



**HAL**  
open science

## Humusica 1, article 2: Essential bases - Functional considerations

Augusto Zanella, Björn Berg, Jean-François Ponge, Rolf Kemmers

► **To cite this version:**

Augusto Zanella, Björn Berg, Jean-François Ponge, Rolf Kemmers. Humusica 1, article 2: Essential bases - Functional considerations. Applied Soil Ecology, 2018, 122 (Part 1), pp.22-41. 10.1016/j.apsoil.2017.07.010 . hal-01658448

**HAL Id: hal-01658448**

**<https://hal.science/hal-01658448>**

Submitted on 7 Dec 2017

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Public Domain

## Humusica 1, article 2: Essential bases – Functional considerations <sup>\*</sup>

Augusto Zanella<sup>a,†</sup>, Björn Berg<sup>b</sup>, Jean-François Ponge<sup>c</sup>, Rolf H. Kemmers<sup>d</sup>

<sup>a</sup> *University of Padova, Department TESAF, Italy*

<sup>b</sup> *University of Helsinki, Finland*

<sup>c</sup> *Muséum National d'Histoire Naturelle, Paris, France*

<sup>d</sup> *Alterra, Wageningen University and Research Centre, The Netherlands*

*Keywords:* Humus; Soil functioning; SOM; SOC; Litter; Biodegradation; Soil ecology; Humusica; Decomposition and temperature

### ABSTRACT

Humusica 1 and 2 Applied Soil Ecology Special issues are field guides for humipedon classification. Contrary to other similar manuals dedicated to soil, the objects that one can describe with these guides are living, dynamic, functional, and relatively independent soil units. This is the reason to why the authors dedicated the whole article 2 to functional considerations even before readers could go in the field and face the matter to be classified. Experienced lectors can overstep many of the sections reported in this article. If the titles of sections "1. A functional classification", "2. What is a humus system?" and "3. Energetic considerations in terrestrial systems" stimulate the reader's curiosity, then we suggest to pass through them. Otherwise, only section "4. Climatic, plant litter, or nutritional constraints?" is crucial. Readers will understand how the soil works in terms of litter and carbon accumulation, which one(s) among climatic, vegetation, or geological factors intervene and strongly affect the formation of terrestrial (oxygenated) soils. The article concludes with a debate about a tergiversated question: can temperature influence humus decomposition? Preceding statements were used for explaining how the biological soil net can store in the soil a maximum of energy in the form of SOM, by raising a plateau partially independent of climatic conditions.

---

<sup>\*</sup> Supplementary information in: Humusica 1, article 8: Terrestrial humus systems and forms – Biological activity and soil aggregates, space-time dynamics; Humusica 3, many articles or short communications about pedofauna, symbioses, roots, biodiversity... and functioning (e.g., driving factors, carbon storage, humeomics), particularly B. Berg: "Decomposing litter; Limit values; Humus accumulation, locally and regionally"; and R. Kölli: "Dynamics of annual falling debris decomposition and forest floor accumulation".

<sup>†</sup> Corresponding author and not mentioned author of figures. Listen to music while reading: Why? Anna RF (Alps): <https://www.youtube.com/watch?v=YdXBWsFc-0U>.

E-mail addresses: [augusto.zanella@unipd.it](mailto:augusto.zanella@unipd.it) (A. Zanella), [bb0708212424@gmail.com](mailto:bb0708212424@gmail.com) (B. Berg), [ponge@mnhn.fr](mailto:ponge@mnhn.fr) (J.-F. Ponge), [Rolf.Kemmers@wur.nl](mailto:Rolf.Kemmers@wur.nl) (R.H. Kemmers).

## 1. A functional classification

Classifying makes sense only if the established categories of objects correspond to a few references allowing us to better understand the observable real world (see also in *Humusica* 1, article 1: Essential bases – Vocabulary and article 7: Terrestrial humus systems and forms – Field practice and sampling problems). We have named these references Humus forms (= theoretical groups of humus profiles displaying the same series of diagnostic horizons) and Humus systems (= theoretical groups of humus forms sharing the same biological/functional properties). If we want to use these references for understanding the real world, some well-known theoretical/practical principles have to be considered:

*1- Objects of the real world are organized in complex units made of smaller systems embedded in larger ones* (theory and examples in natural environments, papers in English, French or Italian: Odum, 1953, 1997; Johnson, 1998; Botkin, 1990; Zanella, 1995, 1996; Camaret et al., 2000; Saugier et al., 2001; Begon et al., 2005; few among many possible examples in forest ecosystems: Susmel et al., 1976; Susmel, 1980, 1988; Oldeman, 1990; Zanella, 1994; Carletti et al., 2009; Nocentini, 2011; Mason and Zapponi, 2015). Concerning humus systems, we would like to classify humus profiles observing features detectable in the field by the naked eye or with a 10×-magnifying lens. This scale allows us to describe objects whose smallest dimension is 1/10 mm (when magnified 10 times with a lens it becomes 1 mm large, which is visible by the naked eye);

*2- Admitting a fractal structure of the soil, accepting that time and space are related to each other and scale dependent* (Mandelbrot, 2004; Anderson et al., 1998; Young et al., 2008). In other words, this means that ecological processes at different scales are working in corresponding different times. Humus and soil specialists cannot exchange information and debate as well as expected (example: the discussion engaged in ResearchGate by P. Baveye: Should soil scientists stop using terms like “humus”, “humic”, or “humification”?

[https://www.researchgate.net/post/Should\\_soil\\_scientists\\_stop\\_using\\_terms\\_like\\_humus\\_humic\\_or\\_humification](https://www.researchgate.net/post/Should_soil_scientists_stop_using_terms_like_humus_humic_or_humification)) because they are studying the same soil system at different time-space scales.

“Humus” scientists analyse litter biodegradation and biological molecules implementation in the topsoil during days to decades of years, in cubic millimetres or meters of soil volumes; soil scientists work on rock transformation and soil genesis, considering decades or hundred to thousand years of history and larger soil volumes (regional surfaces and metres of soil depth). Examples will facilitate our purposes. Humus specialists consider a Mull system strongly influenced by large earthworms. Simplifying their view, it is possible to write that the higher the number of earthworms, the better the soil quality (for data, refer to Cluzeau et al., 1987, 2012, 2014). However, this soil quality does not depend directly from the number of individuals of earthworms but from the quality and quantity of the organic matter these animals are able to store in their droppings, which depends on the type of soil exploitation (e.g. use of pesticides, organic or mineral fertilisation, irrigation, type of culture, recent review in Bertrand et al., 2015). Even worse, to free the potential energy and nutrient content in the organic matter that earthworm activity could have stored in the soil, it is necessary to wake up microbial communities, purposely fed by plant exudates or even stimulated by a complex interaction with other organisms (Fitter and Garbaye, 1994; Blouin et al., 2013; Kardol et al., 2016). Earthworms are organisms working at a scale observable by the naked eye, and their numbers change following

seasonal variations; bacteria occupy microscopic spaces and on one side (Stevenson, 1972, 1985, 1994; Gobat et al., 1998; Janzen, 2006; Legros, 2007) that the stability of the content in bases depends of the capacity of exchange (CEC) of the soil, which takes place at the level of organic macromolecules, edge of mineral microstructures; on the other side (Schulten and Schnitzer, 1997; Leinweber and Schulten, 1998; Piccolo, 2001; van Heerwaarden et al., 2003; Kelleher and Simpson, 2006; Lehmann et al., 2008; Kleber et al., 2011) nutrients may take place between organic-mineral aggregates made by earthworms and microorganisms, or even be attracted by electrostatic forces of organic molecules generated by them. Finally, the functioning of the soil may be summarized by a multitude of processes, each one at a given limited space-time scale, interconnected and influenced by each other at a larger scale.

Humus and soil scientists should accentuate their collaboration. Together they could translate complex realities (made of a multitude of coevolving processes) into understandable "models" human "brain-models", and take practical decisions. For instance, following different simplified functional models of sustainable agriculture, humus scientists may promote the biological quality (example: a higher number of earthworms), soil scientists the mineral quality (high quantity of crop nutrients) of a same field. Both decisions are interconnected on a functional plan and need consultation for finding the right soil-plant system harmony in human "brain-models".

*3- The process of comprehension needs to play with the scale of phenomena.* It has to start from a large-scale model, easy to understand, and in a second step to include more detailed information at a finer resolution, until reaching the limit of a personal (historical) knowledge. The inverse way has to be taken too, from smaller to larger scales, and the movement, in both directions, has to find a final relative harmony in a functional model that could be observed at the same time at both large and small scales. A detective feeling comes along with this harmony in progress [examples for forest management in Zanella et al. (2001, 2003, 2008); Cavalli and Mason (2003); Scattolin et al. (2004a, 2004b); Corona et al. (2005); Ciancio and Nocentini (2005); Ciancio (2014); pedofauna and soil interactions in: Salmon et al. (2006); Galvan et al. (2006, 2008); ecology and evolution in: Barot et al. (2007); relationships between soil biology and climate/land use in: Ascher et al. (2012); Blouin et al. (2013); Spurgeon et al. (2013); Sverdrup-Thygeson et al. (2014a); Sverdrup-Thygeson et al. (2014b); Clause et al. (2014); Nielsen et al. (2015); Fusaro (2015).

We have to accept that a proposed functional model could only represent a new starting point for further search. The final agreement should not be different from an anthropomorphic statement.

## **2. What is a humus system?**

The humipedon – the upper part of a soil made of organic and/or organic-mineral horizons – is directly under the influence of the aboveground parts of an ecosystem. The humipedon constitutes an interaction system born to manage a functional transition between organic and mineral worlds. This humus system has the possibility to degrade structured organic matter and use it as a source of energy. Further, it may act as a sink and a source of energy. Due to the process of photosynthesis,

plant activity produces organic matter, which feeds a complex system of consumers. On the other hand, living organisms lose mineralised compounds such as water, carbon dioxide, ammonia, nitrate, and organic matter (urine, organic waste products) in order to renew their structures, thereby creating a substrate rich in energy, which can be utilized by numerous interconnected decomposers. Both the process of production and that of mineralisation of organic matter are interdependent and can or cannot be well shared. All this activity is organized like a chain from the largest to the tiniest organisms. At each step, part of its energy is extracted from the substrate. Curiously, the result of the process of biodegradation is not the complete mineralisation of the previously built organic matter, but a new “body”, corresponding to functional organic, organic-mineral and mineral interacting “humus horizons” (Fig. 1). On one side this new structure is able to form and/or retain vital elements while on the other side it can release these elements both in mineral form and in more sophisticated molecules (e.g., humic acids, hormone like substances). This new substrate behaves like a biological matrix in which microorganisms as well as meso- and macro-organisms live and evolve in tight association. The result seems helpful for the producing photosynthetic system (aboveground), which finds in it water and nutrients in relatively equilibrated association all along its lifetime. We suggest that such systems of interactions between biotic and abiotic components taking place in the humipedon be called “humus interaction systems” or in short “humus systems”. They are designed to provide a name for still imperfectly known conditions for the common life and evolution of the immense variety of organisms which ensure, in a coordinated manner, the sustainability of terrestrial ecosystems. Since a limited number of strategies were selected in the course of Earth’s history, taking into account the variety of conditions (climate, nutrient availability, vegetation types) prevailing in terrestrial environments, several humus systems have been described, featuring the bulk of existing variation (Ponge, 2003).

### 3. Energetic considerations in terrestrial systems

The large-scale approach (point 2 of Section 1) has to consider the most important parameter while discussing ecosystem functioning: energy. No energy, no life. Sun sends high amounts of energy to Earth. Ignoring clouds, the average insolation for the Earth is approximately 250 W per square meter (= 6 kWhm<sup>-2</sup> day<sup>-1</sup>). In fact, over the course of a year the average solar radiation arriving at the top of the Earth's atmosphere is roughly 1366 W per square meter of ground. Sun rays are attenuated as they pass through the atmosphere, thus reducing the insolation at the Earth's surface to approximately 1000 W per square meter for a surface at right angle to sun rays at sea level on a clear day. Then, taking into account the lower radiation intensity in early mornings and evenings, the sun angle at different seasons of the year and the fact that only half of the Earth spherical surface receives sun radiation – the other half being in night – the average insolation per square meter reduces itself to 250 W (1 W = 1 J s<sup>-1</sup>). Still, this represents (250 × 60 × 60 × 24 = 21,600,000 = 21 MJ day<sup>-1</sup>) about twice the power necessary to cover the daily energy expenditure of an adult human being (nearly 10 MJ day<sup>-1</sup>; Roberts and Dallal (2005).

On a clear day, at noon (universal time), in a temperate zone, the carbon flux absorbed by a plan’s mass shifts from 10 to 40 μmol carbon m<sup>-2</sup> s<sup>-1</sup>. As for the insolation, considering the night/day cycle and the changing height of the sun in the sky during the year, only a quarter of this value

measured at noon may be taken as average over the course of a year. This means 2.5 to 10  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Then, on each meter square of the terrestrial green Earth, a flux of 0.2 to 0.8 mol of carbon could be assimilated every day, corresponding to 2.4 – 10  $\text{g C m}^{-2} \text{day}^{-1}$ , or 876 to 3,650  $\text{g C m}^{-2} \text{year}^{-1}$ . Taking into account the respiration of the photosynthetic mass (wasting 50% of the fixed C), the estimated net primary production (NPP) per square meter of terrestrial green Earth rises from 0.4 to 1.8  $\text{kg C m}^{-2} \text{year}^{-1}$ . Effectively, in a temperate climate, an annual production of biomass (biomass = 2 x C) of 1–3  $\text{kg m}^{-2}$  has been recorded.

In the Alps, organic carbon data have been collected for some forest ecosystems:

- 1) In Rodeghiero (2003), Rodeghiero et al. (2010), InFoCarb (2007) (Italy): aboveground total carbon (essentially in trees): 3.9–15.9  $\text{kg m}^{-2}$ ; belowground total carbon (first 30 cm): 2.3–11.5  $\text{kg m}^{-2}$ ; total carbon of the system: 6.2–27.4  $\text{kg m}^{-2}$ ; litter carbon (freshly shed litter, aboveground): 0.21–0.65  $\text{kg m}^{-2}$ .
- 2) In Perruchoud et al. (1999a, 1999b) (Switzerland): aboveground total carbon (essentially in trees): 7.6–13.5  $\text{kg m}^{-2}$ ; belowground total carbon (first 20 cm): 4.8–7.4  $\text{kg m}^{-2}$ ; total carbon of the system: 12.4–20.9  $\text{kg m}^{-2}$ ; litter carbon (freshly shed litter, above- and belowground): 1.1–2.1  $\text{kg m}^{-2}$ .

[For further information in specialized databases and peer reviewed papers, refer to Luysaert et al. (2007): <http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2007.01439.x/abstract>]

Observing these data, and using a simple but realistic model; for an undisturbed forest ecosystem with all growth phases being in equilibrium, while an annual carbon mass of 0.5–1.5  $\text{kg m}^{-2}$  is assimilated, an equal mass of carbon reaches the soil as litter, half above- and half belowground (root litter: roots and exudates). All the “assimilated solar energy” is then being recycled and feeds a “forest engine” such as gasoline fuels a car engine (Fig. 2). The main difference between forest ecosystems and cars is that the former produce their own gasoline in the form of litter by extracting energy from sunlight. The produced carbon mass, the “static mass” of this standard forest ecosystem, considering the roots living in the first 20–30 cm of soil, amounts to nearly 20  $\text{kg m}^{-2}$ . In an Alpine environment, the biomass of living forest represents about 10 times the “turning dead mass”, i.e. the sum of above- and belowground litter (Fig. 3).

Going further in understanding our model, a useful way is to study – separately – the processes of production and respiration of glucose; in fact, though partially, Calvin and Krebs cycles represent the series of chemical reactions characterizing these processes that effectively occur in different periods of time and spaces. They coexist at the level of ecosystems; they act together: no production without respiration. For understanding the functioning of an ecosystem, one has to consider both processes: production and respiration, or construction of biostructures and their degradation. Concerning the evolution of terrestrial ecosystems, two kinds of dynamic changes have been well described:

- a linear evolution: under favourable conditions, space-time is increasing, the system grows from an initial step of bare rock towards a better organized forest or grassland ecosystem, crossing a long series of intermediate levels of increasing complexity. The direction of the evolution may be inverted (collapse) in case of unfavourable

- conditions. More simply, when the biomass of the system is growing, the photosynthetic production has to be larger than the mass decomposed and respired;
- a cyclic evolution: as for an individual life, each system comes into existence, develops, becomes adult, ages, and finally dies. A forest, for example, knows innovation, aggradation, biostatic, and collapse phases (Oldeman, 1990). Observing attentively the formerly described linear evolution, it occurs that this process is made of a series of cyclic evolutions (Fig. 4). A force seems to push the natural systems to increase their complexity, in response to a better use of solar energy. For the systems, this means being able to retain on Earth the largest part of energy coming from Space. Finally, adapting the topsoil to local constraints corresponds to a survival strategy, a need of parsimony in the use of a limited amount of energy.

#### 4. Climatic, plant litter, or nutritional constraints?

It is not astonishing that this fundamental question was raised by eminent naturalists. They proposed, however, discording solutions.

##### 4.1. Darwin, Dokuchaev, or Jenny?

In an attempt to see further into the future, let us climb onto the shoulders of some fathers of soil science. There are two instructive articles that resume the debate in question since about a century ago, when scientific minds believed that they were able to understand the relationships between plants, soils, and animals. We have come further, but the question is still unresolved:

- Role of the plant factor in pedogenetic functions (Jenny, 1958)
- Reflexions on the nature of soil and its biomantle (Johnson et al., 2005).

**The first article** (Jenny, 1958): “We shall set up models and imaginary experiments. Although they deviate from natural systems by an uncomfortable margin, these over-simplifications are most helpful in clarifying the independent and dependent aspects of the biotic factor and allied conceptual questions of system analysis.”

We report here three of Jenny’s imaginary sympathetic experiments. He wanted to illustrate the influence of plants on soil development. The question is still under investigation (Andreetta et al., 2016).

*First experiment:* three boxes (climate-controlled) in which we may imagine: 1) bare soil; 2) bare soil +grass seeds; 3) bare soil + legume seeds.

Question: in the three boxes, how would be the soil be after 50 years?

Jenny's answer: only the "biotic factor" would change; climate, topography, and parent material would remain the same. Plants would grow and generate different soils, the one made by legumes (symbiotic fixation of  $N_2$ ) would become richer in N and organic matter compared to the one made by grasses.

*Second experiment:* two boxes, the same loessic parent material: 1) ten per cent oak and ninety per cent pine seeds; 2) ten per cent pine and ninety per cent oak seeds; he reseeds annually but does not cut the trees.

Question: How will these two systems evolve?

Jenny's answer: If the two mixed-culture boxes are left to themselves for many centuries, their stands and proportions of species will become more and more alike, even if we keep adding annually the original seed mixture. Adult trees produce seeds and will self-determine the evolution.

Jenny's deductions: the soil under pine is different from the one under oak because of a species-specific effect. Plants make a specific soil: "if we cut the forest of one of the two boxes in the preceding experiment and replant it to an entirely new set of species, a new development cycle is instigated."

*Third experiment:* interaction between two large phytotrons, separated by a partition wall which prevents transfer of matter: 1) with a dense grass sod; 2) with a eucalyptus grove.

Question: after the partition wall is removed, how will the interacting system evolve?

Jenny's answer: "eucalyptus will move slowly into grass, along a narrow fringe, in which the grassland soil – in this case, a parent material – is transformed into a new soil, which is not necessarily identical to the original eucalyptus soil".

With the same spirit, Hans Jenny proposed analogous imaginary experiments for studying the influence of parent material, topography, climate, initial state, and time on soil formation and evolution. Supported by his examples, he presented the following fundamental function:  $l, v, s = f(cl, o, r, i, t)$ , where:  $l$  = landscape,  $s$  = soil,  $v$  = vegetation and  $cl$  = climate,  $o$  = biotic factor,  $r$  = topography,  $i$  = initial state  $t$  = time. He concluded the article stating that:

- a) If in a given area, the five state factors (second part of the function) vary continuously, soil and vegetation very likely will vary continuously also. Larger systems would be expected to diffuse into each other;
- b) If, in a given area, one or more state factors vary in a discontinuous fashion, soil and vegetation very likely will also exhibit discontinuities. In the field, there will be lines of demarcation.

**In the second article**, Johnson et al. (2005) oppose Darwin's animal-process (Darwin, 1881) and Dokuchaev's terrestrial five-factors (Dokuchaev, 1883), zonal approach.

A clarification, reported at the beginning of the article: Jenny's function, just presented in the preceding section, was in fact proposed 70 years earlier in Russia by Dokuchaev (1883). Focusing on this function, we can see that it is not a real mathematical function. It simply says that vegetation or soil or the result of their co-evolution (the landscape) is dependent on climatic, biotic, topographic,



initial state, and time factors: no mathematical formulas, no numbers, but graphic interpretations, like maps of soil and vegetation or points on a bi-plot considering two or three factors and showing a trend. The point raised by Johnson et al. (2005) is that, in soil formation, by “biotic factor” Dokuchaev (and Jenny) intended a strong influence by plants, and this view might be opposed to that of Darwin for whom, on the contrary, animals [earthworms, in Darwin (1881)] are the biotic factor (named “vegetable mould” by Dokuchaev and Darwin) of soil formation.

Johnson et al. (2005) preferred the “animal” interpretation. In this guide, we link specific humipedons to particular humus “systems”, avoiding the distinction between plant, animal and/or microbial influences: all organisms are in play and their activities are tightly interconnected in this concept.

We can state that climate (summarized in the combined yearly distribution/variation/extremes of incident energy, air temperature, humidity, and precipitation) is the main factor that determines the type of terrestrial ecosystem occurring in a given point of our planet. Climate influences biotic activities and adaptations, on each given initial mineral substrate. Then, biotic (microbial, animal, and plant) activities modify the original natural frame, building an ecological dynamic system, changing with time, in equilibrium within a recognisable finite part of the planet, with structured plant-animal-microbial trophic networks, in a volume including aerial, photosynthetic-evapotranspiring and pedologic, biodegrading-recycling spaces.

Observing the topsoil of different terrestrial ecosystems in Europe, five main humus systems have been pointed out and called Mull, Moder, Mor, Amphi, and Tangel (Zanella et al., 2011a, b; Jabiol et al., 2013). A key of classification, based on characters of diagnostic horizons, allows us to identify humus systems in the field. It has been well-established that the ecological attractors of these five “modalities of litter biodegradation” are to be found in the environment. In fact, litter quality, climate, and nutritional factors influence soil biological activity, the latter being directly responsible for the structures observed in the topsoil. A work hypothesis has been set down (Fig. 5) and needs a supplement of theoretical knowledge, involving the concepts of “humus system strategy” and “limit value” which are discussed below.

#### *4.2. Allocation of net primary production and humus system strategies*

Historical published data and well-known facts (very numerous works listed in Berg and McLaugherty, 2014):

- 1) Litter quality varies with species. Coniferous trees in general have needle litter richer in lignin and poorer in nutrients than litter of broadleaf species (Tables 1 and 2 are discussed in Section 4.3);
- 2) Litter is produced above the soil (e.g. leaves, branches, bark) and within the soil (roots, exudates) in equivalent quantities (in all about  $\frac{3}{4}$  of annual NPP). In boreal forests, these quantities encompass  $\frac{3}{4}$  of  $20\text{--}30 \text{ t ha}^{-1} \text{ yr}^{-1}$  = about  $10\text{--}15 \text{ t ha}^{-1}$  above the soil and  $10\text{--}15 \text{ t ha}^{-1}$  within the soil =  $1.5\text{--}2.25 \text{ kg m}^{-2} \text{ yr}^{-1}$ , about 1 kg above and 1 kg within the soil (synthesis of several papers, approximate values);

- 3) With different efficiencies, half of the mineral elements are retranslocated by trees before shedding litter onto the ground (among many works: Killingbeck, 1996; Hagen-Thorn et al., 2006; Fischer, 2007; Marchin et al., 2010; Teija Ruuhola, 2011; Maillardet et al., 2015);
- 4) After a first stage of passive leaching of soluble compounds, shed litter undergoes a selective attack by living organisms (fungi, bacteria, animals), physical factors (leaching), and chemical agents (oxidation) as well as a progressive transformation until it has lost more than half its weight. During this transformation, we observe the formation of a complex organic material, richer in N, lignin, and lignin-like compounds (humus in chemical sense) than the original litter, and more resistant to biodegradation (Berg and McClaugherty, 2008; Berg and Cortina, 1995; Berg and Dise, 2004; Berg and Lundmark, 1985, 1987). In a last stage, the remaining recalcitrant mass is decomposed very/extremely slowly and accumulates (Mor, Tangel) or becomes incorporated to underlying soil horizons by the activity of soil animals (Mull, Moder, Amphi)
- 5) Using solar energy a forest system produces organic matter by utilizing mineral matter in air (CO<sub>2</sub>, N<sub>2</sub>) and in soil (H<sub>2</sub>O, N, S, P, Mn....). Quantifying the cycle, even approximately, we obtain the following data (Fig. 6):
  - 1/4 of NPP is added to the living body (biomass) of the producing system,
  - 3/4 end up outside of this living body as litter. Of these, 1 part is stored in the soil and 2 are biodegraded. This means that at the end of the year, an average of 1/3 of the organic matter furnished to the soil as "litter" (out and in the soil) is still in the soil.

In other words,  $\frac{1}{4}$  of this annually created organic matter (NPP) becomes living organic matter (living bodies, annual increase of the system), the other  $\frac{3}{4}$  are "invested" out of the producing living body of the system. Of these latter, 1 quarter is fixed in the soil (transformed in an organic mass resistant to biodegradation = humus in a chemical sense) and 2 quarters are forced into a perennial cycle, releasing energy, water, and minerals through the process of biodegradation and again feeding the system (Fig. 6).

Readers wanting finer definitions of components of primary production allocations may refer to Luysaert et al. (2007): <http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2007.01439.x/abstract>. The presented data allow a synthesis at the scale of humus systems, following the spirit announced in the introduction (Section 1). Litter is attacked by microorganisms and pedofauna. The more important decomposers are fungi and bacteria (enzymatic activities). These living organisms have an "r" strategy (high reproductive rate) and are very sensitive to environmental factors that influence their development on Earth: temperature, water, nutrients such as C, N, P, as well as basic metal elements necessary for composing indispensable functional enzymes. Everything that can limit the availability of these essential factors and elements necessary for the development/growth of fungi and bacteria inevitably influences the process of litter biodegradation (Berg et al., 1997, 2000, 2001, 2007; Wardle, 2005; Standing et al., 2005; Bastow, 2012a; Ascher et al., 2012; Sverdrup et al., 2014a, b). However, even if fungi and bacteria are mainly responsible for the mineralization of litter, they are far from being the sole agents of its transformation and fragmentation. Soil saprophagous animals ingest litter and transform it into faecal material, both organic and organic-mineral. Thus, even if their direct impact on weight loss is

far less than that of the microflora, their impact on litter disappearance from the ground surface and incorporation into underlying mineral matter is of paramount importance. Both microbial and faunal litter-processing chains are tightly interconnected and benefit from each other (Ponge, 2013). In Figure 7 we present the annual bi-phasic cycle of litter (nOL horizon) in a temperate broadleaved forest.

Following the main environmental factors, in terrestrial condition (aerated soils), five different main strategies of litter transformation are possible (for detailed description of humus horizons and classification refer to Humusica 1, articles 4 and 5):

#### 4.2.1. Mull humus system strategy (Fig. 8)

- ecological conditions: temperate climate and/or base-rich siliceous or calcareous parent material and/or easily biodegradable litter (C/N < 30) and/or no major environmental constraint;
- dominant actors of biodegradation: anecic and large endogeic earthworms, fungi and bacteria;
- actors' action: fast biodegradation and consequent disappearance of litter from the topsoil ( $\leq 3$  years), carbon mainly stocked in the A horizon;
- $\text{pH}_{\text{water}}$  of the A horizon: generally  $\geq 5$ ;
- diagnostic characters (morpho-functional result of specific biological activities): OH never present, A biomacro or biomeso, very sharp transition ( $< 3$  mm) between organic and organic-mineral horizons.

#### 4.2.2. Moder humus system strategy (Fig. 9)

- ecological conditions: mild to moderately cold climate, generally on base-poor substrate;
- dominant actors of biodegradation: arthropods, epigeic earthworms and enchytraeids; bacteria and fungi;
- actors' action: slow biodegradation (2–7 years), carbon stocked in both organic and organic-mineral horizons;
- $\text{pH}_{\text{water}}$  of the A horizon: generally  $< 5$ ;
- diagnostic characters: OH always present, nozOF never present, A biomicro, massive or single grain, no sharp transition ( $\geq 5$  mm) between organic and organic-mineral horizons.

#### 4.2.3. Amphi humus system strategy (Fig. 9)

- ecological conditions: highly contrasting climate conditions with prolonged periods of biological inactivity (dry summer or cold winter) alternating with favourable (mild) seasons, generally on base-rich carbonated or siliceous substrate; an artificial

substitution of vegetation, with a consequent shift from nutrient rich and palatable broad-leaf litter ( $C/N < 20$ ) to recalcitrant coniferous litter ( $C/N > 40$ ), leads generally to a transformation of the original Mull into Amphi. This dynamic process can also generate a Moder on base-poor substrate or in cold climate conditions.

- dominant actors of biodegradation: endogeic and anecic earthworms in the organic-mineral horizon; arthropods, enchytraeids and epigeic earthworms in the organic horizons; fungi;
- actors' action: slow biodegradation (2–7 years), high carbon content in both organic and organic-mineral horizons;
- $pH_{\text{water}}$  of the A horizon: generally  $\geq 5$ ;
- diagnostic characters (morpho-functional result of specific biological activities): OH always present, nozOF never present, thickness of A horizon  $\geq \frac{1}{2}$  OH; A biomacro and sharp transition ( $< 5$  mm) between organic and organic-mineral horizons, or A biomeso (biomicro possible, but only in addition to A biomeso) and no sharp transition ( $\geq 5$  mm) between organic and organic-mineral horizons.

#### 4.2.4. Mor humus system strategy (Fig. 10)

- ecological conditions: cold climate, and/or base-poor siliceous substrate, poorly degradable litter (rich in resins, phenolics, thick cuticle,  $C/N > 40$ );
- dominant actors of biodegradation: fungi (mostly mycorrhizal, review in Ponge, 2003, 2013) and other non-faunal processes;
- actors' action: very slow biodegradation ( $> 7$  years), highest carbon content in organic horizons;
- $pH_{\text{water}}$  of E or AE or A horizon:  $< 4.5$ ;
- diagnostic characters (morpho-functional result of specific biological activities): nozOF (always present); nozOH (not always present and often difficult to recognize especially in wet conditions), E horizon or A massive or single grain, very sharp transition ( $< 3$  mm) between organic and organic-mineral (or mineral) horizons.

#### 4.2.5. Tangel humus system strategy (Fig. 10)

- ecological conditions: mountain climate (subalpine or upper montane belts) on carbonated (calcareous and/or dolomitic) or mixt dominated by carbonated substrates;
- dominant actors of biodegradation: epigeic earthworms, enchytraeids, and arthropods within organic horizons; fungi;
- - actors' action: very slow biodegradation ( $> 7$  years), carbon stocked
- actors' action: very slow biodegradation ( $> 7$  years), carbon stocked mainly in organic horizons;
- $pH_{\text{water}}$  of the A horizon  $\geq 5$ ;

- diagnostic characters (morpho-functional characters, due to specific biological activities): nozOF never present but thick organic horizons [(zoOF + OH) > 10 cm]; if present, thickness of A horizon < ½ OH; if present, A biomeso or A massive.

#### 4.3. Which are the main factors arresting litter biodegradation?

This question cannot be answered without considering the milestone concept of “limit value”.

##### 4.3.1. The concept of limit value

Litter biodegradation is a biological process, depending on climate, substrate chemistry, and litter quality. Following biological laws, the process probably shows a logistic curve, beginning at a low rate, which increases when climate or litter chemical composition becomes progressively more favourable, increasing exponentially at optimum climate and/or chemical composition to decrease when conditions become unfavourable, for example due to limiting factors, such as sub-zero temperatures, summer drought, limited availability to nutrients, or when all litter has been decomposed. The thick red descending line in Figure 7 represents this process. There may be a biodegradation even in winter (illustrated by the feeble slope of the top part of the thick red line), after which the process rate increases again with favourable conditions. In the figure this is represented as a commonly observed case of resource, when all available litter disappears before climate (or chemical) conditions arrest the natural biodegradation process. The rate of the process changes when climate conditions, or litter quality, e.g., nutrient availability, become limiting, as seen in Figures 8 and 9. The process may last over several years and the annual cycle thus is repeated for several years. The curve of litter accumulation/disappearance looks like a saw-tooth line (Fig. 8).

The rate of the process changes and decreases when litter quality (nutrient availability) or climate conditions becomes limiting (concept of limiting value expressed in Figure 11). Several successive years of the biodegradation process are represented in Figures 9 and 10 and correspond to the genesis of Amphi or Moder and Tangel or Mor humus systems. In these cases, not all the yearly produced litter is consumed by biodegradation and we observe an accumulation of undecomposed litter (which stays on the soil even partially transformed: fragmented =OF horizon; humified = OH horizon). The system seems to produce more litter than it is able to degrade or “digest”. In Figures 9 and 10 we represented both, a theoretical accumulation, hypothesizing a yearly biodegradation of half the new litter, and the observed accumulation, which continues until a plateau is reached. The harsher are the conditions for decomposition, the higher is the thickness of the organic horizons of the humipedon and the further in time the plateau is reached. At the plateau level, the system degrades an amount of litter and organic matter which corresponds to the amount of new litter produced and the organic layer covering the organic-mineral and mineral soil maintains a constant thickness (stable fraction). This phenomenon is described in Berg and McLaugherty (2008, 2014) with the use of a function (Fig. 11). The growth of the stable fraction may be followed by summing the stable residues (100–limit value) of each year’s litter fall. The simple formula  $\Sigma(100-$

limit value) over  $n$  years may give the accumulation. Such a calculation has been made for close to 3000 years ( $n = 2984$ ) (Berg et al., 2001; Berg and Dise, 2004) for a boreal Mor system.

When the system reaches the plateau, the thickness of the organic horizons may remain stable even if new litter continues to fall onto the soil. This means that at this point, all the litter input is biodegraded and organic matter disappears not at the top but within the mass or at the bottom of the organic horizons. We think that at the plateau level, litter could have formed an enough temperature-insulating blanket that allows pedofauna and microorganisms activities for a litter biodegradation that compensates the annual addition of litter. We may point out that such a steady state has never been proven and with a humipedon still growing well after 2500 years (Berg et al., 2001), we may conclude that we deal with a concept which in practice is theoretical. Further, the equilibrium plateau may be different among ecosystems and vary with the litter components and climate.

The limit-value curve resembles the top lines that smooth out the toothed trend represented in Figures 9 and 10. We can say that a limit value of 100% is raised in Figures 7 and 8. In Figures 9 and 10 the limit value is less than 100% and we observe an accumulation of litter year by year until raising a threshold value. In Figures 8–10 are also represented the results of litter transformation, i.e. different types of underlying A, OF, and OH (zoogenic or not) horizons. The evolution of the humipedon is arrested when the humus system has reached a point of dynamic equilibrium (a plateau). However, such equilibrium has not yet been identified and may vary with dominant species and ecosystems. Above this plateau level there is the same annual amount of mineralised carbon (as  $\text{CO}_2$ ) as is fuelled to the soil in the form of litter.

Although a plateau has been theorized, we must state that at present we know just part of what regulates the growth rate until the plateau. It has been proven (many works collected and explained in Berg and McLaugherty, 2014) that the limit value depends on litter quality and particularly its content in mineral elements and contents of lignin, nitrogen, and manganese.

The accumulation rate depends on (i) the amount of annual litter fall, which is related to climate, (ii) the size of the residual fraction estimated by (100-limit value), which determines the fraction of the annual litter fall that is accumulated. These aspects will be illustrated here with the help of selected data and figures extracted from Berg and McLaugherty (2014).

#### *4.3.2. Litter quality and its content of mineral elements*

Except for Mn, coniferous needle litter is generally poorer in mineral nutrients than the litter of broadleaf trees (e.g., Table 1). Coniferous needle litter is richer in cellulose and its woody litter is richer in lignin (Table 2); deciduous leaf litter is richer in water-soluble compounds, and its woody litter is richer in cellulose and pectin (component of primary cell walls).

The litter content in mineral elements mainly increases during the process of biodegradation. The litter organic matter is decomposed in a process known as “mineralization”. This process takes place in the soil (physical and biological attacks) and within living bodies of animals. Mineralization liberates mineral elements into the soil, fine colloidal organic particles and soluble organic compounds that can be leached out of the litter by percolating water. Further, delivered energy and

minerals are invested in new living bodies and droppings, which in turn may be consumed by other consumers. “Humification” is the process of storage in the soil of “organic matter other than fresh litter,” meaning organic (living and dead) and mineral products that remain in the soil and result from the two abovementioned processes of litter degradation: 1) physical and chemical mineralization by living organisms, whose bodies remain in the soil and 2) transformation inside living bodies and production of biomass and faeces, which may be consumed several times by other soil organisms.

Humification may also result from the abiotic transformation of plant residues (mainly wood and cuticles, but also tannins), which slowly evolve by incorporating oxygen (incomplete oxidation) and nitrogen (proteins, amino acids) without undergoing mineralization: lignin and polyphenol theories (Stevenson, 1994).

The process of mineralisation has been schematized in Figure 12. Among the different compounds, gravimetric lignin shows a particular trend: its concentration increases and so does the concentration of new compounds due to incorporation of N in litter aromatic structures.

A process in which new stable compounds are formed from lignin and N has been described producing an increased concentration of these stable compounds. In the forest floor the concentrations of such stable compounds increase as does the amount due to the annual addition of a new undecomposed mass of lignin and ‘reactive’ N. In each given environment, an equilibrium point will be reached where all components stabilize. This point corresponds to the stable formation of a humus system, with its specific horizons and living actors of biodegradation.

The humification process is much more complex and differs according to the humus system, each system being adapted to particular environmental conditions. The aim of the present guide is mainly to illustrate how to individuate and describe all these different humus systems. Plotting annual litter mass loss (= % of biodegraded and disappeared litter) versus litter lignin concentration at the start of each year Berg and McClaugherty (2008, 2014) discovered a strange “point of convergence” (Fig. 13): concentration of gravimetric lignin increases in the first years until a concentration of about  $500 \text{ mg g}^{-1}$ , which remains constant for the following years. The process is correlated to the actual evapotranspiration of the site in which the process occurs. High evapotranspiration also means high potential production of photosynthetic biomass. When the system is highly productive, the biological process of decomposition is also very active and the slope of the line of regression of litter mass loss versus lignin concentration is steep. At the point of convergence, the litter mass-loss rate is the same irrespective of the site temperature, suggesting that litter chemistry may ensure a regulatory function.

Expressing a well shared opinion among soil scientists, Davidson and Janssens (2006) resumed the question of the climatic influence on SOM in few phrases:

“If carbon stored belowground is transferred to the atmosphere by a warming-induced acceleration of its decomposition, a positive feedback to climate change would occur. Conversely, if increases of plant-derived carbon inputs to soils exceed increases in decomposition, the feedback would be negative.” The problem seemed relatively simple to solve, even if “several environmental constraints obscure the intrinsic temperature sensitivity of substrate decomposition, causing lower observed ‘apparent’ temperature sensitivity, and these constraints may, themselves, be sensitive to climate”.

Few years later, Schmidt et al. (2011) were still trying to clear the relationship between intrinsic and apparent temperature sensitivity of the SOM, concluding that “experimental advances have demonstrated that molecular structure alone does not control SOM stability and that environmental and biological controls predominate”.

Recently, Lehmann and Kleber (2015) supported a theory proposed by Stevenson (1985, 1994) and largely proved by Piccolo and Mbagwu (1999), Piccolo (2001), Canellas et al. (2010) and Nebbioso and Piccolo (2012), for which SOM is a continuum of progressively decomposing organic compounds. All these authors sustain that there are no large molecular-size ‘humic substances’, but aggregates of small molecules which persistence in the soil depends from nature of SOM, ecological/climatic frame and type of soil management.

We strongly believe the same and would say in addition that the biological control of the quantity and quality of SOM is so strong that a living soil-system may act as buffer for SOM and guarantee a relative independence from climatic conditions.

## **5. Humus systems as an eco-device**

Why are we interested in humus forms? Why are we trying to classify them? Why are we investigating processes of biodegradation? All these questions go back to the intuitive feeling that humus is useful for human beings. It might be useful as a source of ‘free’ nutrients needed for crop growth or timber production. It might provide a structure protecting soils from erosion. It might be an interesting sink for carbon sequestration in respect to the problem of climate warming. Also, the humus system can be considered as a habitat for an abundant and diversified soil life highly contributing to global biodiversity. At the same time the heterogeneity of the soil might result in a broad niche differentiation providing a competition-free environment and consequently a blue print for plant biodiversity. Without being exhaustive it will be clear that the humus system has a manifold purpose character for human use. Depending on one’s interest the humus system will be used in different ways. In this context, the humus system can be considered as a tool, or better a device and still better an eco-device, the functional outputs (in terms of utility for humans) of which should be in line with the user interest. In other words, there are many ways to investigate the humus system. Trying to provide a common ground for these diverging interests, the eco-device concept will be introduced as a metaphor.

Analogous to an electric device an eco-device can only produce utility if connected to a potential field between a source and a sink. In this way house-keeping devices are connected to an electricity field and eco-devices to an ecological field. It will be clear that solar energy will be the main driving force for this ecological field. Other ecological fields may also occur, such as hydrological gradients between recharge and discharge areas.

It is the internal structure of the eco-device that determines its usefulness. An electric razor has quite another structure than a radio tuner although both use a difference of 230 V out of the same potential field. The internal structure of an eco-device is a function of local site factors (texture, pH, mineral composition, etc.), vegetation, and soil organisms. The main terrestrial structures are



known as Mor, Mull, Moder, Amphi, and Tangel. Each of these structures provides a distinct utility of the humus system: for example: a Mor is better equipped for carbon sequestration in cold climate than a Mull; but a Mull is better equipped in providing nutrients for plant or crop in temperate climate; an Amphi might generate favourable habitats for soil biodiversity and niche differentiation, in more contrasted climate conditions...

The eco-device is founded on four main ecological functions: supply and resistance at the input side and disposal (release) and retention at the output side (Fig. 14a). The eco-device makes use of these four functions to control its functionality for human beings or more specifically the operational environment for individual organisms, communities, habitats, ecosystems, landscapes and finally our Earth. Also, the eco-device can be considered as a fractal structure: at each lower level the eco-device is embedded in a higher level with fundamentally the same fractal structure (Fig. 14b). Conservation of energy is actually ensured by the chain of eco-devices. Disposal of energy from eco-device 1 will be a source (supply) of energy for eco-device 2. This approach even fits to the general ecosystem theory of Jenny (1941) in which the humus system clearly shows its dependent character (Fig. 14b).

By its four main functions the eco-device is capable to maintain boundary conditions between maximally acceptable and minimally necessary energy and/or matter. Shortages can be prevented by supply or retention. Disposal or resistance protect against over-feeding. These functions can be applied to the humus system as well in a way that is preferred by the user, be it a human being, a soil organism or any plant species.

Some examples: a Mor humus system clearly displays its retention function for climate control by carbon sequestration, but also for hydrological control by its water holding capacity or nutrient retention by its low mineralisation rate. A Mull humus system on the other side has an excellent supply function for nutrients, which might be in favour of the activity of soil organisms and plant growth. In Agro Mull on arable land this function is overactive and disposal by leakage is necessary to prevent eutrophication. Mull also generates high nutrient cycling rates and consequently has an explicit disposal function for nutrient (N, P, K, Ca) release but a bad behaviour with respect to climate control. Even in most Dutch natural fen meadows mowing and harvesting without manuring is a human measure to prevent an excess of nitrogen by atmospheric deposition. Actually, this management replaces the ecosystem disposal function. Without human aid these meadows should suffer from over-grazing, i.e. eutrophication. Resistance might finally play a role in the protection of seed banks, roots, soil organisms etc. by a thick OL or OF horizon acting as an isolator during cold or dry periods. Mull has a high resistance against the loss of nutrients by forest fire, as the main source of nutrients is in the endorganic part that is protected against fire. The same holds true most probably and for the same reasons for protection against climate warming. In contrast Mor has hardly any resistance against loss of nutrients in case of forest fires, as all nutrients are stocked in the ectorganic layer. Finally, many other examples probably can be found to illustrate these distinct functions.

Humus systems can also be seen as devices that convert energy into information. It is challenging to discuss the applicability of thermodynamic laws to eco-devices in general and to humus systems in particular. According to the First Law of thermodynamics energy cannot be lost and the Second Law states that open systems strive to the lowest energy levels and maximum

entropy, corresponding to disorder and unpredictability (uncertainty sensu Heisenberg). In other words, loss of energy coincides with increasing disorder. Order can only be achieved by input and storage of energy. According to thermodynamic laws the storage of energy in humus systems (by carbon sequestration) should therefore inevitably lead to decreasing entropy and subsequently to increasing organizational levels. Horizon differentiation mirrors this increasing degree of organization in humus systems. These highly ordered structures are reliable and predictable environments for organisms, including man, using any product of the humus system. By niche differentiation the competitive exclusion of organisms in their competition for nutrient resources is prevented. Many species will find a niche, which is a favourable condition for a high biodiversity (Fig. 15).

However, the application of this law to the soil is not so simple. Following it, the more horizons there are, the more the living soil is organized, and the more it allows species to coexist. However, the higher level of biodiversity is actually achieved by Mull, not Moder or Mor (Ponge, 2003, 2013). Here the notion of stability takes place and should prevail when speaking about biodiversity. It is generally acknowledged that biodiversity first increases and then decreases with the level of disturbance according to a hump-shaped curve (Ponge, 2013). As most real objects, humus systems are the result of trade-offs (compromises) between independent, opposed forces (the so-called “laws”, which are true only in theory, within a given set of conditions, rarely fulfilled in the real world, to the exception of man-made “devices”). The apparent “disorder” visible in Mull is in fact the result of many disturbances such as temperature and moisture “highs” and “lows”, activities of burrowing animals, root growth pulses, etc., which counteract competitive exclusion (only demonstrated in artificial systems) and favour the coexistence of many species and functions. Despite and due to its “disorder” Mull maximizes biodiversity and associated functions such as high productivity (Ponge, 2003). Energy is dissipated, according to the Second Law of thermodynamics, but this energy is not lost to the grassland or forest ecosystem, being rather circulated between plants, microbes, and animals: energy (and in the same way nutrients) is conserved, but in a state of permanent, or seasonal change. This is the force, but also the weakness of Mull, which is sensitive to any decrease in its integrity, such as when land-use changes, or when key organisms are killed or replaced by man (e.g., conifer plantation, hunting). Mull thus violates both the Second Law of thermodynamics and Darwin’s rule of species coexistence, the famous “struggle for life”. On the opposite side, Mor is strongly “organized” in the form of a variety of horizons, each inhabited by a specific assemblage of organisms, but Mor is much poorer than Mull from the point of view of biodiversity. This is not the result of competition, but – on the contrary – an effect of environmental factors which are detrimental to most organisms, namely harsh conditions: cold, acidity, sometimes pollution as in heavy metal-polluted sites (Gillet and Ponge, 2002). The Mor strategy is the best compromise between the need to ensure the sustainability of the ecosystem and an otherwise unfavourable context. In Mor the conservation of nutrients and energy is ensured by the soil, not by the vegetation. Moder is an intermediate between these two opposite strategies, allowing some level of nutrient and energy circulation between soil and vegetation, although at a lower level than Mull (Ponge, 2013). However, the all-round champion of compromises is Amphi. This humus system combines the advantages of Mull and Moder, by offering conditions of life for all types of organisms, while avoiding the main weakness of Mull, its lack of protection against climate hazards. By its dual nature, Amphi is able to sustain ecosystems through ecological crises such as present-day global warming and associated threats such as increased aridity (Ponge et al., 2011).

The organizational level of Agro Mull systems (see Humusica 2, article 15 for a description of these anthropogenic humus systems) is low and close to a chaotic state. Homogenized “chaotic” humus profiles are illustrative for low organizational levels and poor biodiversity. The homogenization of the soil is obtained by the application of mechanical agricultural machineries (e.g., plows, rotating blades) which mix the soil but cannot mimic organic-mineral and microbe-rich earthworm aggregates. By lack of organized (humus) structures the environment of Agro Mull is unpredictable and organisms have to compete for nutrient sources instead of relying on niche differentiation or repeated disturbances. Survival of the strongest is the adagio and monoculture the result. The most extreme example is an Anthropogenic poorly zoogenic massive A horizon (described in Humusica 2, article 15). In this system, a large part of the circulating energy is transferred to crop production, which is exported (thus is lost) at the end of the cycle. Crops have also to compete with weeds, which try to counteract the Second Law and restore a more complex and ordered state. According to thermodynamics energy is needed to reduce entropy and to favour ordered structures like soil structures and more interactive ecosystems. In the same time inputs of energy (e.g., fertilizers, pesticides, tillage) are needed to maintain these poorly ordered and simplified systems, depending on humans for their maintenance. In other words, under temperate climate conditions, allowing a complex organization of the living network, simplified and poorly biodiverse ecosystems such as arable crops are possible only at the cost of a high investment in energy inputs. On the other hand, more ‘natural’ ecosystems such as woodland, heathland or grassland (pastures, conservation grade agricultural crops and hay meadows being good compromises) are organized in order to conserve energy (First Law) but at the same time by converting it into an infinite number of localized structures (minimum level of entropy), rendering the whole compatible with the Second Law (Bormann and Likens, 2012).

## **6. Can temperature influence humus decomposition? Can temperature influence humus/carbon sequestration rate? How?**

### *6.1. Carbon sequestration and decomposition 1*

The title covers part of a complex concept and it may be a good start telling a short story. While telling the story we will focus on three main points, which are connected, namely (i) sequestration of carbon in humus, (ii) steady state for humus, (iii) humus decomposition vs rate-regulating factors.

#### 6.1.1. The story including an overview

We may use – as an example – data from two well-studied ecosystems, one with Scots pine (*Pinus sylvestris*) and one with Norway spruce (*Picea abies*) located in climate gradients ranging from subarctic to temperate sites with a range in mean annual temperature, MAT from  $-1.7$  to  $10 - 11^{\circ}\text{C}$ .

Studying measured data for foliar litter fall we may see that for both Scots pine and Norway spruce there is a higher litter inflow with increasing temperature, and highly significant positive relationships to MAT (Berg and Meentemeyer, 2001; Akselsson et al., 2005). Such relationships are common and in the present case they were found for a region from the Arctic Circle in Scandinavia to NW France, including stands under subarctic, boreal, and temperate climates. Over the gradient litter fall increased exponentially (B. Berg, unpubl.) and by simplifying the relationships we may see that with an increase in temperature of 2°C the foliar litter fall increased by a factor of 3.7 for pine and 2.9 for spruce. In addition – foliar litter fall for Norway spruce was higher than that for Scots pine. A simple conclusion is that the input of organic matter (foliar litter) to the forest floor/humus layer becomes higher with increasing site temperature and may vary with tree species.

Decomposition of foliar litter in a climate gradient – early stage – newly shed litter. The newly shed litter starts decomposing, and for that of Scots pine temperature (MAT) is positively related to mass loss – initially – in the early stage (Berg et al., 1993, 1996; Bradford et al., 2016). For newly-shed Norway spruce litter there was no relationship to MAT or MAP but a positive one to Mn (Berg et al., 2000). Also, for the decomposition study we used the above gradients with a MAT range from -1.7 to 8 °C.

Decomposition of foliar litter – partly and far-decomposed litter (late stage) in a climate gradient. We may see that initially the litter is decomposing at very different rates – related positively to MAT – a very traditional image. Figure 13 gives data for Scots pine litter. As decomposition progresses the decomposition rate decreases. Further – as litter becomes gradually richer in gravimetric lignin (acid unhydrolyzable residue, AUR) the difference in decomposition rates between sites with different MAT/AET becomes smaller – the effect of MAT decreases. Finally, as shown in the red circle (Fig. 13) the lines converge and in the original figure they even cross each other. This means that decomposing litter – once it has reached the far-decomposed state site – mainly is decomposed at the same rate. A consequence and conclusion is that – at that stage – temperature is much less/not important and that above a certain decomposition level MAT does not influence decomposition rate. Rather, some other factor(s) is more important and more limiting (below). A similar conclusion was reached by Marie-Madeleine Coûteaux and her group in Montpellier, using standard wheat straw in a climate gradient ranging from northern Sweden to the Mediterranean region (Dalias et al., 2001).

There has been an attempt to evaluate the effect of MAT vs that of substrate quality – which changes during decomposition – using another approach (Berg et al., 2015). They related four main properties of site and litter, namely site MAT, and litter concentrations of Mn, N, and AUR (gravimetric lignin) to annual mass loss using in all 93 values for annual mass loss. That study was made in a Scots pine climate gradient using local pine litter that was decomposed to at least 30% accumulated mass loss, thus the more readily decomposable matter was decomposed and the litter was in a late stage. There was a clearly significant, negative effect of MAT ( $p = 0.017$ ). That the effect of MAT was negative is in accordance with the studies by Johansson et al. (1995) and Dalias et al. (2001). The more pronounced effects were those of litter chemistry, namely a positive effect of litter Mn concentration ( $p = 0.0046$ ) and negative ones of N and AUR concentrations, both at  $p < 0.0001$ .

Annual mass loss of late-stage litter of Norway spruce was found to be positively related to litter Mn concentration ( $p < 0.001$ ) (Berg et al., 2007), with no relationship to MAT. Also for this litter species the decomposition rate decreases as decomposition proceeds.

We may conclude that the decomposition of a main part of the foliar litter for these two species, namely the far-decomposed or near-humus part is not regulated by temperature, although there may be a possible negative effect. Both Mn and N appear to be dominant regulating factors.

The limit value is a calculated property and gives a stage at which the progressively decreasing decomposition rate has reached the rate zero. That value may be calculated using litter accumulated mass loss (Berg and McClaugherty, 2014). Thus, part of the litter may be considered 'stable' and that residue may be expected to decompose at a very low rate if not at all. We investigated relationships between limit values – for pine species, mainly Scots pine – and potentially regulating factors. Ten factors including climate (MAT, MAP; P= Precipitation) and substrate quality (N, P, K, Ca, Mg, Mn, AUR, and water solubles; AUR = Acid Unhydrolyzable Residue) were related (linear relationships) to limit values and the only significant relationship was that to Mn concentration. Decomposition data from a climate gradient were used but there was no effect of MAT on limit values (Berg et al., 2010). The genus *Pinus* is so far the only genus/species that has been investigated for regulating factors for limit values.

Limit values for different pine species may be related negatively to N and positively to Mn (Berg et al., 1999, 2013; Berg and McClaugherty, 2014). Norway spruce litter has a somewhat larger stable residue (lower limit value) than litter of Scots pine and lodgepole pine litter a smaller (Berg, 2000a, 2000b, 2000c). The stability of this stable residue is uncertain but should vary likely depending on its chemistry.

The slowly degraded (or stable) residue may be expected to degrade so slowly that a net accumulation of stable residues may take place. That such an accumulation takes place is evident as we can observe the formation of humus layers. In fact, such a reconstruction of growth rate has been done using limit values and humus accumulated for close to 3,000 years (Wardle et al., 1997; Berg et al., 2001). By using calculated stable residues, we may quantify the growth rate simply by adding amounts of stable residues based on foliar litter fall.

### 6.1.2. Steady state in humus layers

It is very likely that the concept of 'steady state' is just a theoretical one. So far there appears not to be any proof of the existence of a humus layer that has reached a steady state (Berg and McClaugherty, 2014). Considering the influencing factors on limit values/stable humus as well as the range in values we may expect that even as a theoretical concept 'steady state' would be very different among ecosystems and stands. An often-used argument in favour of a steady state is that an 'infinite growth' is impossible or at least would give absurd values. Still, such an argument may be an exaggeration. However, without drawing any conclusion we may consider (and just accept) the fact that there are organic layers some 100 m deep, today with peat on top and coal/brown coal further down, but we can at least exclude the terms 'absurd' and 'impossible'. With depths of at least 75 to 400 m given and given periods of 'millions of years' we may take an arbitrary value for an

organic layer of 100 m. With a growth rate of 0.1 mm (cf. above) it would take ca. 1 million years for that 100-m-deep layer to be formed. Clymo (1987) has an interesting discussion about peat, peat depth, age and coal formation.

Above we cited a measured growth rate of c. 0.5 mm per year over a recorded period of 3,000 years resulting in an accumulation that reached 1.5 m (Wardle et al., 1997; Berg et al., 2001). Of course, over a period of a few thousand years there may be rather violent changes or variations in climate, which may change the system in which the humus layer grows (Charpentier-Ljunkvist, 2009). A warm and dry period may result in fires and a very wet period may more or less drown the system with growing humus layers and make it anaerobic.

For the forested land of Sweden the measured annual increase ranged from 0.57 (region Low, in the north, subarctic/boreal) to 1.05 mm (region High, in the south, temperate climate) in Berg et al. (2009), which fits well with the recorded growth rate in the accumulated humus.

### *6.1.3. Humus in large-scale field measurements – a synthesis*

We may take a long step to an investigation made on humus growth along Sweden (climate gradient range from  $-1.7$  to  $8^{\circ}\text{C}$ ; Berg et al., 2009). They used about half a million humus-depth values in Mor humus (see Humusica 1, article 5 for a detailed description of this humus system), collected over a 41-year period. Measurements were distributed all over Sweden and could be subdivided into grid plots of  $25 \times 25$  km. The annual measurements started in the 1960, i.e. when wild-fire protection had been well built up.

After a first investigation of the data we divided the grid plots into three climate zones (Berg et al., 2009) based on temperature sum. For each of the grid plots temperature sum was determined, and related to C sequestration rate. The measured humus layer was OF plus OH or the (OF + OH) layer (see Humusica 1, article 4 for details about these humus horizons). We may comment on that this layer would be made up of stable litter residues and judging from data (cf. Figure 13 and results from a limit-value study: Berg et al., 2010) its decomposition would not be sensitive to temperature.

First, in all the three climate zones there was an increase in humus depth (and C sequestration) with time. Initially there was a difference between them, with the thickest layers in the south (region High) and the thinnest ones in the north (region Low). The long-term increase was shown to be highest in the south (region High) and lowest in the north (region Low) (Berg et al., 2009). They also found a positive correlation between temperature sum and the increase rate in humus layers ( $R^2 = 0.29$ ;  $n = 548$ ;  $p < 0.0001$ ).

These data may allow us to conclude that the net increase in humus layers is positively related to the site temperature and its effect on the amount of litter fall. Of course, such a conclusion is based on the existence of a relatively stable residue.

Berg et al. (2009) also found a significant difference in increase rate between pine- and spruce-dominated plots with a higher sequestration rate for pine ( $p < 0.0001$ ), in spite of a higher foliar litter fall for spruce. Further, with a higher inflow of litter to spruce stands and a lower sequestration in organic layers we may conclude that there are different humus build-up rates

among species and that litter chemistry may be a dominant factor as there are really high differences in chemistry between pine and spruce litter, e.g. in Mn concentration.

## 6.2. Carbon sequestration and decomposition 2

Main points of the preceding story:

- 1) we can apply a theoretical concept of “steady state”, which could be very different among ecosystems and stands. It corresponds to a concept of “humus system in equilibrium with its environment”, or even (which is easier to be discussed) to a Not Influenced by Temperature humus (NIT-humus);
- 2) there is a positive correlation between temperature sum and increase rate in humus layers (OF + OH of a Mor humus system);
- 3) there is a significant difference in increase rate between pine- and spruce-dominated plots with a higher sequestration rate for pine;
- 4) this significant difference in increase rate between pine- and spruce-dominated plots occurs in spite of a higher foliar litter fall for spruce.

### 6.2.1. What is a not-influenced-by-temperature humus (NIT-humus)?

Studying soil humic compounds and microbial communities in Alpine spruce forests, Carletti et al. (2009) found a significantly higher mean organic carbon content in north-facing acid parent material sites compared to other sites, even if a south-facing basic substrate site made exception. The concentration of humic substances with high molecular weight (> 100 kDa) was higher in the A horizons of north-facing acid sites compared to the corresponding south-facing one; as a contrast, small-size humic fractions (< 10 kDa) were more abundant in south-facing sites. These authors measured average microbial biomass will almost double the carbon/nitrogen ratios in acid soils compared to basic soils. Higher ratios can be associated with higher presence of fungal mycelia (Pennanen et al., 1999), which may behave as the main decomposers in acid soils (Verburg et al., 1999). Concerning the bacterial communities, it appears that they are foremost shaped by the geological substrate (calcareous opposed to acid parent materials), secondly by mountain slope orientation, (temperature), and thirdly by forest stage (soil nutrients availability). Finally, less bacterial taxa, specialized in more distinct communities, were found in north-facing acid soils; in opposition, more bacterial taxa, more uniform and universal bacterial communities were found in warmer climatic conditions on base-richer soils.

Ascher et al. (2012) investigated comparable Alpine forest ecosystems and furnished additional information. In fact, in Italian spruce forests with equivalent parent material, age, topography, and vegetation, these authors compared south and north exposures at different altitudes. They stated that the thickness of the organic layer and the acidification of the subjacent mineral horizon increase under cooler conditions (north-exposure; higher altitude = higher thickness of OL + OF + OH horizons); the microbial biomass is higher in the cooler soils, where specialized

Gram-negative bacteria can develop on a larger amount of less decomposed organic matter. However, the concentrations of these bacteria and even soil faunal activity, especially that of micro-annelids, are higher at lower altitude or at south exposure compared to north-facing sites (which means a higher biological activity). As a consequence, the humipedon horizons were different in thickness and composition and the authors concluded that humus forms are good indicators for soil biota (both micro- and macro-biology).

Following the same line of reasoning, we may compare the well-known (in *Humusica* 1, article 4, figures and detailed description of each horizon) standard humus genesis in three different climatic situations.

Standard steps of humipedon genesis:

1. OL (fallen litter) may become an OF horizon (fragmented litter), then
2. OF may become an OH horizon (humified litter) and finally
3. OH may become an A horizon (organic-mineral aggregates).

The process is cyclic: the soil carbon is transferred to the air by respiration/mineralisation from shed litter (even dead organisms), the air carbon is newly integrated in living organisms (plants, animals, and microorganisms consuming plants in a pyramidal structure), carbon in living organisms returns to the soil after organism's death and goes through another mineralisation step (short overview in Sections 2–4 of this article, or in specialized articles of *Humusica* 3; more detailed information in Hopkins and Gregorich (2005), O'Donnell et al. (2005), Standing et al. (2005), Wardle (2005), Schmidt et al. (2011), Bastow (2012a), Berg (2012), Maillard et al. (2015). We do not consider CaCO<sub>3</sub> formation/alteration and the related water cycle, a longer and very important process that has been let aside (nevertheless crucial: Baudin et al., 2007), accepting as an approximation for the present discussion that it does not have an influence.

However, simplifying “not too much” and considering three types of climatic conditions, few common plant and animal groups, which are easy to recognize (see *Humusica* 1, article 8), we can write that:

*In very cold zones* (e.g., high latitudes areas, taiga latitudes, high altitude mountains, zones characterized by very harsh conditions for soil organisms) we generally observe the presence of organic horizons and absence of A organic-mineral horizons (*Humusica* 1, article 5 for detailed description of Mor humus systems). We call these humipedons Mor systems, i.e. a relatively thick horizon (OL+ OF +OH) directly lying on mineral substrates. In these cases, NIT-humus corresponds to still not decomposed organic residues (needle and leaf litter and other organic bodies). In this type of systems, we do not find any anecic or endogeic earthworms mixing organic and mineral matter in large casts. In extreme conditions, very few or no soil animals can survive. Litter stays as litter, slowly becoming OF horizon and eventually breaking down like an inert substrate. Accumulation is stopped by fungi, which maintain a balance between organic matter inflow (litter fall) and outcome (litter biodegradation), the “plateau” of Figures 10–12. Fungi mostly act at the level of OL and OF horizons (OH horizon made of animal droppings may be present but generated in warmer conditions) and are able to attack even coniferous litter, very rich in lignin. The process depends on the succession of wet/dry periods, some years being favourable to the formation of a high numbers of fungal



carpophores, other years/periods being less favourable, in a cyclic casual frequency. In the long run fungi are able to stop the increase in thickness of organic horizons. Fire may also play a great role, freeing in a short time a considerable amount of carbon, mineralizing the soil organic layers of a forest in a few days ([http://www.nytimes.com/2016/05/11/science/global-warming-cited-as-wildfires-increase-in-fragile-boreal-forest.html?\\_r=0](http://www.nytimes.com/2016/05/11/science/global-warming-cited-as-wildfires-increase-in-fragile-boreal-forest.html?_r=0)). The canopy may also be opened during processes of natural/artificial regeneration of these forests, when old trees fall onto the soil or are harvested and sunlight, warming the soil, activates the process of biological decomposition involving cyclic fauna migrations and sylvogenesis (examples in Bernier and Ponge, 1994).

*In temperate zones* (e.g., European plains, areas with relatively high air temperature and no water or mineral elements constraints) OL horizons directly become A horizons, setting a Mull system. This system consists essentially in a machinery of earthworms consuming the leaf litter (broadleaf plants dominate in this climatic zone, see Humusica 1, article 5 for details about Mull humus systems). Leaf litter is transformed and transferred into the soil as organic-mineral casts. In this case, NIT-humus corresponds to “earthworm casts”. In them, organic matter is linked with mineral clay and bound to not very accessible places (see Humusica 1, article 8 for details). Roots cannot directly consume this organic matter, but bacteria and fungi must release it first (see Humusica 2, article 19; Schmidt et al., 2011; Blouin et al., 2013; Maillard et al., 2015). It seems that plants need to activate these microorganisms (simply by feeding them), which then can develop and consume this humus. In a second step these microorganisms would die and free the consumed organic matter in the soil in the form of dead microorganisms, when their protective constitutive membranes break and free their cytoplasm. Mostly at this secondary stage, plants and other macro-organisms can use this organic matter, previously stored by large earthworms in casts (examples in Janzen, 1980; Bastow, 2012a, b; Berg, 2012; Blouin et al., 2005, 2013). At this stage, a “plateau” (= equilibrium between input and output of carbon/organic matter) is dependent on: 1) input: living earthworms feeding on leaf litter and restoring the soil with their casts; 2) output: roots, microorganisms activated by plants pinching organic matter from earthworm casts, soil biodegradation and respiration.

*Between temperate and very cold climate zones*, in forests dominated by conifers or mixed broadleaved trees, we may find high numbers of small animals feeding on litter, animals of a size that allows them to go even inside pine or spruce needles, feeding on the tissues around the xylem of these organs (details in Humusica 1, article 5 for Moder and Amphi humus systems and Humusica 1, article 8 for biological considerations). In the nlitter but on the outside of the needles, we may find other animals like collembolans, enchytraeids, and insect larvae in thousands per square meter. In this case, the minute excrements of these animals accumulate under the fresh litter horizon (= OL) and form OF and OH horizons, which may rise to even more than 10 cm in thickness. Biologically formed, OF and OH horizons disappear under biological control, the whole system finding an equilibrium as a result of different processes:

1. Biodegradation by fungi and bacteria as well as by specific groups of arthropods and enchytraeids which intervene and biodegrade OL into OF and OH horizons. Finally, a Moder system substitutes the Mor humus system described for temperate to very cold conditions;
2. In a Moder system, the NIT-humus corresponds to a (OF + OH) layer, i.e. organic residues and excrements of small arthropods and potworms;

3. Formation of (OF + OH) horizons: activity of animals and deposition of droppings;
4. Disappearance of (OF + OH): biodegradation and respiration; soil animal mortality and mineralization; nutrients leaching; root uptake of nutrients and organic molecules;
5. When climatic and underground conditions allow earthworms to enter the system (they arrive when canopy is opened, when old trees die and fall, for instance), earthworms feed on and integrate the organic horizons in underlying organic-mineral A horizons. In this case, Amphi system substitutes potential Mor or Moder systems;
6. In the process of formation of this dynamic Amphi system, the former NIT-humus (OF + OH) becomes another bipartite NIT-humus (OH + A). The equilibrium is now due to droppings of arthropods and enchytraeids (forming organic OH) and casts of large earthworms (generating organic-mineral A) depending from animals evolving in two different related but independent niches and habitats;
7. In Amphi, NIT-humus shows a more dynamic and plastic reaction to climatic conditions. Amphi is a system able to glide from temperate zones to very cold zones in response to climatic variations.

The Amphi humus system is potentially a more adaptable humipedon and may become more common on a planet under the influence of a forecasted warmer and more variable and contrasted climate (Ponge et al., 2014). Future climate/carbon-cycle feedbacks may depend more strongly on changes in the hydrological cycle than is expected at present (Carvalhais et al., 2014).

*6.2.2. Why is there a positive correlation between temperature sum and increase rate in humus layers (OF +OH) of a Mor humus system?*

Because there is also a positive relationship between temperature sum and litter production, this last related to the net primary production. And in case of a Mor humus system, where litter biodegradation is slow and strongly limited by climatic conditions, it is possible that the process of litter production (photosynthesis and needle fall) might be faster than the one of litter mineralization and disappearance (biodegradation at soil level, under an evergreen coniferous cover).

*6.2.3. Why is there a significant difference in increase rate between pine and spruce-dominated plots with a higher sequestration rate for pine?*

Because Norway spruce litter is chemically different from that of Scots pine. In Table 1, Norway spruce litter shows a higher Ca mineral content. This probably affects biological decomposition, rising the pH and opening the door to a faster Moder “device” under spruce.

*6.2.4. Why this significant difference in increase rate between pine- and spruce-dominated plots occurs despite the higher foliar litter fall for spruce?*

Norway spruce litter is faster mineralised than that of the Scots pine. We assume a difference in humus systems and a slipping towards Moder conditions in case of Norway spruce litter. Moder being a more active humus system, the transfer of SOM from superficial organic to deeper organic-mineral horizons is possible thanks to the intervention of arthropods and enchytraeids and may explain the measured difference in organic horizon thickness between pine (Mor) and spruce (Moder) sites. A more accurate classification of the topsoil is indeed necessary for verifying this hypothesis.

### *6.3. A long-term perspective*

Production and accumulation should be larger than biodegradation (mineralization), as biodegradation is a secondary process and even may be halted before the substrate (litter) is decomposed. In natural populations, genetic variation may generate species progressively more adapted to each other and thus able to progressively increase the system's capacity to return organic matter. In fact, the natural evolution that characterizes our planet has been recorded as a non-stop process of increasing biodiversity, punctuated by five mass extinctions.

The expansion of "functional-organized-biomass" (as regards e.g., habitats, species, biodiversity) needs energy – sun radiation. The life cycle of the sun is well-known (<http://www.universetoday.com/18847/life-of-the-sun/>) and we know that the pressure of the star core rises and the conversion of hydrogen into helium increases sun luminosity by 1% every 100 million years resulting in a constant growth in radiant energy arriving on Earth. The long-term trend over the period of the last 100 million years is a striking long-term increase in biodiversity ([https://commons.wikimedia.org/wiki/File:Phanerozoic\\_Biodiversity-2.png](https://commons.wikimedia.org/wiki/File:Phanerozoic_Biodiversity-2.png)), with a striking increase from the late Mesozoic until today corresponding to the appearance of the flowering plants, which boosted the process.

An era ago or even more, a remarkable difference in the potential structure of a biological complex might have found its source in new soils, related to flowering plants. Receiving more organic matter (litter) than necessary for entertaining the ecosystems, these soils got progressively richer in organic matter. The finalization of the use of this secondary source of energy – the genesis of new humus systems – allowed the ecosystems to increase their mass and biodiversity. This hypothesis could explain why even today in a climatically homogeneous region we can observe the genesis of successions over time from pioneer young ecosystems with thin soil to old forest ecosystems with deeper soils. More precisely, the part of the soil interesting for this process may be the NIT-humus (described above; humus, the degradation of which is not influenced by temperature). NIT-humus, naturally, seems always to be induced to grow, fast in temperate regions and more slowly under harsher climatic conditions. Soils submitted to traditional agriculture have lost 50 to 75% of their historical pool of organic matter in less than a century (Lal, 2007; Chan, 2008; Li et al., 2013; Schwartz, 2014). To stop this destructive process would be in negative contrast to this reported long-term trend. With the content of Humusica we would like to convince people to take reason and inverse the course, restoring organic matter in agricultural soils and re-establishing an equilibrium with respect for the dynamic process revealed in natural soils. A model of slow, never-stopping

accumulation of NIT-humus may even be accredited, and be a source for a never-ending diversification of a living.... Gaia.

## References

- Akselsson, C., Berg, B., Meentemeyer, V., Westling, O., 2005. Carbon sequestration rates in organic layers of boreal and temperate forest soils: Sweden as a case study. *Global Ecol. Biogeogr.* 14, 77–84.
- Anderson, A.N., McBratney, A.B., Crawford, J.W., 1998. Application of fractals to soil studies. *Adv. Agron.* 63, 1–76.
- Andreetta, A., Cecchini, G., Bonifacio, E., Comolli, R., Vingiani, S., Carnicelli, S., 2016. Tree or soil? Factors influencing humus form differentiation in Italian forests. *Geoderma* 264, 195–204.
- Ascher, J., Sartori, G., Graefe, U., Thornton, B., Ceccherini, M.T., Pietramellara, G., Egli, M., 2012. Are humus forms, mesofauna and microflora in subalpine forest soils sensitive to thermal conditions? *Biol. Fert. Soils* 48, 709–725.
- Barot, S., Blouin, M., Fontaine, S., Jouquet, P., Lata, J.C., Mathieu, J., 2007. A tale of four stories: soil ecology, theory, evolution and the publication system. *PLoS ONE* 2, e1248.
- Bastow, J., 2012a. Succession, resource processing, and diversity in detrital food webs. In: Wall, D.H., Bardgett, R.D., Behan-Pelletier, V., Herrick, J.E., Jones, T.H., Ritz, K., Six, J., Strong, D.R., Van der Putten, W.H. (Eds.), *Soil Ecology and Ecosystem Services*. Oxford University Press, Oxford, pp. 117–135.
- Bastow, J.L., 2012b. Resource quality in a soil food web: is nitrogen or labile carbon more important for soil nematodes? *Biol. Fertil. Soils* 48, 501–510.
- Baudin, F., Tribouvillard, N., Trichet, J., 2007. *Géologie de la Matière Organique*. Vuibert, Paris.
- Begon, M., Townsend, C.R., Harper, J.L., 2005. *Ecology: from Individuals to Ecosystems*, 4<sup>th</sup> ed. Blackwell, Oxford.
- Berg, B., 1998. *A Maximum Limit for Foliar Litter Decomposition: a Synthesis of Data from Forest Systems*. Swedish University of Agricultural Sciences, Departments of Forest Ecology and Forest Soils, Uppsala.
- Berg, B., 2000a. Initial rates and limit values for decomposition of Scots pine and Norway spruce needle litter: a synthesis for N-fertilized forest stands. *Can. J. For. Res.* 30, 122–135.
- Berg, B., 2000b. Litter decomposition and organic matter turnover in northern forest soils. *For. Ecol. Manage.* 133, 13–22.
- Berg, B., 2000c. Initial rates and limit values for decomposition of Scots pine and Norway spruce needle litter: a synthesis for N-fertilized forest stands. *Can. J. For. Res.* 30, 122–135.

- Berg, M.P., 2012. Patterns of biodiversity at fine and small spatial scales. In: Wall, D.H., Bardgett, R.D., Behan-Pelletier, V., Herrick, J.E., Jones, T.H., Ritz, K., Six, J., Strong, D.R., Van der Putten, W.H. (Eds.), *Soil Ecology and Ecosystem Services*. Oxford University Press, Oxford, pp. 136–152.
- Berg, B., Berg, M., Bottner, P., Box, E., Breymeyer, A., Calvo de Anta, R., Couteaux, M., Gallardo, A., Escudero, A., Kratz, W., Madeira, M., Mälkönen, E., Meentemeyer, V., Munöz, F., Piusi, P., Remacle, J., Virzo de Santo, A., 1993. Litter mass loss in pine forests of Europe and eastern United States as compared to actual evapotranspiration on a European scale. *Biogeochemistry* 20, 127–153.
- Berg, B., Booltink, H.G.W., Breymeyer, A., Ewertsson, A., Gallardo, A., Holm, B., Johansson, M.B., Koivuova, S., Meentemeyer, V., Nyman, P., Olofsson, J., Pettersson, A.S., Reurslag, A., Staaf, H., Staaf, I., Uba, L., 1991. Data on needle litter decomposition and soil climate as well as site characteristics for some coniferous forest sites. Section 2. Data on Needle Litter Decomposition, 2<sup>nd</sup> ed. Swedish University of Agricultural Sciences, Department of Ecology and Environmental Research, Uppsala.
- Berg, B., Calvo de Anta, R., Escudero, A., Johansson, M.B., Laskowski, R., Madeira, M., McLaugherty, C., Meentemeyer, V., Reurslag, A., Virzo de Santo, A., 1995. The chemical composition of newly shed needle litter of different pine species and Scots pine in a climatic transect. Long-term decomposition in a Scots pine forest X. *Can. J. Bot.* 73, 1423–1435.
- Berg, B., Cortina, J., 1995. Nutrient dynamics in some leaf and needle litter types of different chemical composition in a Scots pine forest. *Scand. J. For. Res.* 10, 1–11.
- Berg, B., Davey, M.P., De Marc, A., Emmett, B., Faituri, M., Hobbie, S.E., Johansson, M.B., Liu, C., McLaugherty, C., Norell, L., Rutigliano, F.A., Vesterdal, L., Virzo de Santo, A., 2010. Factors influencing limit values for pine needle litter decomposition: a synthesis for boreal and temperate pine forest systems. *Biogeochemistry* 100, 57–73.
- Berg, B., Dise, N., 2004. Validating a new model for N sequestration in forest soil organic matter. In: Wieder, R.K., Novák, M., Vile, M.A. (Eds.), *Biogeochemical Investigations of Terrestrial, Freshwater, and Wetland Ecosystems across the Globe*. Springer, Dordrecht, pp. 343–358.
- Berg, B., Ekbohm, G., 1991. Litter mass-loss rates and decomposition patterns in some needle and leaf litter types. Long-term decomposition in a Scots pine forest VII. *Can. J. Bot.* 69, 1449–1456.
- Berg, B., Ekbohm, G., Johansson, M.B., McLaugherty, C., Rutigliano, F., Virzo de Santo, A., 1996. Some foliar litter types have a maximum limit for decomposition: a synthesis of data from forest systems. *Can. J. Bot.* 74, 659–672.
- Berg, B., Erhagen, B., Johansson, M.B., Vesterdal, L., Faituri, M., Sanborn, P., Nilsson, M., 2013. Manganese dynamics in decomposing foliar litter: a synthesis. *Can. J. For. Res.* 43, 1127–1136.

- Berg, B., Hannus, K., Popoff, T., Theander, O., 1982. Changes in organic-chemical components during decomposition. Long-term decomposition in a Scots pine forest I. *Can. J. Bot.* 60, 1310–1319.
- Berg, B., Johansson, M.B., Lundmark, J.E., 1997. Site Descriptions for Forest Sites: a Compilation. Swedish University of Agricultural Sciences, Department for Forest Ecology and Forest Soils, Uppsala.
- Berg, B., Johansson, M.B., Meentemeyer, V., 2000. Litter decomposition in a transect of Norway spruce forests: substrate quality and climate control of mass-loss rates. *Can. J. For. Res.* 30, 1136–1147.
- Berg, B., Johansson, M.B., Nilsson, Å., Gundersen, P., Norell, L., 2009. Sequestration of carbon in the humus layer of Swedish forests: direct measurements. *Can. J. For. Res.* 39, 962–975.
- Berg, B., Kjønaas, J., Johansson, M.B., Erhagen, B., Åkerblom, S., 2015. Late stage pine litter decomposition: relationships to litter N, Mn and acid unhydrolyzable residue (AUR) concentrations and climatic factors. *For. Ecol. Manage.* 358, 41–47.
- Berg, B., Laskowski, R., Virzo de Santo, A., 1999. Estimated N concentration in humus as based on initial N concentration in foliar litter: a synthesis. *Can J Bot* 77, 1712–1722.
- Berg, B., Lundmark, J.E., 1985. Decomposition of Needle and Root Litter in Lodgepole Pine and Scots Pine Monocultural Systems. Swedish University of Agricultural Sciences, Department of Forest Ecology and Forest Soils, Uppsala.
- Berg, B., Lundmark, J.E., 1987. Decomposition of needle litter in lodgepole pine and Scots pine monocultures: a comparison. *Scand. J. For. Res.* 2, 3–12.
- Berg, B., McLaugherty, C., 2008. *Plant Litter: Decomposition, Humus Formation, Carbon Sequestration*, 2<sup>nd</sup> ed. Springer, Berlin.
- Berg, B., McLaugherty, C., 2014. *Plant Litter: Decomposition, Humus Formation, Carbon Sequestration*, 3<sup>rd</sup> ed. Springer, Berlin.
- Berg, B., McLaugherty, C., Virzo de Santo, A., Johnson, D., 2001. Humus build-up in boreal forests: effects of litter fall and its N concentration. *Can. J. For. Res.* 31, 988–998.
- Berg, B., Meentemeyer, V., 2001. Litterfall in some European coniferous forests as dependent on climate: a synthesis. *Can. J. For. Res.* 31, 292–301.
- Berg, B., Meentemeyer, V., 2002. Litter quality in a north European transect versus carbon storage potential. *Plant Soil* 242, 83–92.
- Berg, B., Steffen, K., McLaugherty, C., 2007. Litter decomposition rates as dependent on litter Mn concentration. *Biogeochemistry* 85, 29–39.
- Bernier, N., Ponge, J.F., 1994. Humus form dynamics during the sylvogenetic cycle in a mountain spruce forest. *Soil Biol. Biochem.* 26, 183–220.

- Bertrand, M., Barot, S., Blouin, M., Whalen, J., de Oliveira, T., Roger-Estrade, J., 2015. Earthworm services for cropping systems: a review. *Agron. Sustain. Dev.* 35, 553–567.
- Blouin, M., Hodson, M.E., Delgado, E.A., Baker, G., Brussaard, L., Butt, K.R., Dai, J., Dendooven, L., Peres, G., Tondoh, J.E., Cluzeau, D., Brun, J.J., 2013. A review of earthworm impact on soil function and ecosystem services. *Eur. J. Soil Sci.* 64, 161–182.
- Blouin, M., Zuily-Fodil, Y., Pham-Thi, A.T., Laffray, D., Reversat, G., Pando, A., Tondoh, J., Lavelle, P., 2005. Belowground organism activities affect plant aboveground phenotype, inducing plant tolerance to parasites. *Ecol. Lett.* 8, 202–208.
- Bogatyrev L., Berg B., Staaf H., 1983. Leaching of plant nutrients and total phenolic substance from some foliage litter: a laboratory study. Swedish Coniferous Forest Project Technical Report, Uppsala.
- Bormann, F.H., Likens, G., 2012. *Pattern and Process in a Forested Ecosystem: Disturbance, Development and the Steady State Based on the Hubbard Brook Ecosystem Study.* Springer, New York.
- Botkin, D.B., 1990. *Discordant Harmonies: a New Ecology for the Twenty-First Century.* Oxford University Press, New York.
- Camaret, S., Bernier, N., Eynard-Machet, R., Dobremez, J.F., Fay, J., Gauquelin, X., Khelifa, J., Lancon, M.F., Leclerc, D., Merrouche, A., Zanella, A., 2000. *Distribution Spatiale et Évolution Temporelle de la Végétation et de sa Diversité: Relations avec l'Hétérogénéité des Structures des Peuplements en Pessière d'Altitude.* Université de Chambéry, Laboratoire de Dynamique des Écosystèmes d'Altitude, Chambéry.
- Canellas, L.P., Piccolo, A., Dobbss, L.B., Spaccini, R., Olivares, F.L., Zandonadi, D.B., Façanha, A.R., 2010. Chemical composition and bioactivity properties of size-fractions separated from a vermicompost humic acid. *Chemosphere* 78, 457–466.
- Carletti, P., Vendramin, E., Pizzeghello, D., Concheri, G., Zanella, A., Nardi, S., Squartini, A., 2009. Soil humic compounds and microbial communities in six spruce forests as function of parent material, slope aspect and stand age. *Plant Soil* 315, 47–65.
- Carvalhais, N., Forkel, M., Khomik, M., Bellarby, J., Jung, M., Migliavacca, M., Mu, M., Saatchi, S., Santoro, M., Thurner, M., Weber, U., Ahrens, B., Beer, C., Cescatti, A., Randerson, J.T., Reichstein, M., 2014. Global covariation of carbon turnover times with climate in terrestrial ecosystems. *Nature* 514, 213–217.
- Cavalli R, Mason F., 2003. *Techniques for Reestablishment of Dead Wood for Saprophytic Fauna Conservation.* Gianluigi Arcari, Mantova, Italy.
- Chan, Y., 2008. Increasing soil organic carbon of agricultural land. *Primefacts* 735, 1–5.
- Charpentier-Ljunkvist, F., 2009. *Global nedkylning: klimatet och människan under 10 000 år.* Norstedts, Stockholm (in Swedish).

- Ciancio, O., 2014, *Storia del Pensiero Forestale: Selvicoltura, Filosofia, Etica*. Rubettino, Soveria Mannelli.
- Ciancio, O., Nocentini, S., 2005. Biodiversity conservation in Mediterranean forest ecosystems: from theory to operationality. In: Marchetti M (Ed.), *Monitoring and Indicators of Forest Biodiversity in Europe: from Ideas to Operationality*. European Forest Institute, Joensuu, pp. 163–168.
- Clause, J., Barot, S., Richard, B., Decaëns, T., Forey, E., 2014. The interactions between soil type and earthworm species determine the properties of earthworm casts. *Appl. Soil Ecol.* 83. <http://dx.doi.org/10.1016/j.apsoil.2013.12.006>.
- Cluzeau, D., Lebouvier, M., Trehen, P., Bouche, M.B., Badour, C., Perraud, A., 1987. Relations between earthworms and agricultural practices in the vineyards of Champagne. Preliminary results. In: Omodeo, P. (Ed.), *On Earthworms. Selected Symposia and Monographs U.Z.I., Modena, Italie*, pp. 465–484.
- Cluzeau, D., Guernion, M., Chaussod, R., Martin-Laurent, F., Villenave, C., Cortet, J., Ruiz-Camacho, N., Pernin, C., Mateille, T., Philippot, L., Bellido, A., Rougé, L., Arrouays, D., Bispo, A., Pérès, G., 2012. Integration of biodiversity in soil quality monitoring: baselines for microbial and soil fauna parameters for different land-use types. *Eur. J. Soil Biol.* 49, 63–72.
- Cluzeau, D., Descôtes, A., Georget, C., Chaussod, R., Nouaim-Chaussod, R., Pérès, G., Guernion, M., Cylly, D., Rougé, L., Garcia, O., Panigai, L., Moncomble, D., 2014. Les sols vivants du vignoble champenois: comment intégrer ces connaissances acquises sur ce patrimoine pour contribuer à la pérennité de l'A.O.C Champagne? Rapport Final Programme GESSOL. ADEME, Paris.
- Clymo, R.S., 1987. *Rainwater-Fed Peats as a Precursor of Coal*. Geological Society, London.
- Corona, P., Del Favero, R., Marchetti, M., 2005. Forest type approach in Italy: experiences from the last twenty years. In: Marchetti M (Ed.), *Monitoring and Indicators of Forest Biodiversity in Europe: from Ideas to Operationality*. European Forest Institute, Joensuu, pp. 143-152.
- Dalias, P., Anderson, J.M., Bottner, P., Coûteaux, M.M., 2001. Long-term effects of temperature on carbon mineralisation processes. *Soil Biol. Biochem.* 33, 1049–1057.
- Darwin, C., 1881. *The Formation of Vegetable Mould Through the Action of Worms with Some Observations on Their Habits*. John Murray, London.
- Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440, 165–173.
- Dokuchaev, V.V., 1883. *Selected Works of V.V. Dokuchaev, Volume 1, Russian Chernozem*. Israel Program for Scientific Translations, Jerusalem.



- Fischer, A.M., 2007. Nutrient remobilization during leaf senescence. In: Gan, S. (Ed.), *Annual Plant Reviews, Volume 26, Senescence Processes in Plants*. Blackwell, Oxford, pp. 87–107.
- Fitter, A.H., Garbaye, J., 1994. Interactions between mycorrhizal fungi and other soil organisms. *Plant Soil* 159, 123–132.
- Fusaro, S., 2015. Evaluation, maintenance and improvement of biodiversity for environmental protection and crop. Doctorate thesis, Università degli Studi di Padova, Padova.
- Galvan, P., Ponge, J.F., Chersich, S., Zanella, A., 2008. Humus components and soil biogenic structures in Norway spruce ecosystems. *Soil Sci. Soc. Am. J.* 72, 548–557.
- Galvan, P., Solaro, S., Chersich, S., Zanella, A., 2006. Il ruolo della pedofauna nella variabilità spaziale e temporale delle forme di humus: indagini micromorfologiche su sezioni sottili ed osservazioni allo stereoscopio. *Forest@* 3, 555–561.
- Gillet, S., Ponge, J.F., 2002. Humus forms and metal pollution in soil. *Eur. J. Soil Sci.* 53, 529–539.
- Gobat, J.M., Aragno, M., Matthey, W., 1998. *Le Sol Vivant. Bases de Pédologie. Biologie des Sols*. Presses Polytechniques et Universitaires Romandes, Lausanne.
- Hagen-Thorn, A., Varnagiryte, I., Nihlgard, B., Armolaitis, K., 2006. Autumn nutrient resorption and losses in four deciduous forest tree species. *For. Ecol. Manag.* 228, 33–39.
- Hopkins, D.W., Gregorich, E.G., 2005. Carbon is a substrate for soil organisms. In: Bardgett, R.D., Usher, M.B., Hopkins, D.W. (Eds.), *Biological Diversity and Function in Soils*. Cambridge University Press, Cambridge, pp. 57–79.
- InFoCarb, 2007. *Inventario Forestale del Carbonio della Provincia di Trento*. Centro di Ecologia Alpina, Trento.
- Jabiol, B., Zanella, A., Ponge, J.F., Sartori, G., Englisch, M., Van Delft, B., De Waal, R., Le Bayon, R.C., 2013. A proposal for including humus forms in the World Reference Base for Soil Resources (WRB-FAO). *Geoderma* 192, 286–294.
- Janzen, D.H., 1980. When is it coevolution? *Evolution* 34, 611–612.
- Janzen, H.H., 2006. The soil carbon dilemma: shall we hoard it or use it? *Soil Biol. Biochem.* 38, 419–424.
- Jenny, H., 1941. *Factors of Soil Formation: a System of Quantitative Pedology*. McGraw-Hill, New York.
- Jenny, H., 1958. Role of the plant factor in the pedogenic functions. *Ecology* 39, 5–16.
- Johansson, M.B., Berg, B., Meentemeyer, V., 1995. Litter mass-loss rates in late stages of decomposition in a climatic transect of pine forests. Long-term decomposition in a Scots pine forest IX. *Can. J. Bot.* 73, 1509–1521.
- Johnson, D.L., Domier, J.E.J., Johnson, D.N., 2005. Reflections on the nature of soil and its biomantle. *Ann. Assoc. Am. Geogr.* 95, 11–31.

- Johnson, D.L., 1998. A universal definition of soil. *Quaternary Int.* 51/52, 6–7.
- Kardol, P., Throop, H.L., Adkins, J., De Graaff, M.A., 2016. A hierarchical framework for studying the role of biodiversity in soil food web processes and ecosystem services. *Soil Biol. Biochem.* 102, 33–36.
- Kelleher, B.P., Simpson, A.J., 2006. Humic substances in soils: are they really chemically distinct? *Environ. Sci. Technol.* 40, 4605–4611.
- Killingbeck, K.T., 1996. Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. *Ecology* 77, 1716–1727.
- Kleber, M., Nico, P.S., Plante, A., Filley, T., Kramer, M., Swantson, C., Sollins, P., 2011. Old and stable soil organic matter is not necessarily chemically recalcitrant: implications for modeling concepts and temperature sensitivity. *Global Change Biol.* 2, 1097–1107.
- Lal, R., 2007. Carbon management in agricultural soils. *Mitigation Adapt. Strateg. Global Change* 12, 303–322.
- Legros, J.P., 2007. *Les Grands Sols du Monde*. Presses Polytechniques Universitaires Romandes, Lausanne.
- Lehmann, J., Kleber, M., 2015. The contentious nature of soil organic matter. *Nature* 528, 60–68.
- Lehmann, J., Solomon, D., Kinyangi, J., Dathe, L., Wirick, S., Jacobsen, C., 2008. Spatial complexity of soil organic matter forms at nanometre scales. *Nat. Geosci.* 1, 238–242.
- Leinweber, P., Schulten, H.R., 1998. Advances in analytical pyrolysis of soil organic matter. *J. Anal. Appl. Pyrolysis* 47, 165–189.
- Li, X., Wang, Y., Liu, L., Luo, G., Li, Y., Chen, X., 2013. Effect of land use history and pattern on soil carbon storage in arid region of Central Asia. *PLoS ONE* 8, e68372.
- Luysaert, S., Inglima, I., Jung, M., Richardson, A.D., Reichstein, M., Papale, D., Piao, S.L., Schulze, E.D., Wingate, L., Matteucci, G., Aragao, L.E.O.C., Aubinet, M., Beers, C., Bernhofer, C., Black, G.K., Bonal, D., Bonnefond, J.M., Chambers, J., Ciais, P., Cook, B., Davis, K.S., Dolman, A.J., Gielen, B., Goulden, M., Grace, J., Granier, A., Grelle, A., Griffis, T., Grünwald, T., Guidolotti, G., Hanson, P.J., Harding, R., Hollinger, D.Y., Hutyrá, L.R., Kolari, P., Kruijt, B., Kutsch, W.L., Lagergren, F., Laurila, T., Law, B., Le Maire, G., Lindroth, A., Loustau, D., Malhi, Y., Mateu, J., Migliavacca, M., Misson, L., Montagnani, L., Moncrieff, J., Moors, E.J., Munger, J.W., Nikinmaa, E., Ollinger, S.V., Pita, G., Rebmann, C., Rouspard, O., 2007. CO<sub>2</sub> balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biol.* 13, 2509–2537.
- Maillard, A., Diquélou, S., Billard, V., Laîné, P., Garnica, M., Prudent, M., Garcia-Mina, J. M., Yvin, J.C., Ourry, A., 2015. Leaf mineral nutrient remobilization during leaf senescence and modulation by nutrient deficiency. *Front. Plant Sci.* 6, 317.
- Mandelbrot, B., 2004. *Fractals and Chaos: the Mandelbrot Set and Beyond*. Springer;New York.

- Marchin, R., Zeng, H., Hoffmann, W., 2010. Drought-deciduous behavior reduces nutrient losses from temperate deciduous trees under severe drought. *Oecologia* 163, 845–854.
- Mason, F., Zapponi, L., 2015. The forest biodiversity artery: towards forest management for saproxylic conservation. *iForest* 9, 205–216.
- Nebbioso, A., Piccolo, A., 2012. Advances in humeomics: enhanced structural identification of humic molecules after size fractionation of a soil humic acid. *Anal. Chim. Acta* 720, 77–90.
- Nielsen, U.N., Wall, D.H., Six, J., 2015. Soil biodiversity and the environment. *Annu. Rev. Environ. Resour.* 40, 63–90.
- Nocentini, S., 2011. The forest as a complex biological system: theoretical and practical consequences. *L'Italia Forestale e Montana* 66, 191–196.
- O'Donnell, A.G., Colvan, S.R., Malosso, E., Supaphol, S., 2005. Twenty years of molecular analysis of bacterial communities in soils and what have we learned about function? In: Bardgett, R.D., Usher, M.B., Hopkins, D.W. (Eds.), *Biological Diversity and Function in Soils*. Cambridge University Press, Cambridge, pp. 44–56.
- Odum, E.P., 1953. *Fundamentals of Ecology*. Saunders, Philadelphia.
- Odum, E.P., 1997. *Ecology*. Sinauer Associates, Sunderland.
- Oldeman, R.A.A., 1990. *Forests: Elements of Silvology*. Springer, Berlin.
- Pennanen, T., Liski, J., Bååth, E., Kitunen, V., Uotila, J., Westman, C.J., Fritze, H., 1999. Structure of the microbial communities in coniferous forest soils in relation to site fertility and stand development stage. *Microb. Ecol.* 38, 168–179.
- Perruchoud, D.O., Joos, F., Fischlin, A., Hajdas, I., Bonani, G., 1999a. Evaluating time scales of carbon turnover in temperate forest soils with radiocarbon data. *Global Biogeochem. Cycles* 13, 555–573.
- Perruchoud, D.O., Kienast, F., Kaufmann, E., Bräker, O.U., 1999b. 20<sup>th</sup> century carbon budget of forest soils in the Alps. *Ecosystems* 2, 320–337.
- Piccolo, A., 2001. The supramolecular structure of humic substances. *Soil Sci.* 166, 810–832.
- Piccolo, A., Mbagwu, J.S.C., 1999. Role of hydrophobic components of soil organic matter in soil aggregate stability. *Soil Sci. Soc. Am. J.* 63, 1801–1810.
- Ponge, J.F., 2003. Humus forms in terrestrial ecosystems: a framework to biodiversity. *Soil Biol. Biochem.* 35, 935–945.
- Ponge, J.F., 2013. Plant-soil feedbacks mediated by humus forms: a review. *Soil Biol. Biochem.* 57, 1048–1060.
- Ponge, J.F., Sartori, G., Garlato, A., Ungaro, F., Zanella, A., Jabiol, B., Obber, S., 2014. The impact of parent material climate, soil type and vegetation on Venetian forest humus forms: a direct gradient approach. *Geoderma* 226–227, 290–299.

- Roberts, S., Dallal, D.E., 2005. Energy requirements and aging. *Public Health Nutr.* 8, 1028–1036.
- Rodeghiero, M., Tonolli, S., Vescovo, L., Gianelle, D., Cescatti, A., Sottocornola, M., 2010. INFOCARB: a regional scale forest carbon inventory (Provincia Autonoma di Trento, Southern Italian Alps). *For. Ecol. Manage.* 259, 1093–1101.
- Rodeghiero, M., 2003. *Il Ruolo delle Foreste nel Bilancio del Carbonio: Aspetti Ecologici ed Economici.* Centro di Ecologia Alpina, Trento.
- Salmon, S., Mantela, J., Frizzera, L., Zanella, A., 2006. Changes in humus forms and soil animal communities in two developmental phases of Norway spruce on an acidic substrate. *For. Ecol. Manage.* 237, 47–56.
- Saugier, B., Roy, J., Mooney, H.A., 2001. Estimations of global terrestrial productivity: converging toward a single number? In: Roy, J., Saugier, B., Mooney, H.A. (Eds.), *Terrestrial Global Productivity.* Academic Press, San Diego, pp. 543–557.
- Scattolin, L., Galvan, P., Zanella, A., 2004a. Osservare l'humus per conoscere meglio il bosco. *Linea Ecologica* 1, 8–12.
- Scattolin, L., Viola, F., Zanella, A., 2004b. Il contributo dei funghi alla trasformazione delle lettiere in una pecceta altimontana del Trentino. *Linea Ecologica* 4, 12–17.
- Schmidt, M.W.I., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Kleber, M., Kogel-Knabner, I., Lehmann, J., Manning, D.A.C., Nannipieri, P., Rasse, D.P., Weiner, S., Trumbore, S.E., 2011. Persistence of soil organic matter as an ecosystem property. *Nature* 478, 49–56.
- Schulten, H.R., Schnitzer, M., 1997. Chemical model structures for soil organic matter and soils. *Soil Sci.* 162, 115–130.
- Schwartz, J.D., 2014. Soil as carbon storehouse: new weapon in climate fight? *Environnement* 360. [http://e360.yale.edu/feature/soil\\_as\\_carbon\\_storehouse\\_new\\_weapon\\_in\\_climate\\_fight/2744/](http://e360.yale.edu/feature/soil_as_carbon_storehouse_new_weapon_in_climate_fight/2744/).
- Spurgeon, D.J., Keith, A.M., Schmidt, O., Lammertsma, D.R., Faber, J.H., 2013. Land-use and land-management change: relationships with earthworm and fungi communities and soil structural properties. *BMC Ecol.* 13, 46.
- Standing, D.B., Rangel Castro, J.I., Prosser, J.I., Meharg, A., Killham, K., 2005. Rhizosphere carbon flow: a driver of soil microbial diversity? In: Bardgett, R.D., Usher, M.B., Hopkins, D.W. (Eds.), *Biological Diversity and Function in Soils.* Cambridge University Press, Cambridge, pp. 31–43.
- Stevenson, F.J., 1972. Role and function of humus in soil with emphasis on adsorption of herbicides and chelation of micronutrients. *Bioscience* 22, 643–650.
- Stevenson, F.J., 1985. Geochemistry of soil humic substances. In: McKnight, D.M. (Ed.), *Humic Substances in Soil, Sediment and Water: Geochemistry, Isolation and Characterization.* Wiley, New York, pp. 13–52.

- Stevenson, F.J., 1994. Humus Chemistry: Genesis, Composition, Reactions, 2<sup>nd</sup> edition. Wiley, New York.
- Susmel, L., 1980. Normalizzazione delle Foreste Alpine: Basi Ecosistemiche, Equilibrio, Modelli Colturali, Produttività con Applicazione alle Foreste del Trentino. Liviana, Padova.
- Susmel, L., 1988. Principi di Ecologia: Fattori Ecologici, Ecosistemica, Applicazioni. CLEUP, Padova.
- Susmel, L., Viola, F., Bassato, G., 1976. Ecologia della lecceta del supramonte di Orgosolo. Annali del Centro di Economia Montana delle Venezie 10, 121–172.
- Sverdrup-Thygeson, A., Bendiksen, E., Birkemoe, T., Larsson, K.H., 2014a. Do conservation measures in forest work? A comparison of three area-based conservation tools for wood-living species in boreal forests. For. Ecol. Manage. 330, 8–16.
- Sverdrup-Thygeson, A., Gustafsson, L., Kouki, J., 2014b. Spatial and temporal scales relevant for conservation of dead-wood associated species: current status and perspectives. Biodivers. Conserv. 23, 513–535.
- Teija Ruuhola, T.L., 2011a. Retranslocation of nutrients in relation to boron availability during leaf senescence of *Betula pendula* Roth. Plant Soil 344, 227–240.
- Van Heerwaarden, L.M., Toet, S., Aerts, R., 2003. Current measures of nutrient resorption efficiency lead to a substantial underestimation of real resorption efficiency: facts and solutions. Oikos 101, 664–669.
- Verburg, P.S.J., Van Dam, D., Hefting, M.M., Tietema, A., 1999. Microbial transformations of C and N in a boreal forest floor as affected by temperature. Plant Soil 208, 187–197.
- Wardle, D.A., 2005. How plant communities influence decomposer communities. In: Bardgett, R.D., Usher, M.B., Hopkins, D.W. (Eds.), Biological Diversity and Function in Soils. Cambridge University Press, Cambridge, pp. 119–138.
- Young, J.M., Crawford, J.W., Nunan, N., Otten, W., Spiers, A., 2008. Chapter 4: microbial distribution in soils: physics and scaling. Adv. Agron. 100, 81–121.
- Zanella, A., 1994. Proposition pour une Typologie Forestière Intégrée. Exemples d'Application aux Forêts de la Flandre Française Intérieure. Doctorate thesis, Université Paris-Sud, Orsay.
- Zanella, A., 1995. Filosofia olistica ed ecologia: il concetto di ecosistema e la nuova teoria dell'evoluzione cosmica. Linea Ecologica 2, 3–6.
- Zanella, A., 1996. Tipologia delle stazioni forestali: concetti e proposte operative. Linea Ecologica 1, 39–45.
- Zanella, A., Jabiol, B., Ponge, J.F., Sartori, G., De Waal, R., Van Delft, B., Graefe, U., Cools, N., Katzensteiner, K., Hager, H., Englisch, M., 2011b. A European morpho-functional classification of humus forms. Geoderma 164, 138–145.

- Zanella, A., Jabiol, B., Ponge, J.F., Sartori, G., De Waal, R., Van Delft, B., Graefe, U., Cools, N., Katzensteiner, K., Hager, H., Englisch, M., Brêthes, A., Broll, G., Gobat, J.M., Brun, J.J., Milbert, G., Kolb, E., Wolf, U., Frizzera, L., Galvan, P., Kollir, R., Baritz, R., Kemmers, R., Vacca, A., Serra, G., Banas, D., Garlato, A., Chersich, S., Klimo, E., Langohr, R., 2011a. European Humus Forms Reference Base.  
[http://hal.archives-ouvertes.fr/docs/00/56/17/95/PDF/Humus\\_Forms\\_ERB\\_31\\_01\\_2011.pdf](http://hal.archives-ouvertes.fr/docs/00/56/17/95/PDF/Humus_Forms_ERB_31_01_2011.pdf).
- Zanella, A., Secco, R., Tarasconi, L., Jabiol, B., Viola, F., 2008. Struttura degli orizzonti diagnostici e classificazione delle forme di humus. *Forest@* 5, 68–81.
- Zanella, A., Tommasi, M., de Siena, C., Frizzera, L., Jabiol, B., Nicolini, G., Sartori, G., Calabrese, M.S., Mancabelli, A., Nardi, S., Pizzeghello, D., Odasso, M., 2001. Humus Forestali. Manuale di Ecologia per il Riconoscimento e l'Interpretazione. Centro di Ecologia Alpina, Trento.
- Zanella, A., Valenti, A., Bernier, N., Galvan, P., Camaret, S., Frizzera, L., Zampedri, R., Nicolini, G., Viola, F., 2003. Viaggiare sulle scale dell'humus. In: Atti III Congresso Nazionale "Alberi e Foreste per il Nuovo Millennio", Viterbo, Italy, October 15-18, 2001, pp. 331–336.

## Figure captions

**Fig. 1.** The place of a humus system in a terrestrial ecosystem. At the starting point, there were a source of energy, a mineral planet and some small organic molecules. Exploiting the available energy (electromagnetic, gravitational, nuclear and of mass) of a planet-star system, the planetary mineral-organic world produced more complex structures occupying larger and larger space-time on the planet. Simplifying, the interaction between photosynthetic and geological components may explain how a system evolves. The photosynthetic component stores at the right moment/place a small but useful part of electromagnetic energy. The geological component delivers at the right moment/place the mineral elements and water necessary for the functioning of the photosynthetic component. A new “organic matter”, made of a carbon skeleton instead of the pre-existing silica skeleton of the rock, auto-generates from the interaction between the two components. A web of consumers of the produced organic matter may now generate, extracting and using the energy stored in the organic matter. Each structure that originates in a point of the space-time grows, reproduces itself, dies, and is transformed into elemental units, which may be used for building new (generated from the old ones, evolved) structures. Because of the gravity force, the residues of obsolete structures fall and accumulate on the surface of the planet. Their transformation and reuse are influenced by environmental conditions, expressed at small scale by electromagnetic forces and biological interactions. In cold, acid or anoxic situations, biodegradation and reuse of organic residues progress slowly; besides, the more favourable the conditions for decomposition, the faster the residues will be transformed and reused in new processes. Progressively, another component develops and grows between photosynthetic and geological layers: a humipedon, corresponding to a humus system. Curiously, the result of the process of biodegradation is not a complete destruction (until mineral elements) of the previously built organic matter, but a new “complex cover”, a new functional body, an organic and organic-mineral interacting matrix called “humus system”.

**Fig. 2.** Carbon balance. In an undisturbed forest ecosystem, the average annual net production of organic matter is used in the process of respiration by animals and microorganisms. Net primary production equals respiration + leaching and in an undisturbed Alpine forest ecosystem this amounts to  $1\text{--}1.5 \text{ kg C m}^{-2} \text{ year}^{-1}$ .

**Fig. 3.** Flux of mass and energy in a standard forest ecosystem. The flux of mass in a standard forest ecosystem concerns nearly 1/10 of the producing biomass. This “travelling mass” is composed of residues (dead organic matter lost by living organisms). The biodegradation takes place in the topsoil. This “travelling mass” is necessary to maintain the system in a state of equilibrium. The static living mass is represented by a thin blue line, sharing above- and belowground “travelling biomasses”. Legend: E =energy (white arrow, electromagnetic waves at high frequency; red arrow, low frequency electromagnetic waves; the difference of energy becomes the ‘gasoline’ that feeds the forest-engine); 1 =assimilation of water, mineral elements and energy; 2 =storage of energy in the soil. (For interpretation of the references to colours in this figure legend, the reader is referred to the web version of this article).

**Fig. 4.** As for the processes of production and respiration, it is hard to separate linear from cyclic evolution. Both interact at different space-time scales. Day-night cycles succeed within warm/cold seasons, influencing young/old stages, in warm/cold centuries and millennia, on single/shared terrestrial crustal plates and seas... starting in high mountains from a bare rock point, in a medium cold climate, and stepping down through different ecosystems to join a more mesic plain, the natural history of a large territory has been crossed in a linear sequence (time step zero =bare rock; time 1 =crust and mosses carpet; time 2= alpine grassland; time 3 =alpine heath; time 4= coniferous forest; time 5 =broadleaf forest). However, stopping at one level and observing a given ecosystem, the cyclic evolution could be investigated. The more the system grows in complexity and biomass, the higher amount the “travelling mass” of carbon necessary for maintaining the system in good conditions. Quality and quantity of energy in the form of radiation, water, and mass of mineral elements limit the growth of the system. More concise figures of the same concept are available in Cavana (2003).

**Fig. 5.** Graphic model. The main “ecological attractors” in which a topsoil “falls” under the influence of climatic and nutritional constraints and as a consequence of its biological activity and connectedness. Central humus forms in bold (attractors at the level of humus system).

**Fig. 6.** Cycle of annually produced organic matter. 1/4 of the newly created organic matter is living matter, the other 3/4 are “invested” out of the producing living body of the system. Of these latter ones, 1 quarter is fixed in the soil (transformed in order to be resistant to biodegradation) and 2 quarters are forced into a perennial cycle.

**Fig. 7.** The bi-phasic cycle of litter production and biodegradation in a temperate broadleaved forest with the example from a very common European lowland namely *Querceto-Carpinetum*. At fall, all previously fallen litter has generally been integrated into the soil by anecic earthworms.

**Fig. 8.** Mull humus system strategy. The equilibrium point is a biomacrostructured A horizon, essentially generated by anecic and endogeic earthworms, which consume and incorporate all fallen litter in an organic-mineral horizon. The red arrow indicates that the disappearing organic matter is transported into the soil (in this specific humus system mostly by anecic and endogeic earthworms) and partially (the part not dissipated in the process of respiration) ends fixed in organic-mineral aggregates, forming a biomacrostructured A horizon, typical of a Mull system. This process allows stocking the energy needed for the future evolution of the system. It constitutes a sort of warehouse, a bank of energy, exploited first by the earthworms themselves when fresher aliments are no longer available, but also by plants, microorganisms and any organisms living in the soil, directly or indirectly linked to this durable resource. (For interpretation of the references to colours in this figure legend, the reader is referred to the web version of this article).

**Fig. 9.** Moder and Amphi humus form strategies. We observe the formation of a layer of undecomposed litter. The thickness of this layer depends of climate conditions, which periodically stimulate and arrest the biological activity of biodegradation. The Moder strategy has a point of equilibrium which shows transformed litter (zoOF and zoOH) accumulation and thin (< 5–7 cm) biomicrostructured organic-mineral A horizon. Amphi



conditions generate a double humus system (the so-called “twin humus”) with both well-developed organic and organic-mineral layers. Supposing a biodegradation that may “digest” half the yearly arriving litter, we would assist at a never-ending process of accumulation (theoretical accumulation). In the field in aerated soils we instead observe that the process raises a plateau. The process of biodegradation and integration of new litter in the soil increases (we tried to illustrate the collapsing litter with multi-lined teeth and dashed green arrows) with the thickness of the not biodegraded litter and reach an equilibrium dependent on climate and litter quality. (For interpretation of the references to colours in this figure legend, the reader is referred to the web version of this article).

**Fig. 10.** Mor and Tangel humus system strategies. In this case harsh climate conditions favour the formation of very organic soils, with a non-zoogenic OF horizon in very cold and humid aerated conditions where a fungal transformation of the litter dominates (Mor), or with very thick organic zoogenic layers, in cold climates with periodically more favourable conditions for litter biotransformation (Tangel). Supposing a biodegradation that may “digest” half the yearly arriving litter, we would assist at a never-ending process of accumulation (theoretical accumulation). In the field in aerated soils we instead observe that the process raises a plateau. The process of biodegradation and integration of new litter in the soil increases (dashed blue arrows) with the thickness of the not biodegraded litter and reaches an equilibrium dependent on climate and litter quality. (For interpretation of the references to colours in this figure legend, the reader is referred to the web version of this article).

**Fig. 11.** The limit value concept and its mathematical representation (from Berg and McLaugherty, 2008, 2014).

**Fig. 12.** The disappearance of the four quantitatively most important groups of organic compounds from decomposing Scots pine needle litter. Y axis =sum of stable residues; X axis =years. Data in Berg et al. (1982). Amounts of water-soluble compounds, cellulose, hemicellulose, and gravimetric lignin (AUR =Acid Unhydrolyzable Residue) were measured in Scots pine needle litter incubated in litter bags for 5 years. For building the graph, we assumed that the process of decomposition pursued the same pattern for 30 years, itself at the same rate for the series of  $6 \times 5 = 30$  years. During the first 5 years measured by Berg et al. (1982), the total mass of water-soluble compounds, cellulose, hemicellulose, and AUR decreased from 100 to about 20%, half the remaining mass being AUR. We considered that in a Mor system, the remaining mass of litter at the limit value would correspond to a mass of “stable humus” (half the remains after 5 years = 10%= AUR). Please refer to “4.3.1. The concept of limit value”; “6.1.2. Steady state in humus layers”, and “6.2.1. What is a humus not influenced by temperature (NIT-humus)?” for a more detailed explanation. Assuming that the organic horizons are in a state of growth/equilibrium we also assumed that the mass of new, annually added litter would decompose and develop like the litter above, passing from 100 to about 20%, half the remaining mass being AUR and the rest a mixing of the other compounds. Starting each new 5-yr cycle at the level of the top of lignin remains, the line of lignin on the graph reaches a plateau corresponding to 25% of the initial mass at the end of 30 years. In fact, with the input of new litter, the organic horizon thickness increases and the whole organic layer, thermally insulating the bottom part of the system, may allow a faster digestion of non AUR compounds, which decomposition ration is still temperature depending. We added a “grey

cloud” of mineral nutrients resulting from litter mineralization, which may form a plateau, too. The humus system may reach an equilibrium stage with a constant ratio of mineralization related to biological and environmental conditions. Among the mineral elements, Mn and N (in bold) play a major role in decomposition as discussed in the text. In comparison, in a Mull system all litter disappears in few months and the “stable humus” (NIT-humus) is not AUR but microscopic particles protected in micropores of large earthworms droppings. In Tangel and Moder systems, arthropod activity may play a great role in adjusting the mass of NIT-humus to the environmental frame. The Amphi system might be a good answer to global change, switching from arthropod (its Moder face) to earthworm (its Mull face) functionality, following climatic variations.

**Fig. 13.** Convergence of the regression lines of first-year litter mass loss versus concentration of gravimetric lignin to a point of about  $500 \text{ mg g}^{-1}$  at which litter decomposes at about the same rate irrespective of climate. The slope of the regression lines is well correlated to the actual evapotranspiration measured at the sites. High annual litter mass loss occurs at sites with high evapotranspiration which thus are well productive. The terrestrial humus systems described in this guide, from the most active Mull, in favourable climate conditions, to the less active Mor and Tangel, passing through intergrade Amphi and Moder, are indicated in the little graph on top right comparing annual actual evapotranspiration AET and slopes of regression lines.

**Fig. 14.** a) Concept of an eco-device that is composed of four main functions to control input (Supply, Resistance) and output (Disposal, Retention) of energy and to realize its functionality for potential users; b) the humus system can be considered part of a repeated structure of eco-devices at different hierarchical levels and is in its essence a fractal structure (Author: R.H. Kemmers).

**Fig. 15.** The humus system (or more precisely a given humus form) as a function of primary ecosystem factors and vegetation (Author: R.H. Kemmers).

**Table 1**

Concentration of nutrients in coniferous needle and deciduous leaf litters. From Berg and McClaugherty (2008). Data: a) Johansson et al. (1995); b) Berg and Lundmark (1987); c) C. McClaugherty and B. Berg (unpubl. *personal communication*); d) Berg et al. (2000); e) Berg and Ekbohm (1991); f) Bogatyrev et al. (1983). In red the highest value, comparing average for mineral elements in coniferous and deciduous leaf litters. Except for Mn, coniferous needle litter is generally poorer in mineral nutrients than the litter of broadleaf trees (average values in bold).

Litter	Concentration of nutrient (mg/g)						
	N	P	S	K	Ca	Mg	Mn
<i>Pinus sylvestris</i> (a)	4.8	0.33	0.55	1.07	4.4	0.49	0.79
<i>Pinus contorta</i> (b)	3.9	0.34	0.62	0.56	6.4	0.95	1.79
<i>Pinus pinaster</i> (c)	6.8	0.54	1.01	1.95	3.1	1.9	0.59
<i>Pinus resinosa</i> c)	6	0.36	0.73	1.4	8.9	2	0.73
<i>Pinus strobus</i> (c)	5.9	0.21	0.68	0.7	7.2	1.1	0.8
<i>Pinus banksiana</i> (c)	7.8	0.64	0.77	2.3	4	2.1	0.25
<i>Pinus flexilis</i> c)	4.3	0.43	0.52	1.1	5.3	1.1	0.21
<i>Picea abies</i> (d)	4.9	0.45	0.73	0.72	17.9	0.65	na
Average Coniferous needle	5.6	0.41	0.7	1.23	7.2	1.29	0.7
<i>Alnus incana</i> (e)	30.7	1.37	6.12	15.6	12.3	2.32	0.1
<i>Betula pendula</i> (e)	7.7	1.05	0.8	4.7	11.8	3.3	1.23
<i>Fraxinus sp.</i> (f)	8.6	1.96	Na	15.3	33.2	2.28	0.003
<i>Sorbus aucuparia</i> (f)	7.1	0.31	Na	10.8	12.4	2.86	0.3
<i>Populus tremuloides</i> (f)	8.2	0.93	Na	5.1	29.9	4.69	0.53
<i>Acer pseudoplatanus</i> (f)	5.1	3.15	Na	13.1	20.4	1.46	0.12
<i>Fagus sylvatica</i> (d)	9.5	1.4	1.3	2.3	7.4	1.2	1.9
Average Deciduous leaves	10.9	1.45	2.74	9.6	18.2	2.59	0.6

**Table 2**

Compounds (%) in coniferous and broadleaf litters (synthesis of many works: Berg, 1998, 2000a, 2000b; Berg and Meentemeyer, 2002; Berg et al., 1982, 1991, 1995; Berg and McClaugherty, 2008, 2014). Coniferous needle litter is richer in cellulose and its woody litter is richer in lignin (bold values); deciduous leaf litter is richer in water-soluble compounds, and its woody litter is richer in cellulose and pectin (component of primary cell walls).

Litter compounds (%)	Coniferous	Deciduous
Other soluble compounds	10–15	20–25
Ethanol soluble compounds	5–10	5
Cellulose (needles and leaves)	20–30	10–15
Cellulose (wood)	10–15	35–45
Hemicellulose	1–2	1–2
Pectin	3–4	4–6
Lignin (needles and leaves)	20–30	15–25
Lignin (wood)	35–45	20–25

## Terrestrial ecosystem

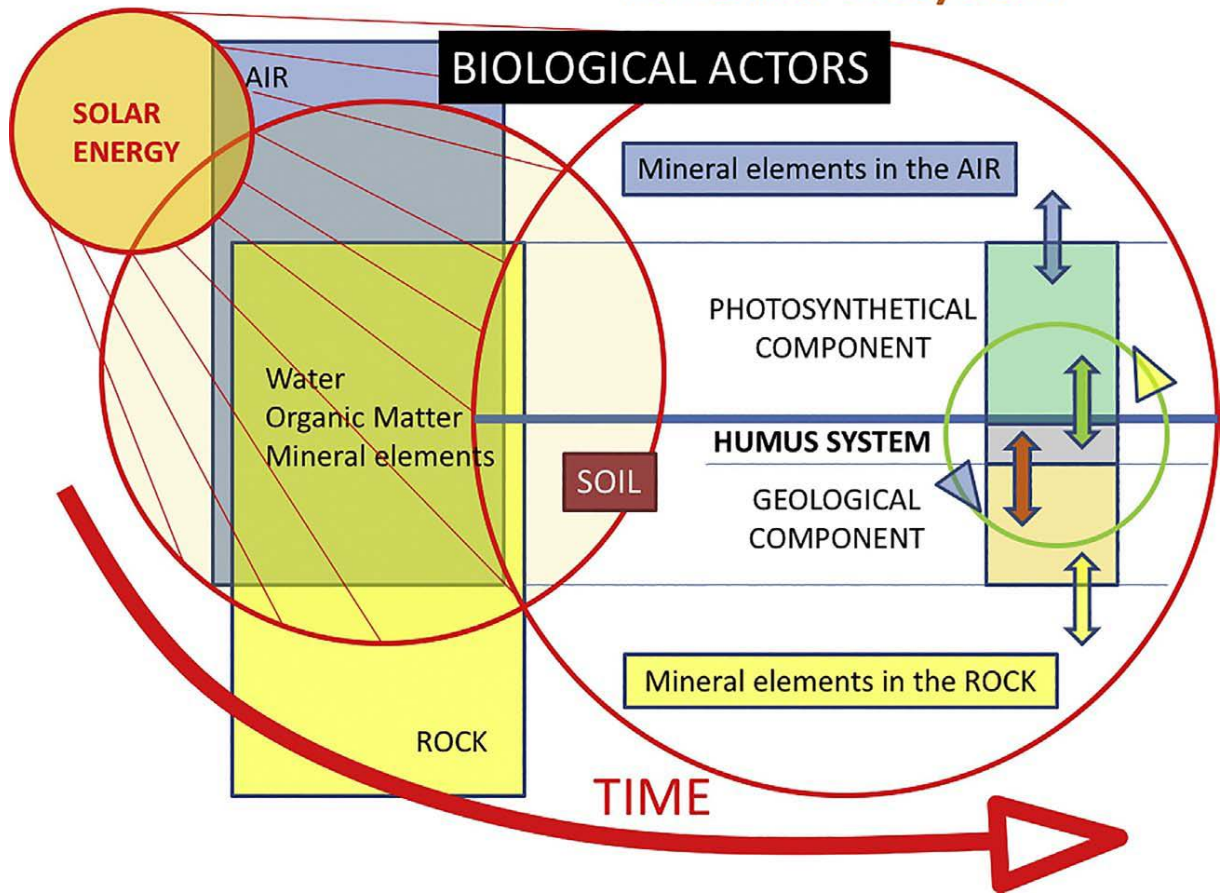
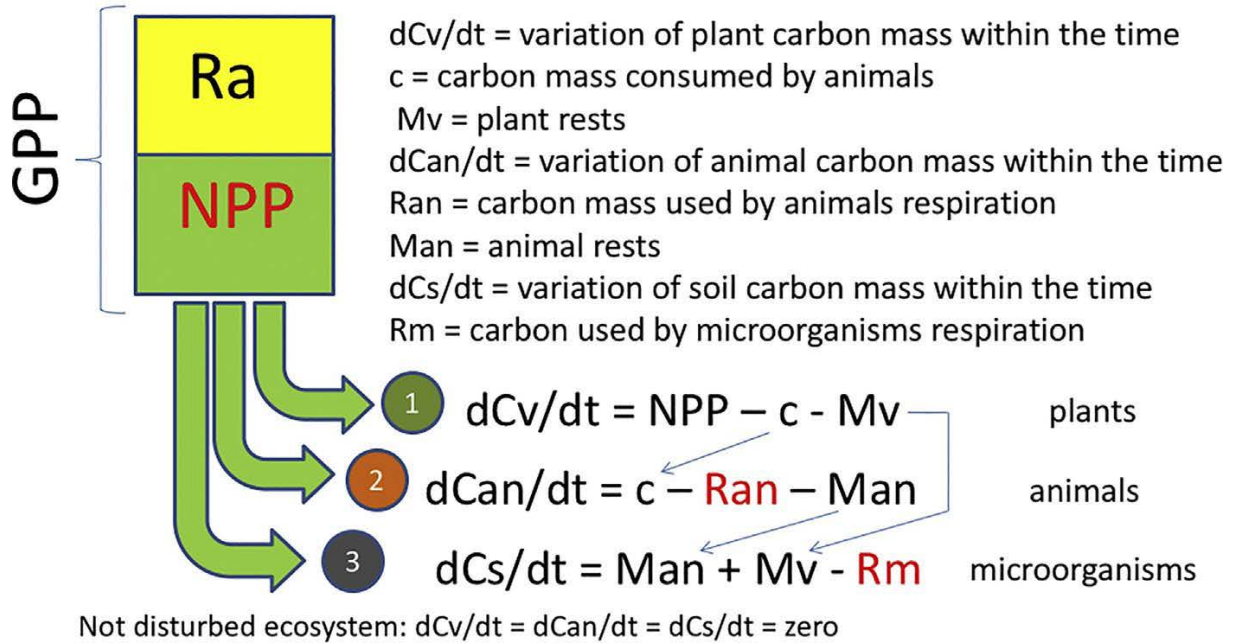


Fig. 1

GPP = gross primary production = carbon mass fixed by plants

Ra = carbon mass used by plants respiration

NPP = Net primary production = GPP - Ra



In not disturbed mountain forest in the Alps:  $NPP = (Ran + Rm) = litter = 1-1.5 \text{ Kg C m}^{-2} \text{ year}^{-1}$

Fig. 2

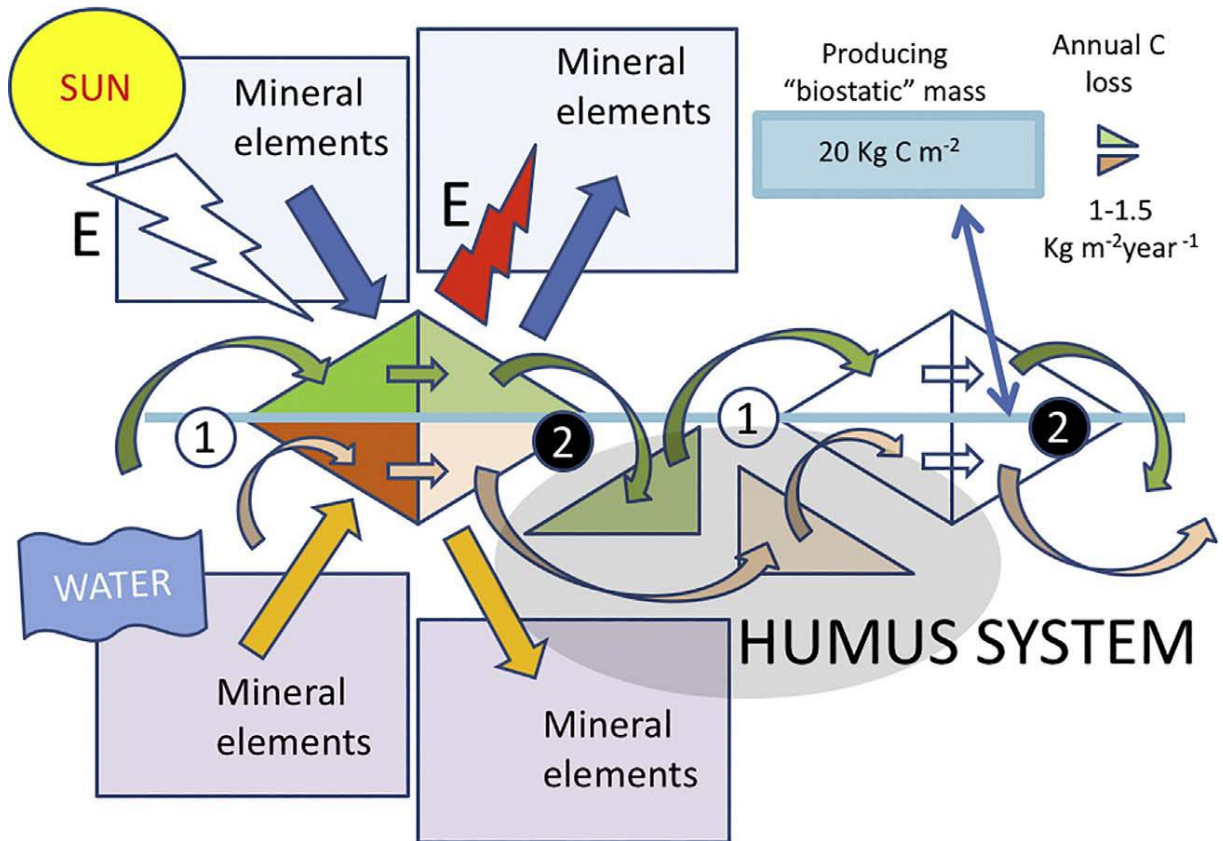


Fig. 3

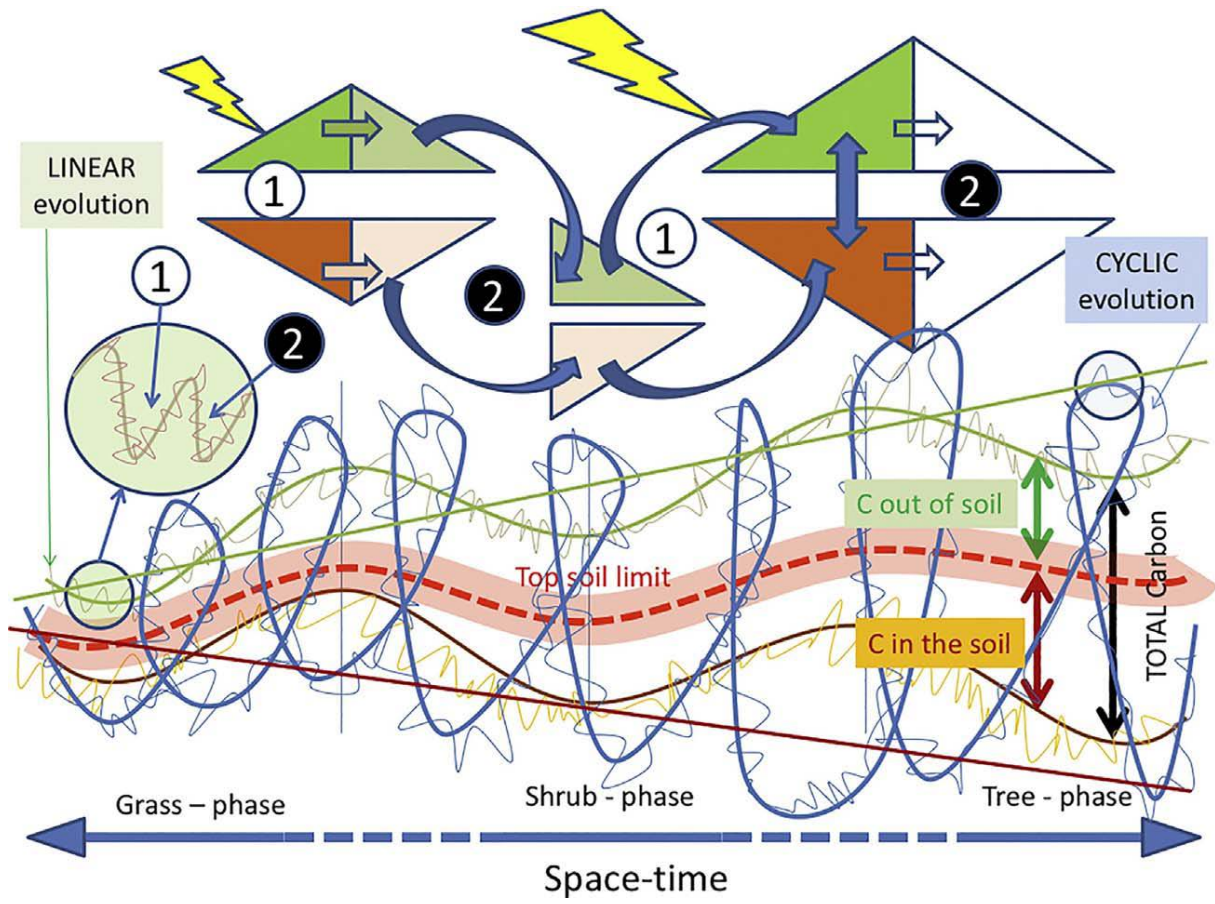


Fig. 4



**TERRESTRIAL HUMUS SYSTEMS  
and main ecological attractors**

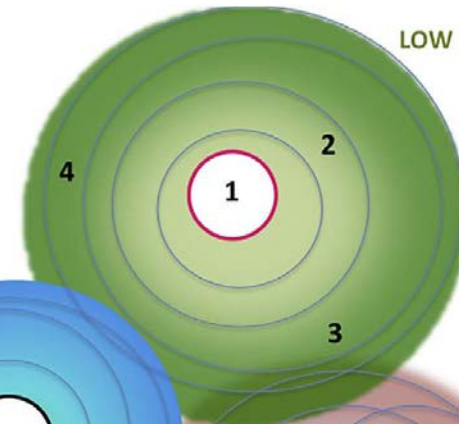
UNFAVOURABLE CONDITIONS for ANECIC WORMS  
but important MESOFAUNA like Arthropods and Enchytraeids  
Base-poor parent material

**MODER** 1- HEMI  
2- EU  
3- DYS

1 - HEMI  
2 - EU  
3 - HUMI

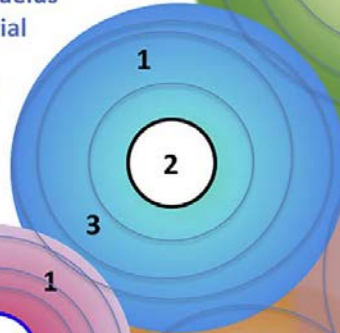
**MOR**

VERY UNFAVOURABLE CONDITIONS for animal activity,  
Base-poor parent material



LOW CLIMATE and NUTRITIONAL CONSTRAINTS for biological activity

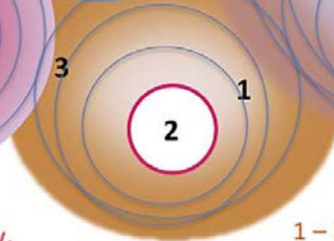
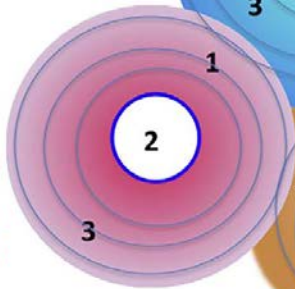
**MULL** 1- EU  
2- MESO  
3- OLIGO  
4- DYS



PERIODICALLY UNFAVOURABLE CLIMATE CONDITIONS for animal activity  
Base-rich parent material

**AMPHI**

1 - LEPTO  
2 - EUMACRO  
3 - EUMESO  
4 PACHY



**TANGEL**

1 - LEPTO PERIODICALLY UNFAVOURABLE  
2 - EU CONDITIONS for animal activity  
3- PACHY Base-rich parent material

Fig. 5

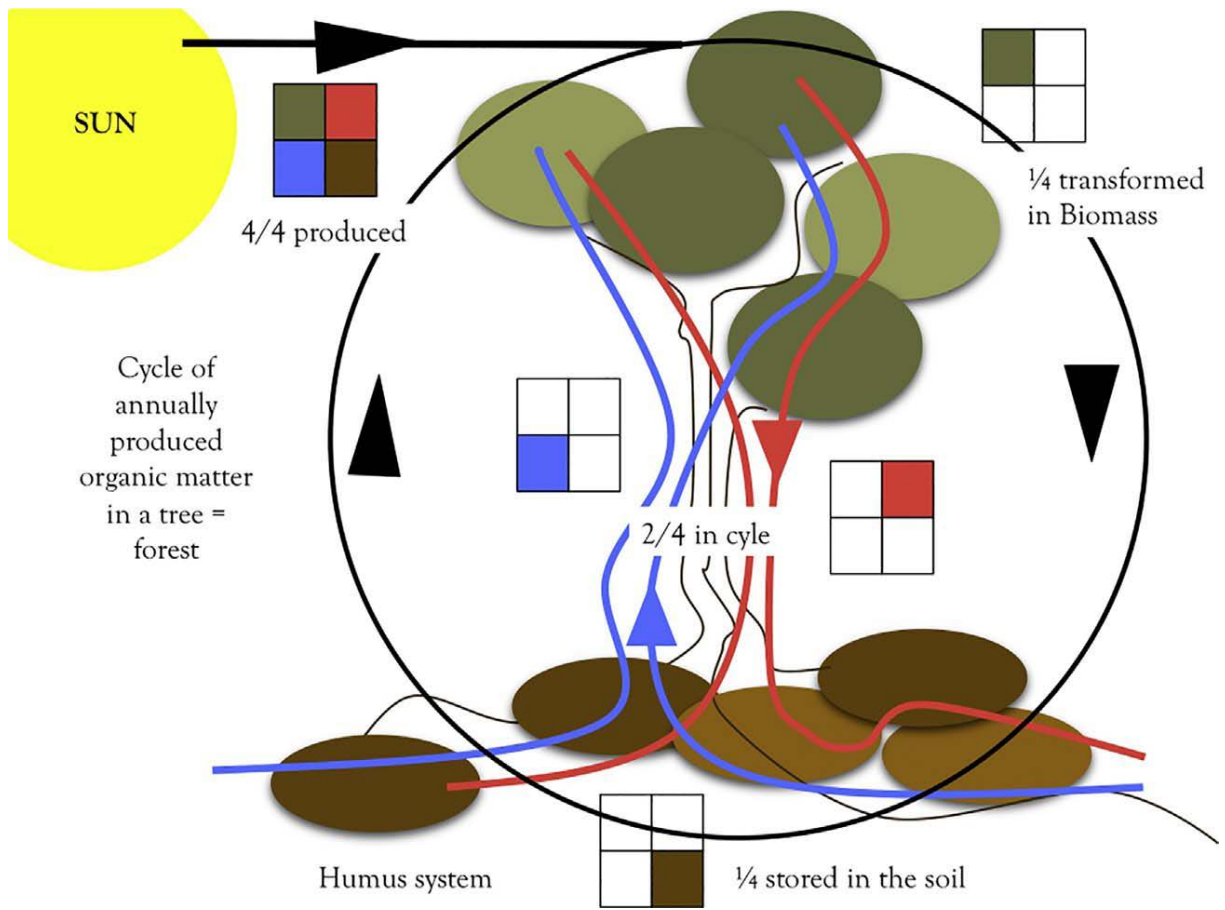


Fig. 6

Litter cycle in a MULL humus system of a temperate broad-leaved forest

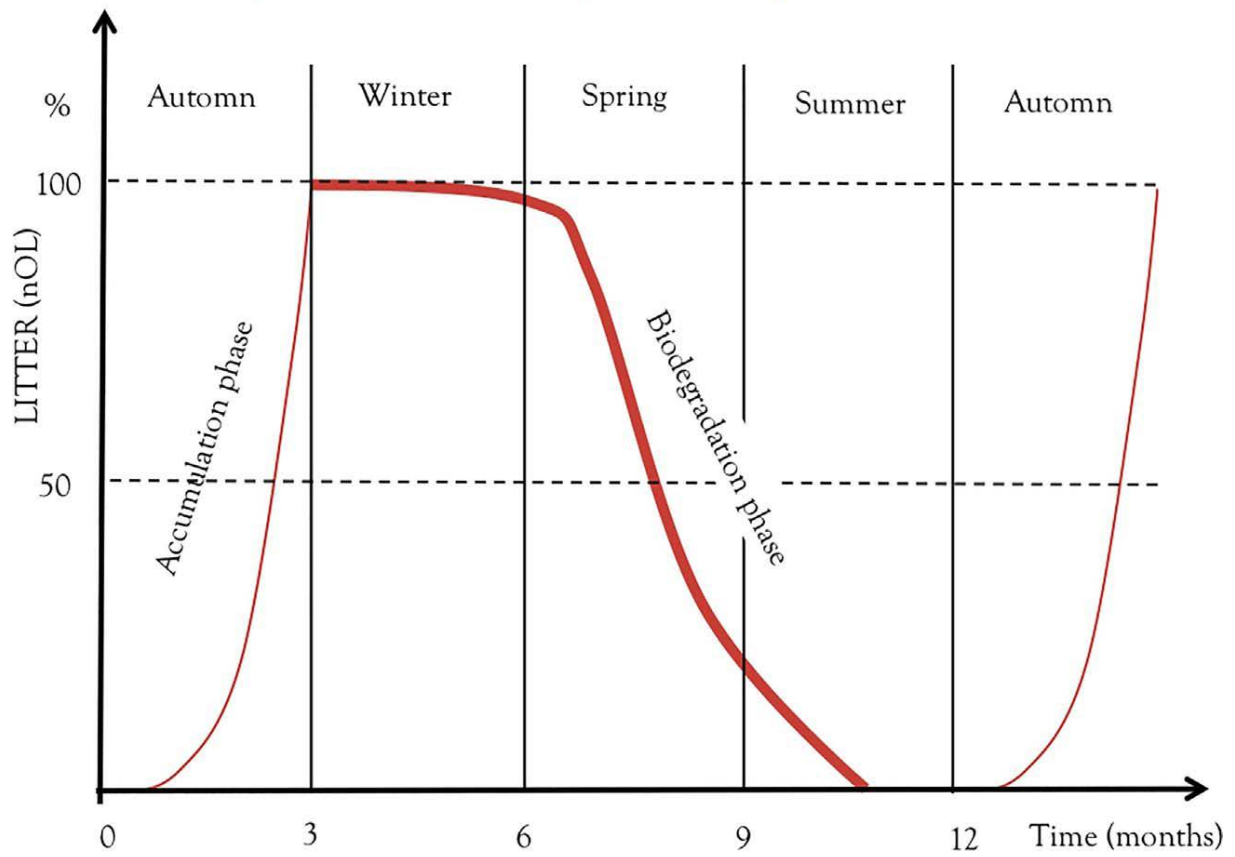


Fig. 7

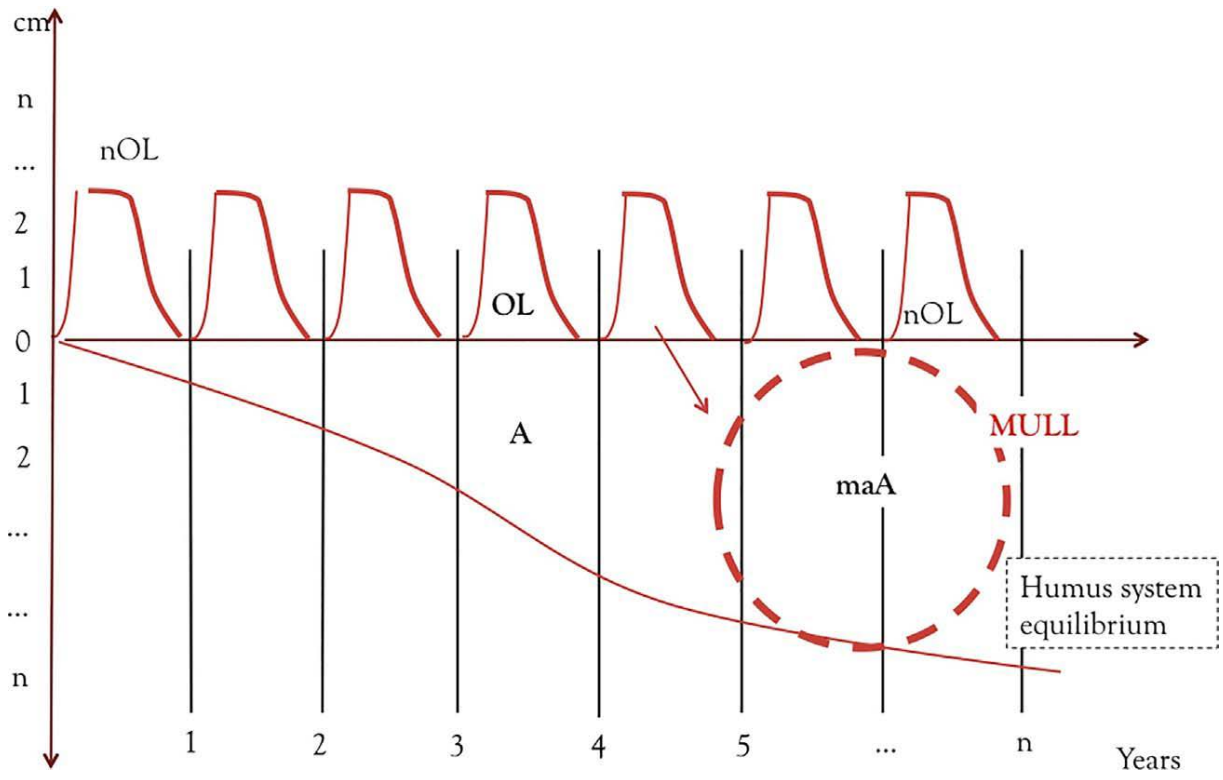


Fig. 8

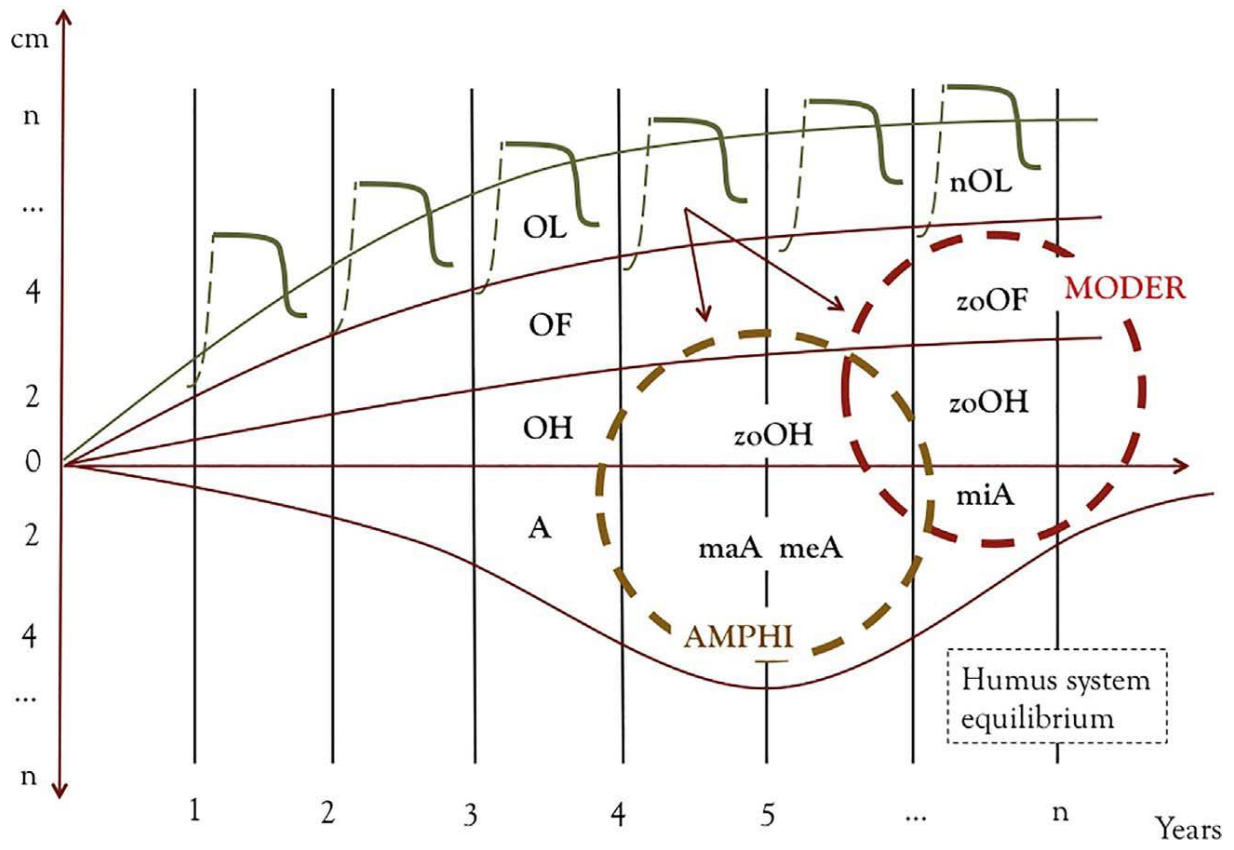


Fig. 9

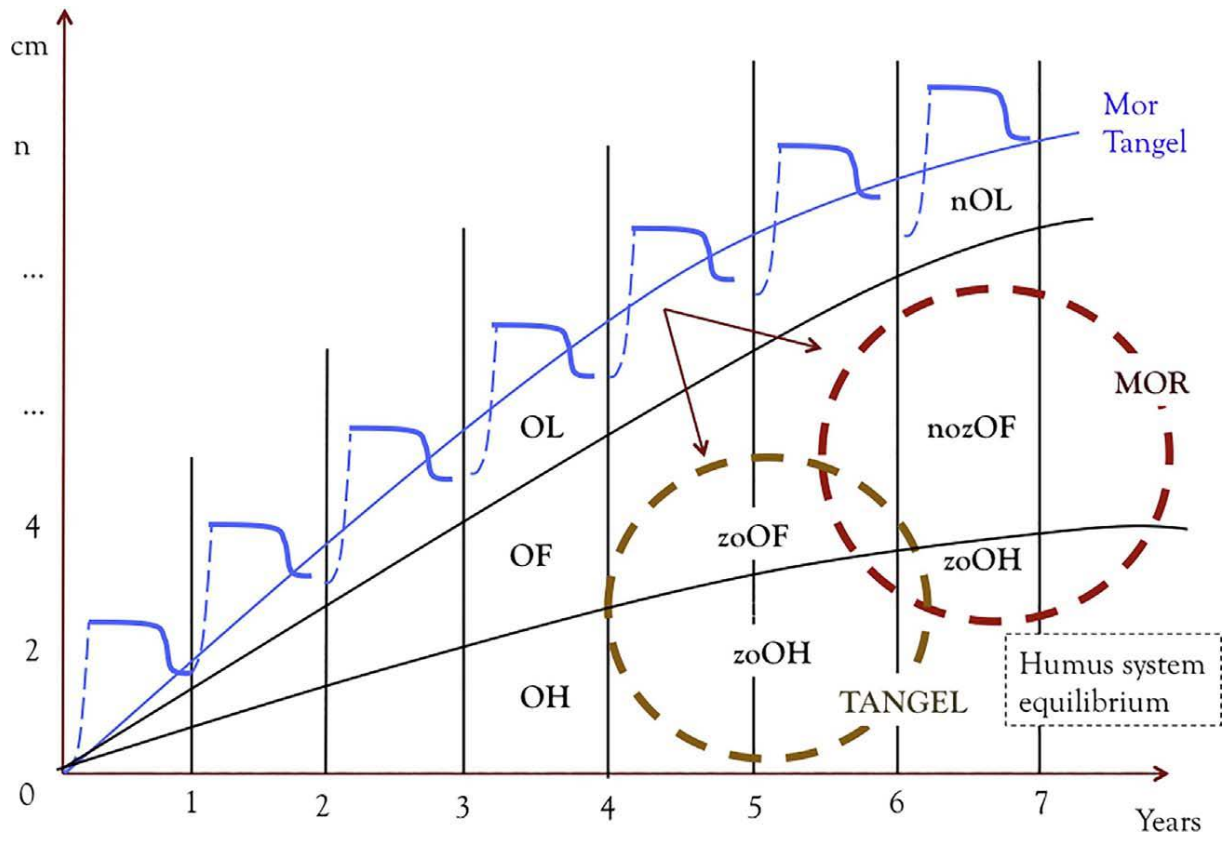


Fig. 10

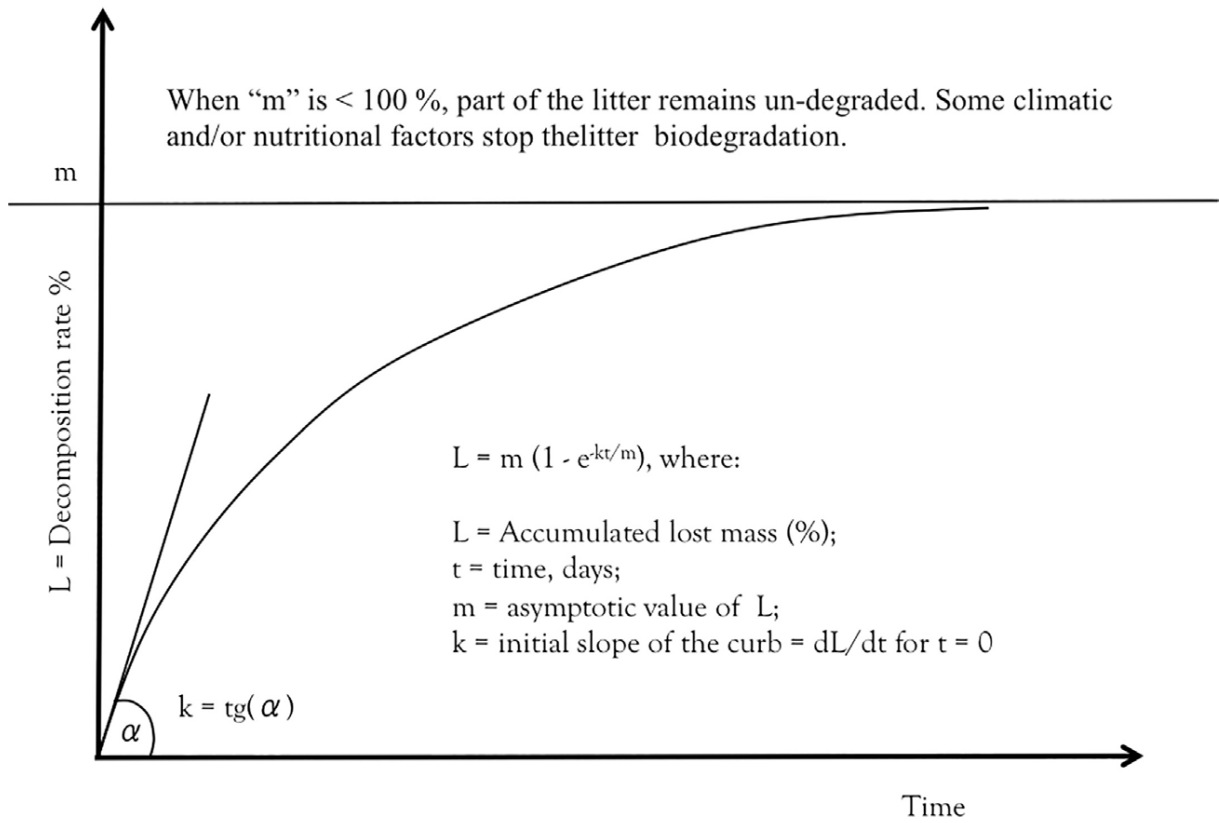


Fig. 11

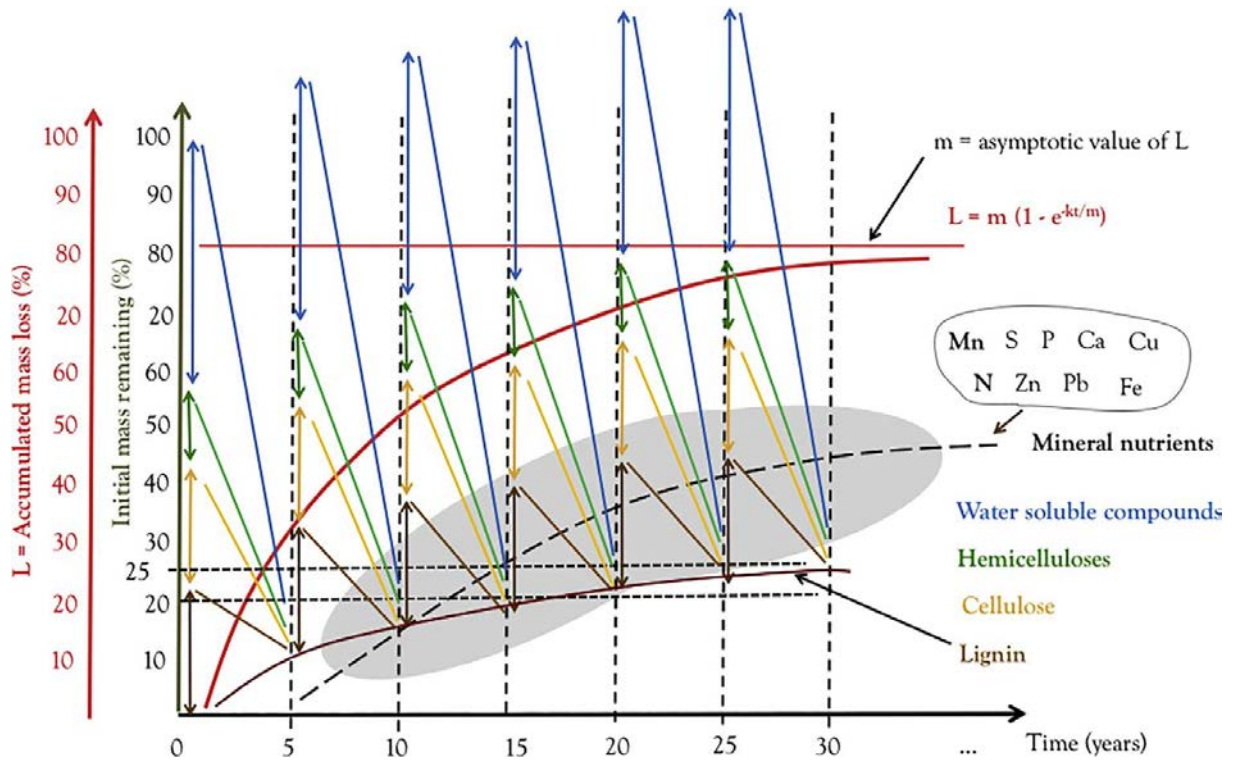


Fig. 12



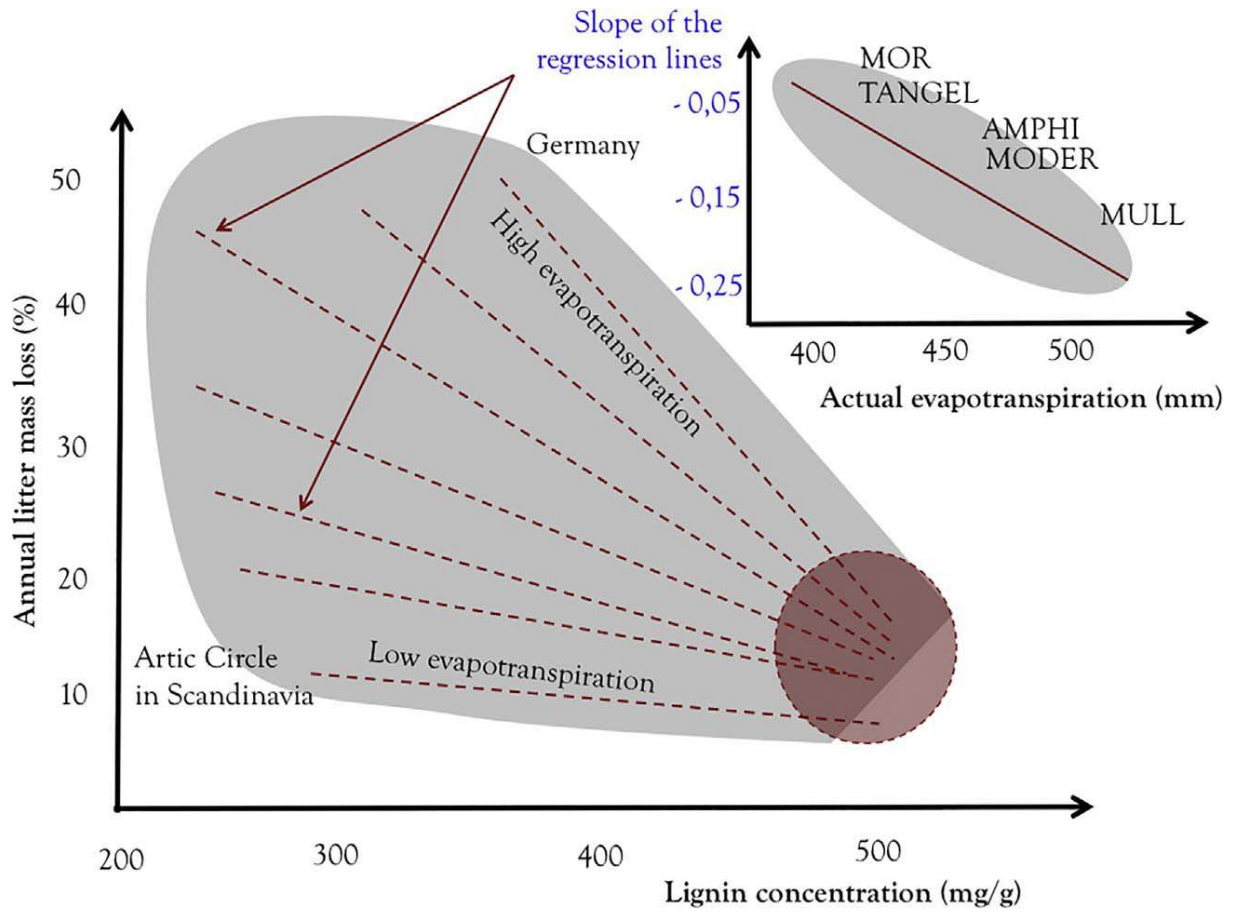
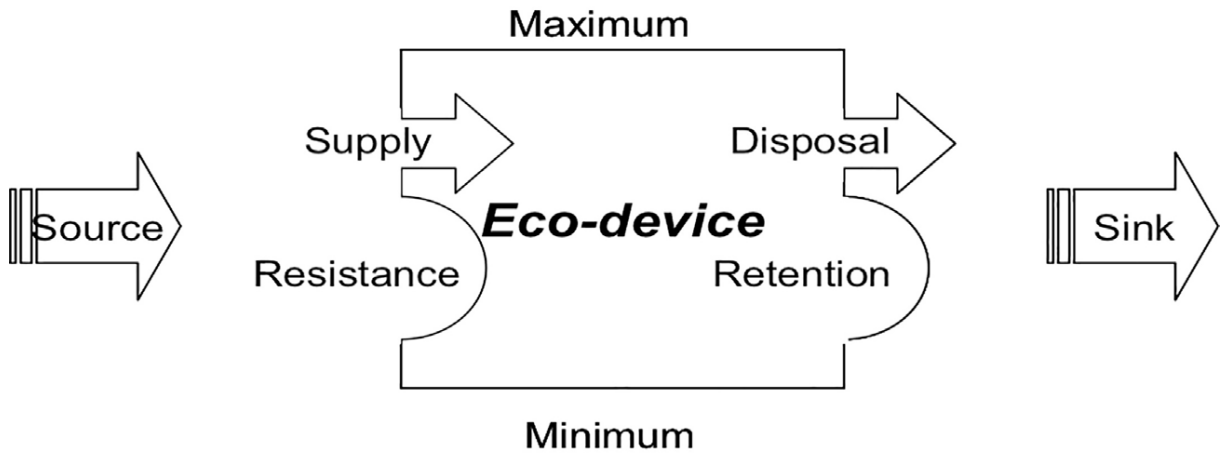


Fig. 13

a)



b)

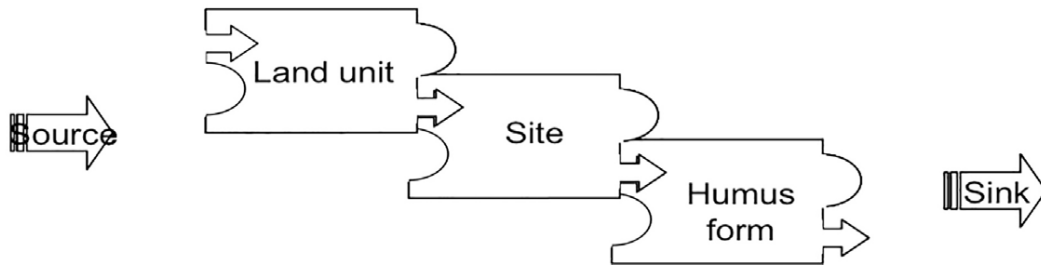


Fig. 14

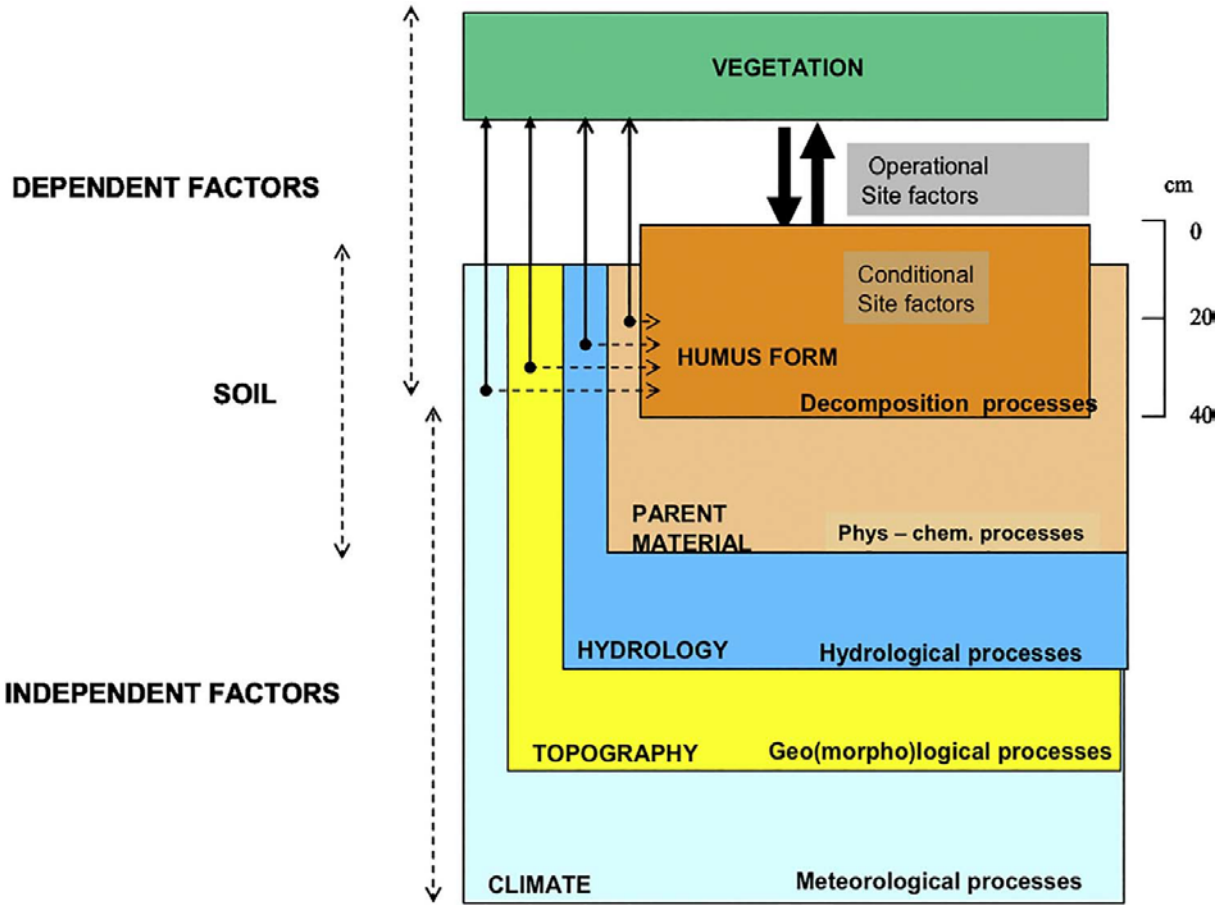


Fig. 15