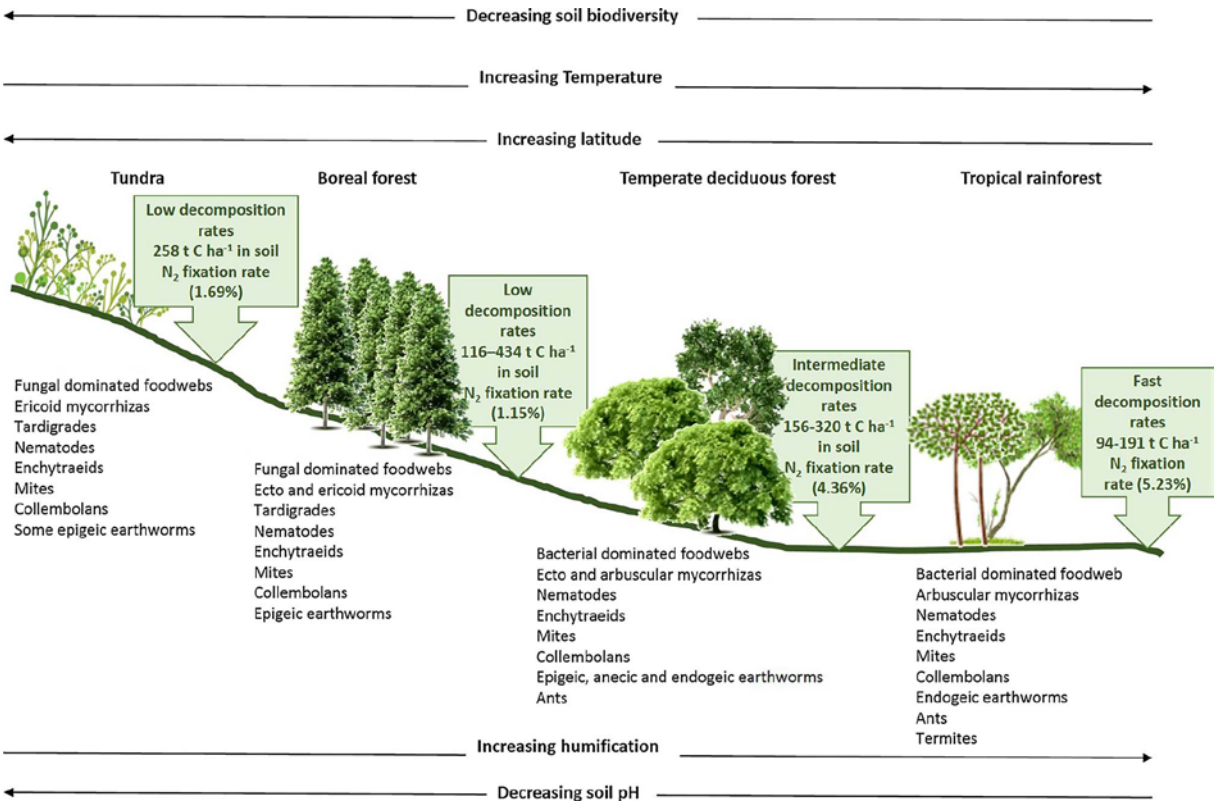

Decreasing soil biodiversity
Increasing Temperature
Increasing latitude
Tundra
Boreal forest
Temperate deciduous forest
Tropical rainforest
Low decomposition rates
258 t C ha-1 in soil
N2 fixation rate
(1.69%)
Low decomposition rates
116–434 t C ha-1 in soil
N2 fixation rate
(1.15%)
Intermediate decomposition rates
156-320 t C ha-1 in soil
N2 fixation rate
(4.36%)
Fast decomposition rates
94-191 t C ha-1
N2 fixation rate (5.23%)
Fungal dominated foodwebs
Ericoid mycorrhizas
Tardigrades
Nematodes
Enchytraeids
Mites
Collembolans
Some epigeic earthworms
Fungal dominated foodwebs
Ecto and ericoid mycorrhizas
Tardigrades
Nematodes
Enchytraeids
Mites
Collembolans
Epigeic earthworms
Bacterial dominated foodwebs
Ecto and arbuscular mycorrhizas
Nematodes
Enchytraeids
Mites
Collembolans
Epigeic, anecic and endogeic earthworms
Ants
Bacterial dominated foodweb
Arbuscular mycorrhizas
Nematodes
Enchytraeids
Mites
Collembolans
Endogeic earthworms
Ants
Termites
Increasing humification
Decreasing soil pH

Fig. 26

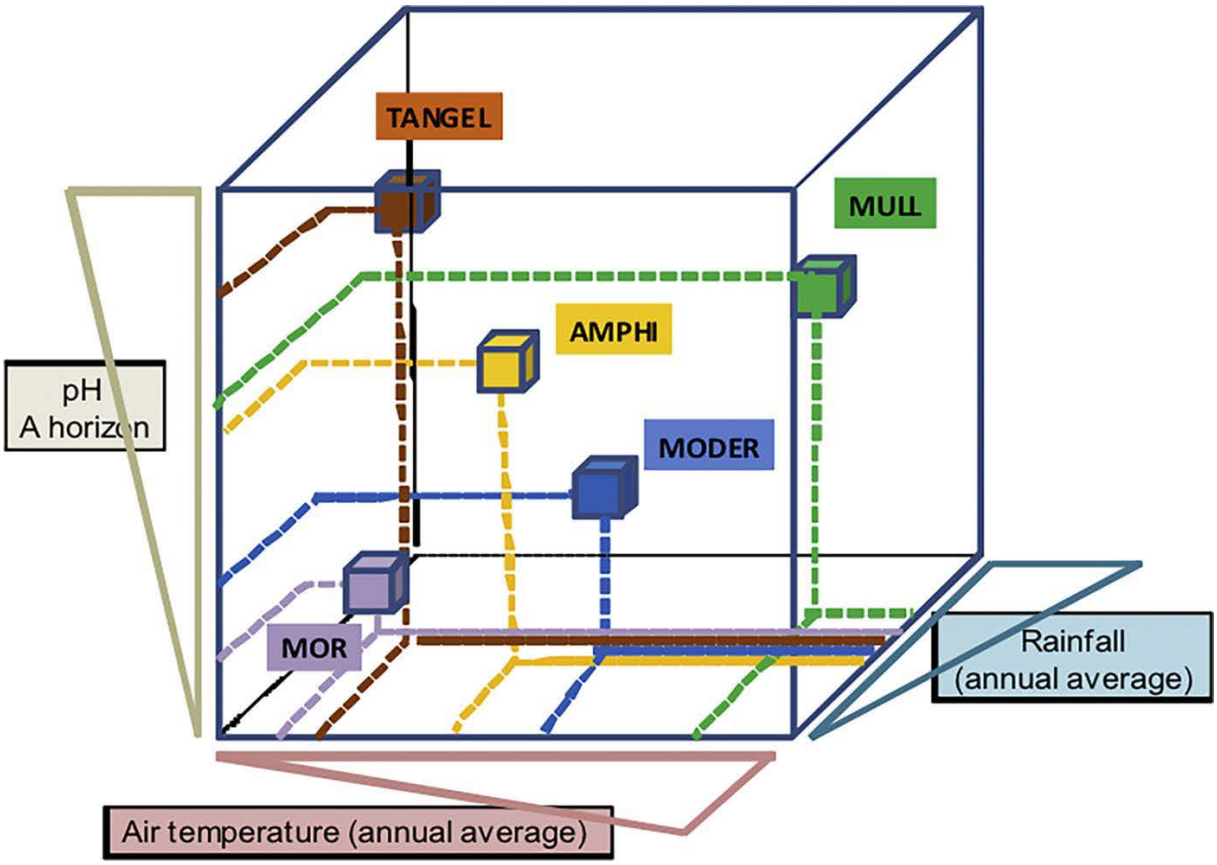

TANGEL
MULL
AMPHI
pH
A horizon
MODER
MOR
Rainfall
(annual average)
Air temperature (annual average)

Fig. 27

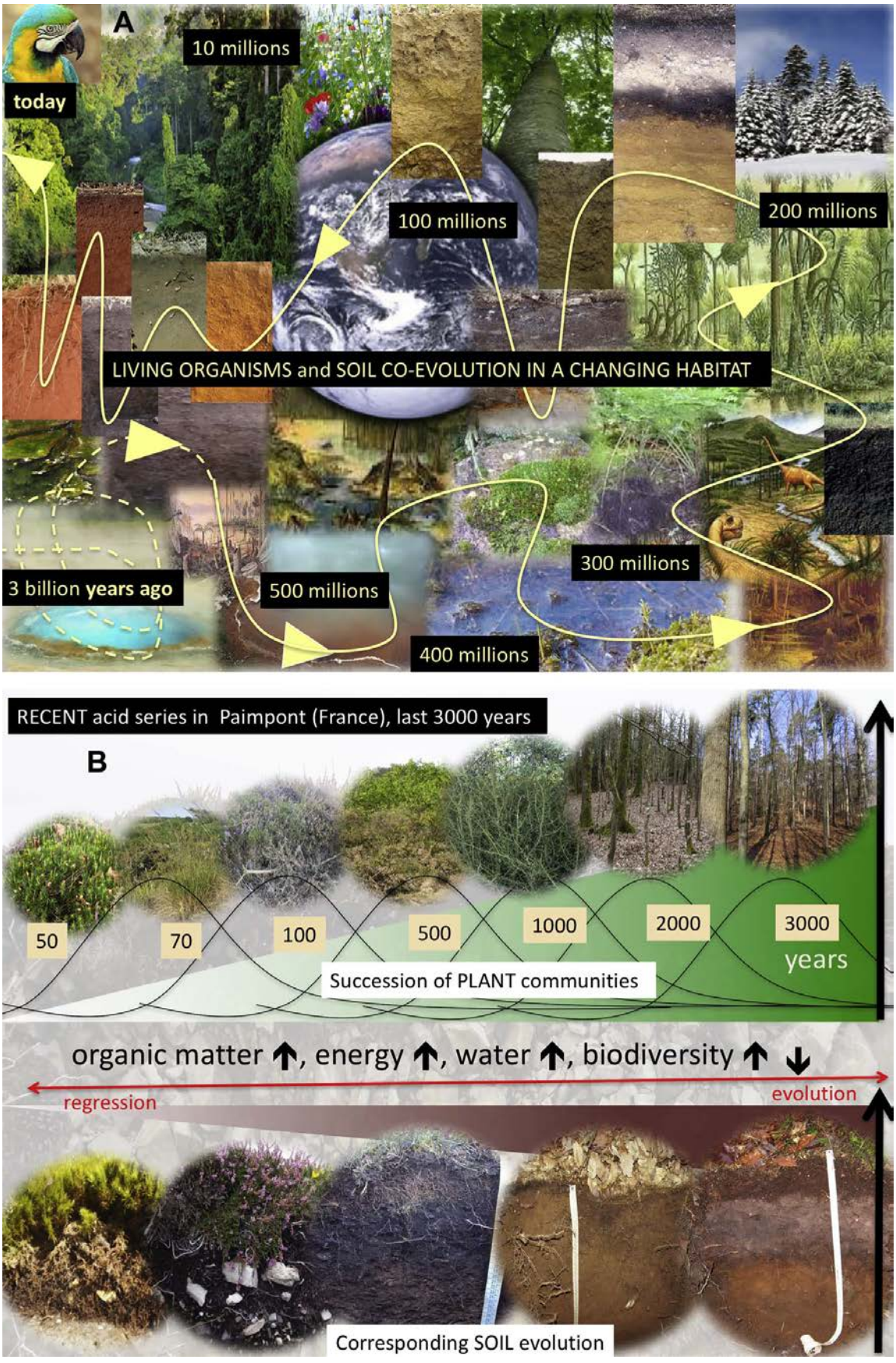
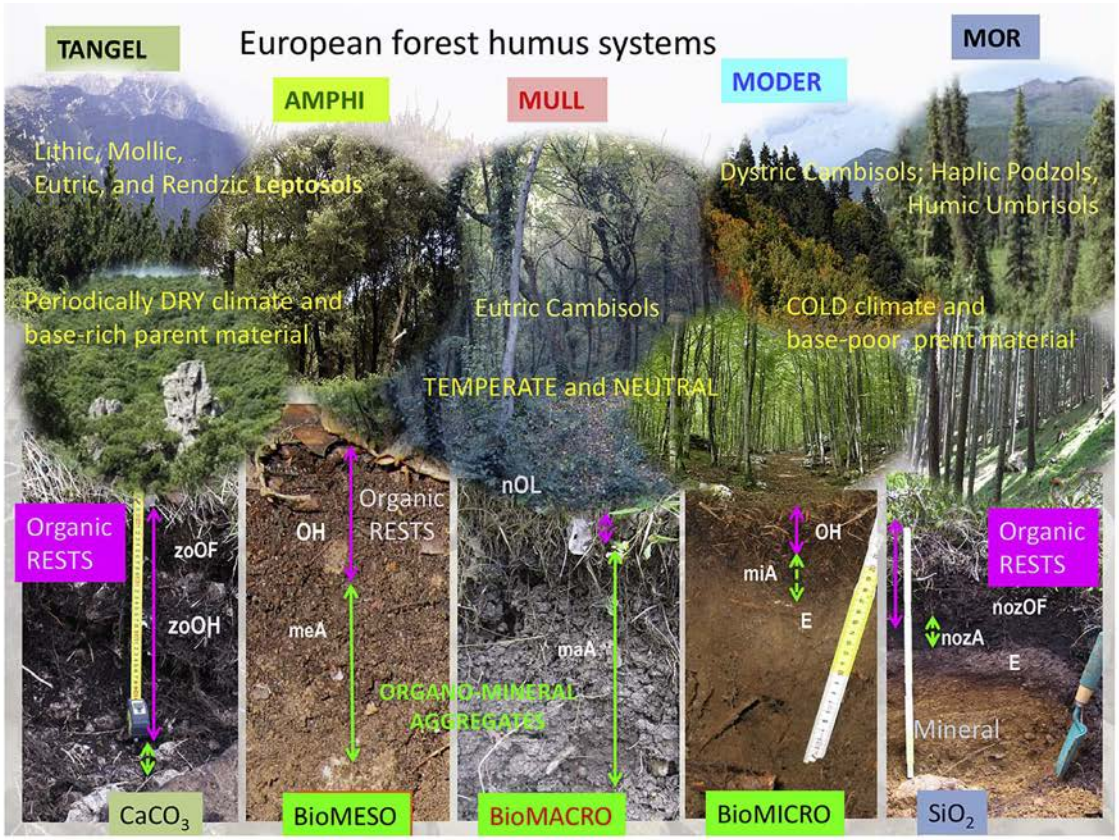

A
today
10 millions
100 millions
200 millions
LIVING ORGANISMS and SOIL CO-EVOLUTION IN A CHANGING HABITAT
3 billion years ago
500 millions
400 millions
300 millions
RECENT acid series in Paimpont (France), last 3000 years
B
50
70
100
500
1000
2000
3000
years
Succession of PLANT communities
organic matter ↑, energy ↑, water ↑, biodiversity ↑ ↓
regression
evolution
Corresponding SOIL evolution

Fig. 28

a.


TANGEL
European forest humus systems
AMPHI
MULL
MODER
MOR
Lithic, Mollic,
Eutric, and Rendzic Leptosols
Dystric Cambisols; Haplic Podzols,
Humic Umbrisols
Periodically DRY climate and
base-rich parent material
Eutric Cambisols
COLD climate and
base-poor parent material
TEMPERATE and NEUTRAL
Organic
RESTS
zoOF
zoOH
OH
Organic
RESTS
meA
nOL
maA
ORGANO-MINERAL
AGGREGATES
OH
miA
E
Organic
RESTS
nozOF
nozA
E
Mineral
CaCO3
BioMESO
BioMACRO
BioMICRO
SiO2

b.

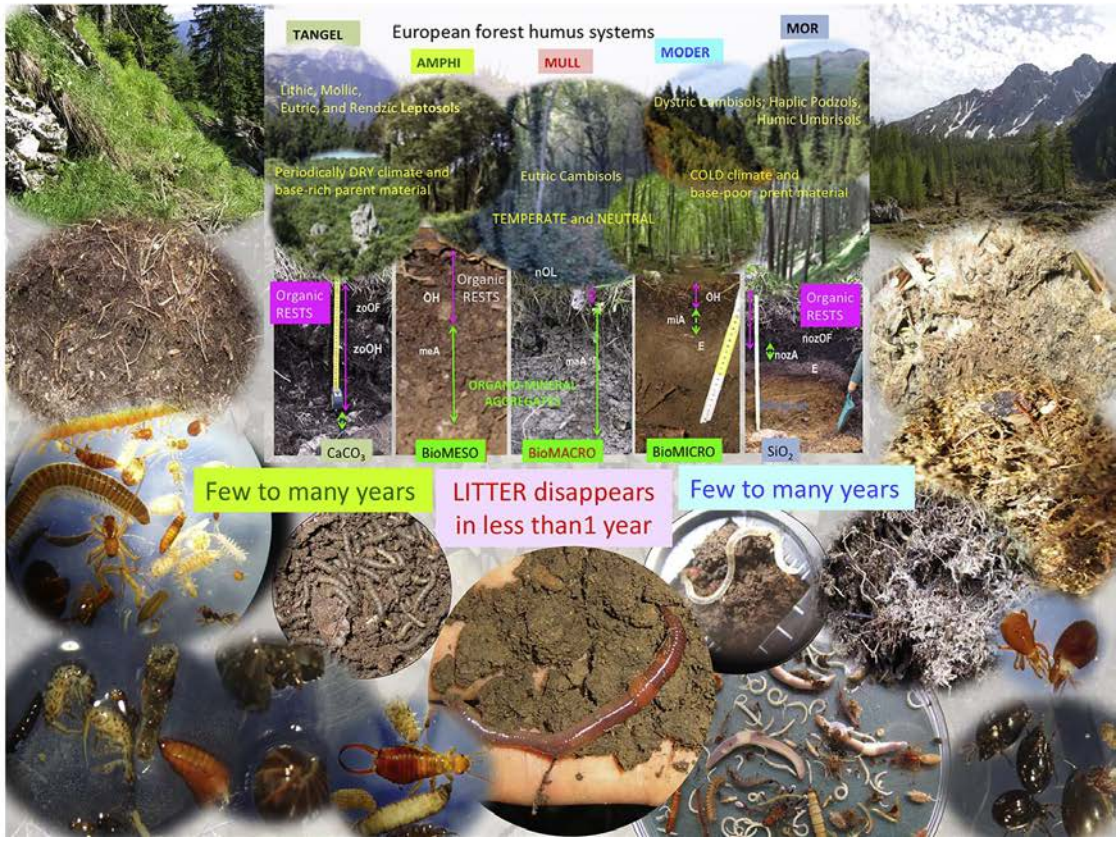

TANGEL
European forest humus systems
AMPHI
MULL
MODER
MOR
Lithic, Mollic,
Eutric, and Rendzic Leptosols
Dystric Cambisols; Haplic Podzols,
Humic Umbrisols
Periodically DRY climate and
base-rich parent material
Eutric Cambisols
COLD climate and
base-poor parent material
TEMPERATE and NEUTRAL
Organic
RESTS
zoOF
zoOH
OH
Organic
RESTS
meA
nOL
maA
ORGANO-MINERAL
AGGREGATES
OH
miA
E
Organic
RESTS
nozOF
nozA
E
CaCO3
BioMESO
BioMACRO
BioMICRO
SiO2
Few to many years
LITTER disappears
in less than1 year
Few to many years

Fig. 29

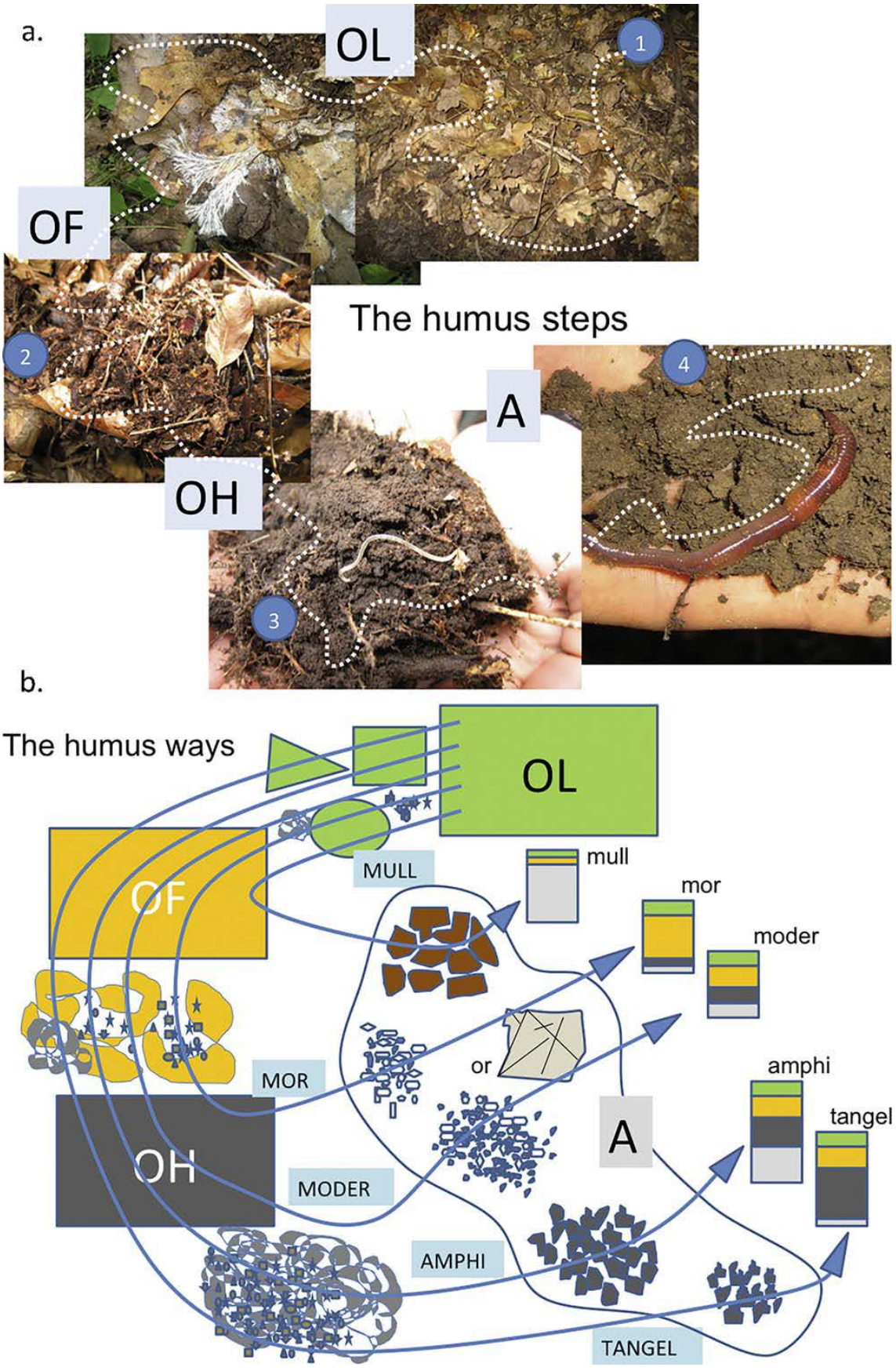

a.
OL
1
OF
2
The humus steps
A
4
OH
3
b.
The humus ways
OL
mull
MULL
mor
OF
moder
or
MOR
amphi
tangel
A
OH
MODER
AMPHI
TANGEL

Fig. 30

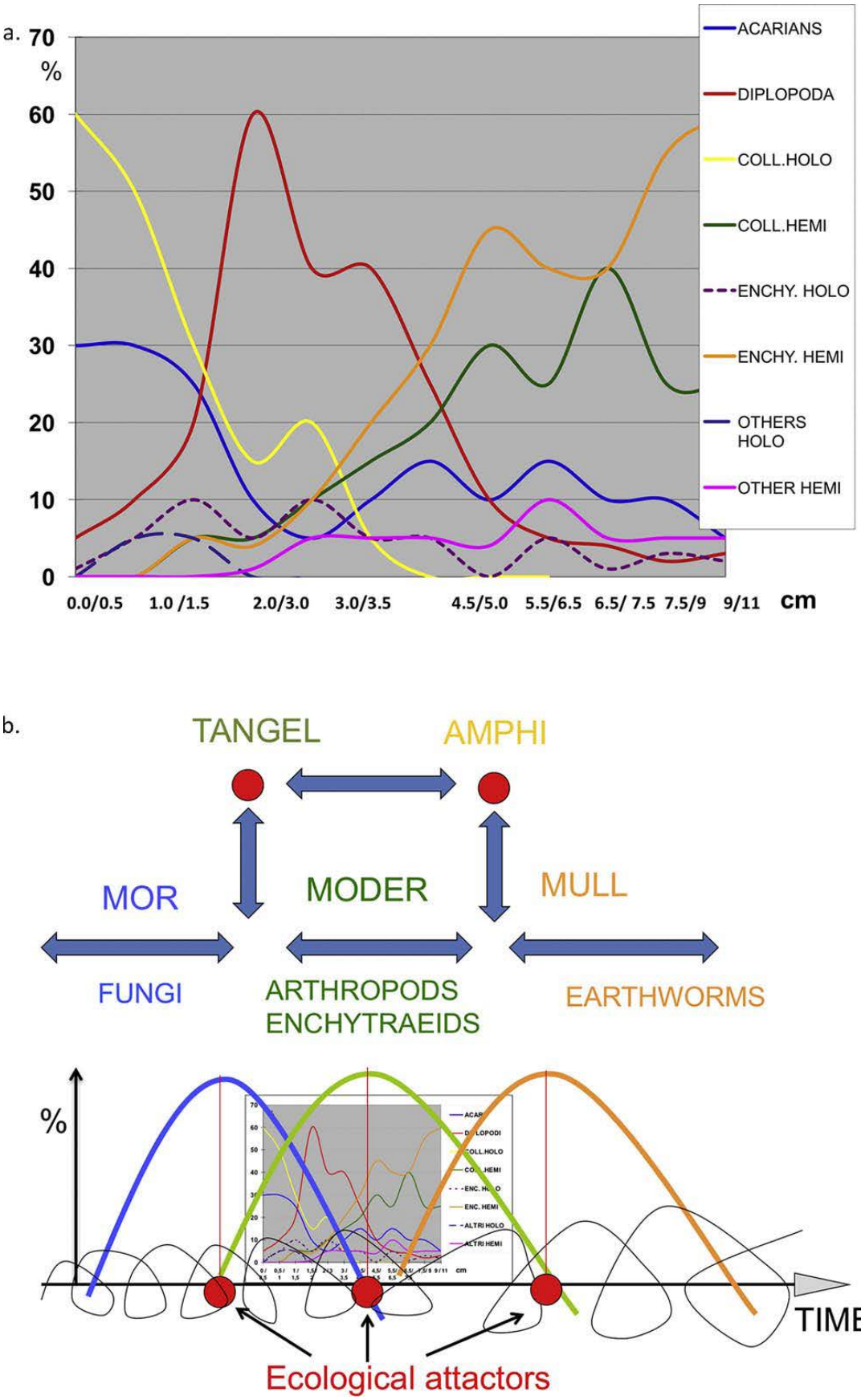

a.
70
%
60
50
40
30
20
10
0
0.0/0.5
1.0 /1.5
2.0/3.0
3.0/3.5
4.5/5.0
5.5/6.5
6.5/ 7.5
7.5/9
9/11
cm
ACARIANS
DIPLOPODA
COLL.HOLO
COLL.HEMI
ENCHY. HOLO
ENCHY. HEMI
OTHERS HOLO
OTHER HEMI
b.
TANGEL
AMPHI
MOR
MODER
MULL
FUNGI
ARTHROPODS
ENCHYTRAEIDS
EARTHWORMS
%
TIME
Ecological attactors

Fig. 31

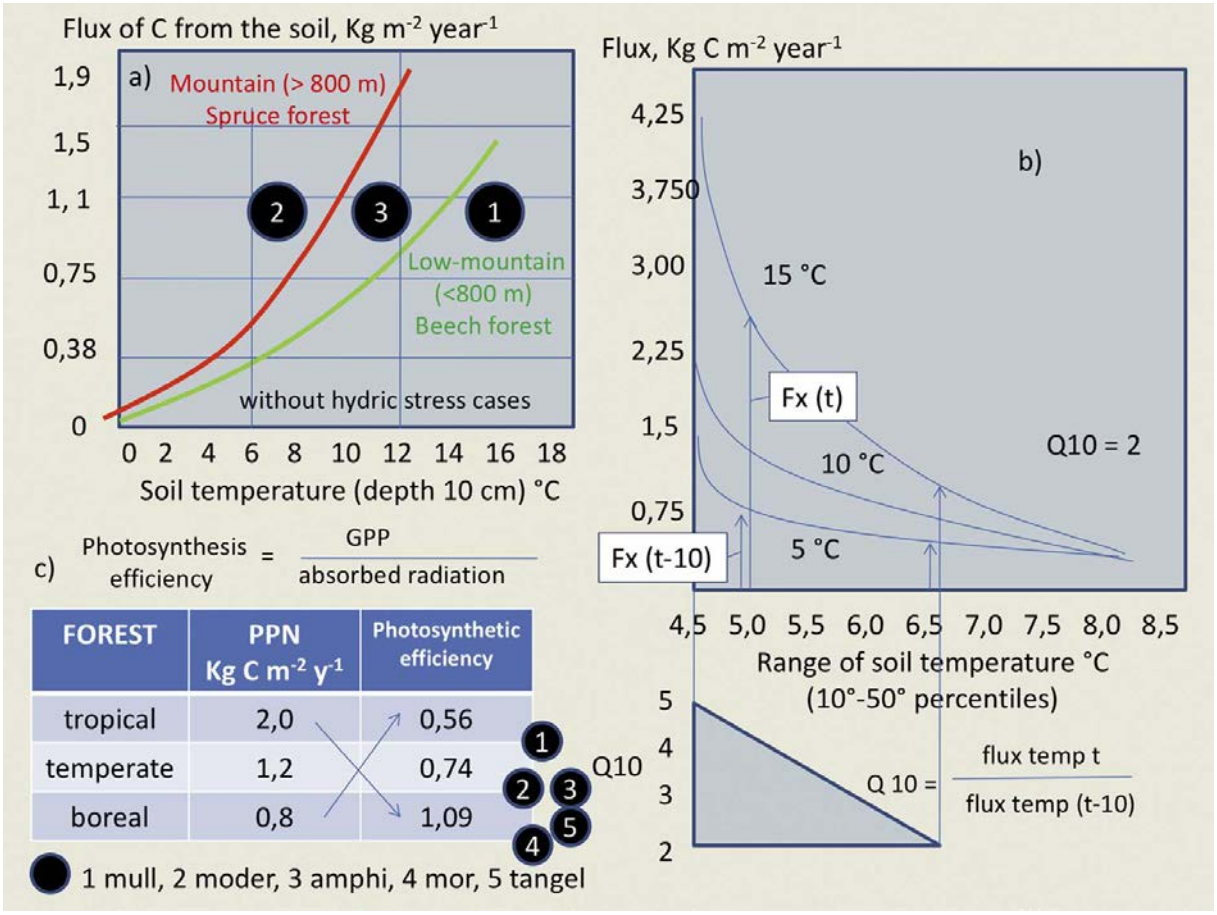

Flux of C from the soil, Kg m-2 year-1
a)
Mountain (> 800 m)
Spruce forest
Low-mountain
(<800 m)
Beech forest
without hydric stress cases
1,9
1,5
1, 1
0,75
0,38
0
0 2 4 6 8 10 12 14 16 18
Soil temperature (depth 10 cm) °C
Flux, Kg C m-2 year-1
b)
15 °C
10 °C
5 °C
Fx (t)
Fx (t-10)
Q10 = 2
4,25
3,750
3,00
2,25
1,5
0,75
4,5 5,0 5,5 6,0 6,5 7,0 7,5 8,0 8,5
Range of soil temperature °C
(10°-50° percentiles)
Q10
5
4
3
2
Q 10 = flux temp t / flux temp (t-10)
c) Photosynthesis efficiency = GPP / absorbed radiation
FOREST
PPN Kg C m-2 y-1
Photosynthetic efficiency
tropical 2,0 0,56
temperate 1,2 0,74
boreal 0,8 1,09
1 mull, 2 moder, 3 amphi, 4 mor, 5 tangel

Fig. 32

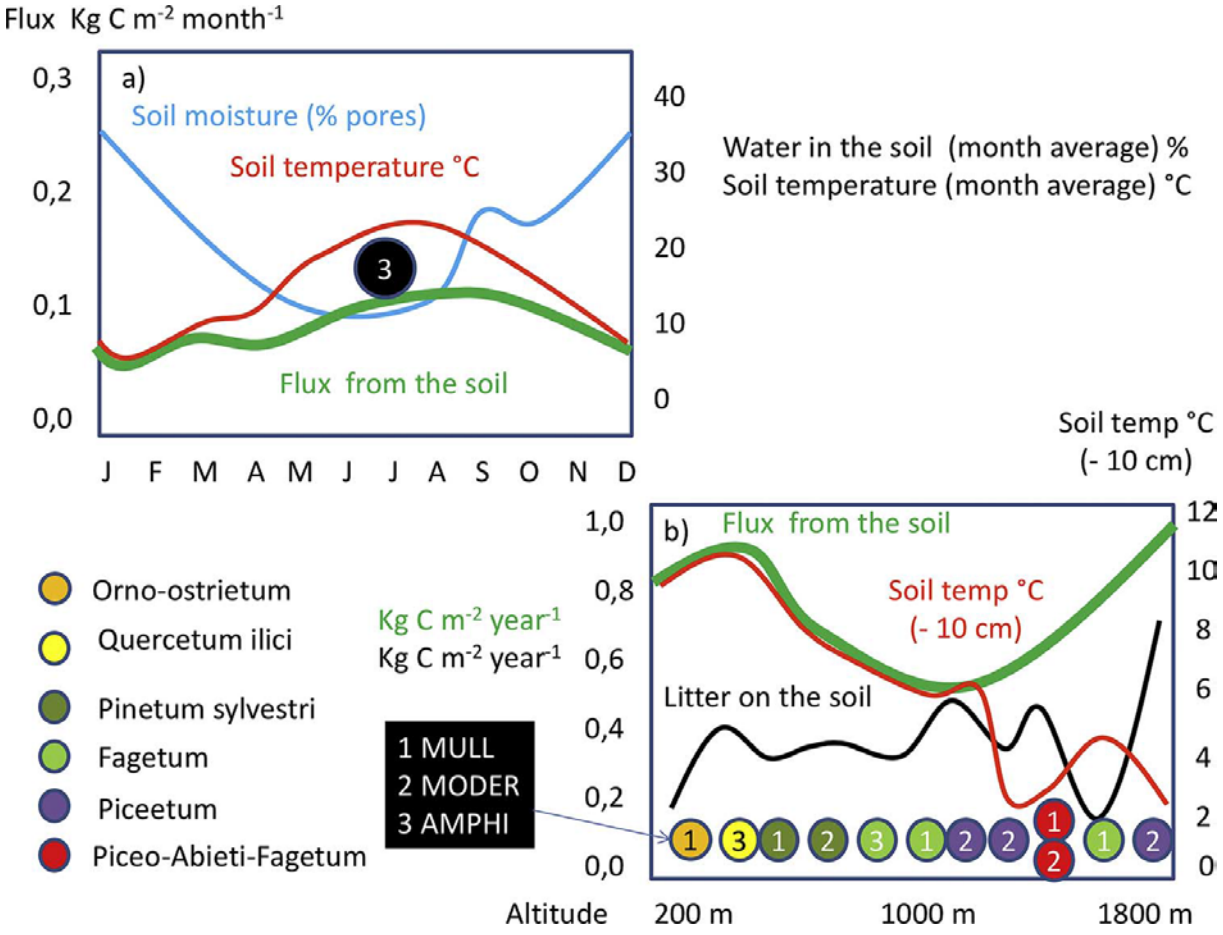

Flux Kg C m-2 month-1
a)
Soil moisture (% pores)
Soil temperature °C
Flux from the soil
0,3
0,2
0,1
0,0
40
30
20
10
0
J F M A M J J A S O N D
Water in the soil (month average) %
Soil temperature (month average) °C
Soil temp °C
(- 10 cm)
Orno-ostrietum
Quercetum ilici
Pinetum sylvestri
Fagetum
Piceetum
Piceo-Abieti-Fagetum
Kg C m-2 year-1
Kg C m-2 year-1
1,0
0,8
0,6
0,4
0,2
0,0
1 MULL
2 MODER
3 AMPHI
b)
Flux from the soil
Soil temp °C
(- 10 cm)
Litter on the soil
12
10
8
6
4
2
0
Altitude
200 m
1000 m
1800 m

Fig. 33

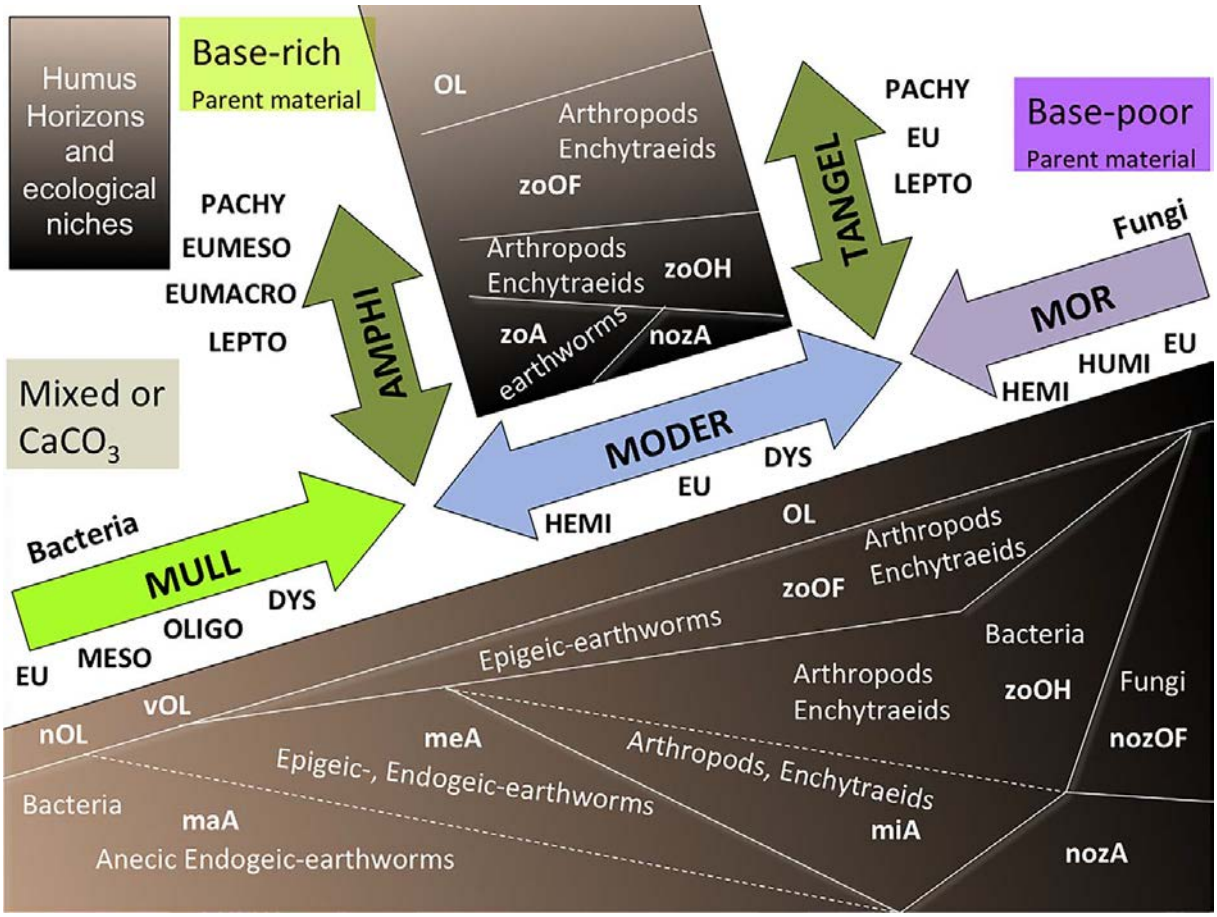

Humus Horizons and ecological niches
Base-rich
Parent material
OL
Arthropods
Enchytraeids
zoOF
Arthropods
Enchytraeids
zoOH
zoA
earthworms
nozA
PACHY
EUMESO
EUMACRO
LEPTO
AMPHI
TANGEL
PACHY
EU
LEPTO
Base-poor
Parent material
Fungi
MOR
HUMI
EU
HEMI
Mixed or $CaCO_3$
MODER
DYS
EU
HEMI
Bacteria
MULL
DYS
OLIGO
MESO
EU
OL
Arthropods
Enchytraeids
zoOF
Epigeic-earthworms
Bacteria
zoOH
Fungi
nozOF
Arthropods
Enchytraeids
vOL
nOL
meA
Epigeic-, Endogeic-earthworms
Arthropods, Enchytraeids
miA
Bacteria
maA
Anecic Endogeic-earthworms
nozA

Fig. 34

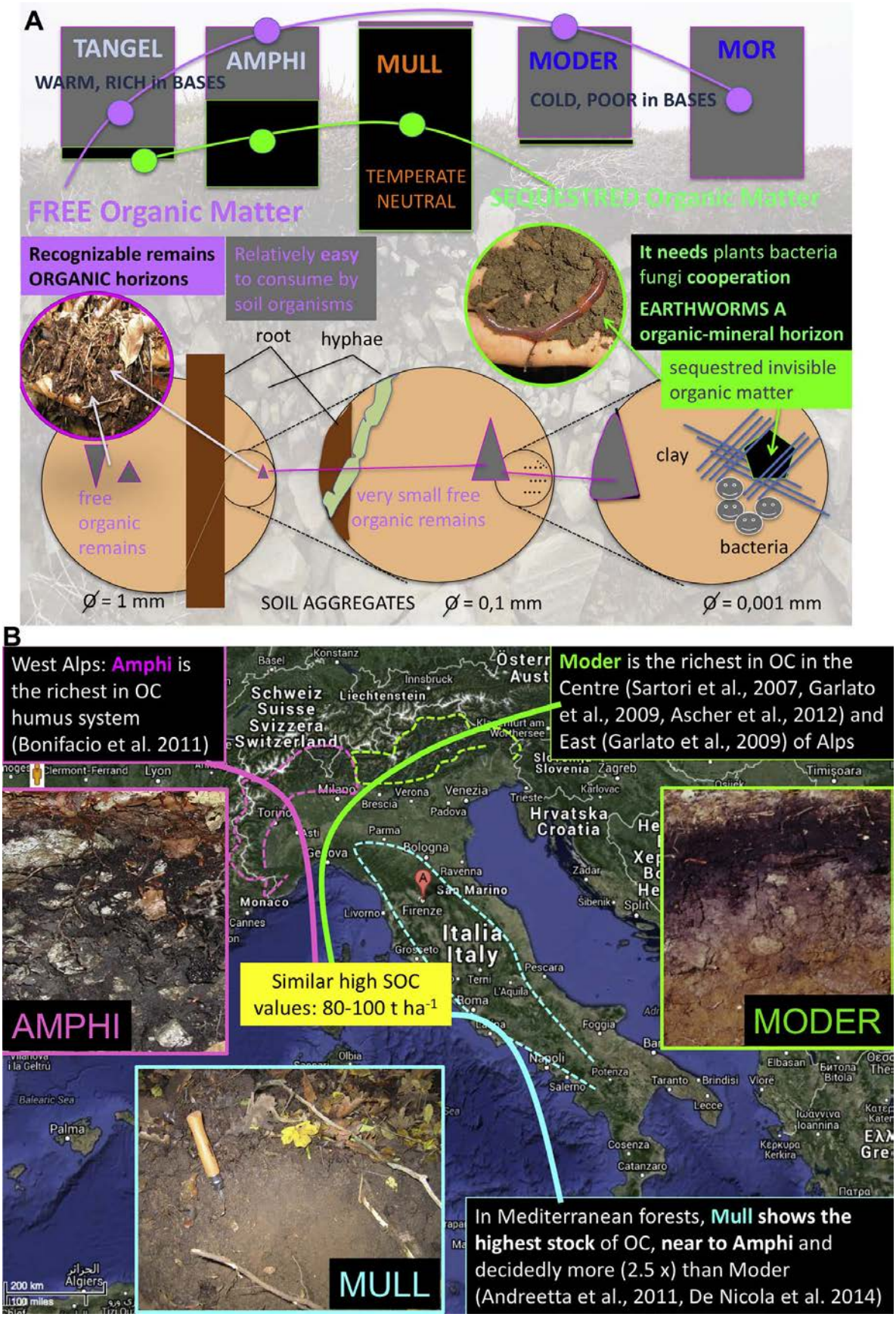

A
TANGEL
WARM, RICH in BASES
AMPHI
MULL
TEMPERATE
NEUTRAL
MODER
COLD, POOR in BASES
MOR
FREE Organic Matter
SEQUESTRED Organic Matter
Recognizable remains
ORGANIC horizons
Relatively easy
to consume by
soil organisms
It needs plants bacteria
fungi cooperation
EARTHWORMS A
organic-mineral horizon
root
hyphae
sequestred invisible
organic matter
clay
free
organic
remains
very small free
organic remains
bacteria
Ø = 1 mm
SOIL AGGREGATES
Ø = 0,1 mm
Ø = 0,001 mm
B
West Alps: Amphi is
the richest in OC
humus system
(Bonifacio et al. 2011)
Moder is the richest in OC in the
Centre (Sartori et al., 2007, Garlato
et al., 2009, Ascher et al., 2012) and
East (Garlato et al., 2009) of Alps
Schweiz
Suisse
Svizzera
Switzerland
Liechtenstein
Innsbruck
Slovenia
Zagreb
Hrvatska
Croatia
Milano
Verona
Venezia
Brescia
Padova
Trieste
Parma
Bologna
Ravenna
San Marino
Firenze
Livorno
Monaco
Cannes
Italia
Italy
Pescara
Roma
Foggia
Napoli
Potenza
Taranto
Brindisi
Lecce
Cosenza
Catanzaro
Palma
Balearic Sea
Algiers
Split
Zadar
Sibenik
Timişoara
Karlovac
Elbasan
Ioannina
Kerkira
Patra
AMPHI
MODER
MULL
Similar high SOC
values: 80-100 t ha-1
In Mediterranean forests, Mull shows the
highest stock of OC, near to Amphi and
decidedly more (2.5 x) than Moder
(Andreetta et al., 2011, De Nicola et al. 2014)

Fig. 35



Fig. 36

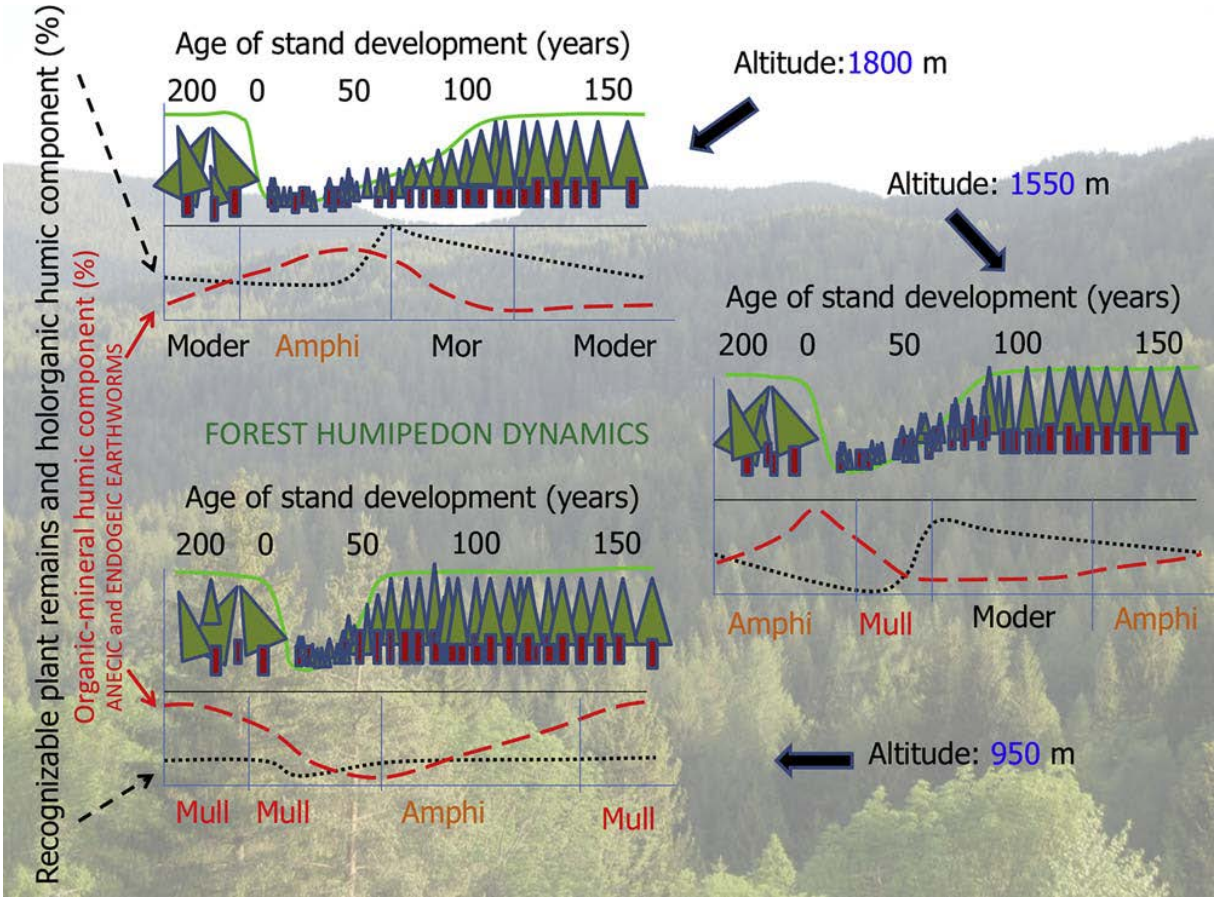

Recognizable plant remains and holorganic humic component (%)
Organic-mineral humic component (%)
ANECIC and ENDOGEIC EARTHWORMS
Age of stand development (years)
200 0 50 100 150
Moder Amphi Mor Moder
Altitude:1800 m
Altitude: 1550 m
Age of stand development (years)
200 0 50 100 150
Amphi Mull Moder Amphi
FOREST HUMIPEDON DYNAMICS
Age of stand development (years)
200 0 50 100 150
Mull Mull Amphi Mull
Altitude: 950 m

Fig. 37

a.



b.



Fig. 38