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1 **Plant-soil feedbacks mediated by humus forms: a review**

2 **Jean-François Ponge***

3 Muséum National d'Histoire Naturelle, CNRS UMR 7179, 4 avenue du Petit-Château, 91800 Brunoy,
4 France

5 Keywords: humus forms, plant-soil relationships, aboveground-belowground biodiversity

6 **ABSTRACT**

7 The present review was undertaken to add more information on the place taken by humus forms in
8 plant-soil interactions. Three questions were asked: *(i)* are humus forms under the control of plant-soil
9 relationships, *(ii)* are humus forms the main seat of these relationships, and *(iii)* can humus forms
10 explain interactions between aboveground and belowground biodiversity. Some conflicting views
11 about humped-back models of species richness may be resolved by considering a limited number of
12 stable humus forms (here considered as ecosystem strategies) which should be treated separately rather
13 than in a single model. Mull, moder and mor pathways are each characterized by a fine tuning between
14 aboveground and belowground communities, the humus form (including litter) being the place where
15 resonance between these communities takes place, both in functional and evolutionary sense.

16

17 **1. Introduction**

18 In their review of aboveground-belowground ecological relationships, Van der Putten et al.
19 (2009) listed case studies and models that explain how terrestrial plant, animal and microbial
20 communities are interconnected and how the study of these interactions may help to predict what
21 happened and will happen in the course of successional processes, landuse change or global change.

* Corresponding author. Tel.: +33 (0) 678930133; fax: +33 (0) 160465719

E-mail address: ponge@mnhn.fr (J.F. Ponge).

1 However, despite their recognition of the importance of soil fertility as a context which might change
2 size and sign of these interactions, they forget the following points:

- 3 • soil fertility is not an invariant but results, at least partly, from recycling and stocking of
4 nutrients by the biotic component of the ecosystem
- 5 • all aboveground-belowground interactions take place in the part of the soil which is enriched
6 in organic matter, i.e. in the humus profile

7 The present review was undertaken to add more information on the place taken by humus forms in
8 plant-soil interactions. In particular we will ask whether:

- 9 • humus forms are under the control of plant-soil relationships
- 10 • humus forms are the main frame of these relationships
- 11 • humus forms can explain interactions between aboveground and belowground biodiversity

12 Both temperate, boreal/mountain and tropical soils are embraced in this review, since according to
13 Anderson and Swift (1983) tropical soils can be only distinguished by the rate at which functions are
14 fulfilled and not by underlying processes.

15 The present approach does not claim to hold the key to all pending questions and facts about
16 aboveground-belowground interactions, which have been debated and detailed by Eisenhauer (2012).
17 Rather, we want to defend the idea that all interactions taking place in the soil between plants,
18 microbes and animals are under the control of a particular environment, the humus form, where these
19 organisms live and evolve together, and contribute in turn to its build-up and maintenance, stemming
20 in an integrated view of the topsoil as a key component of terrestrial ecosystems.

21

22 **2. Are humus forms controlled by plant-soil interactions?**

23 *2.1. What are humus forms?*

1 The concept of humus form has been devised by soil morphologists (Bal, 1970; Pawluk, 1987)
2 to designate and classify the manner humified soil organic matter (SOM), also called humus in
3 chemical sense (Kumada, 1988), appears and segregates from mineral matter along soil profiles. When
4 SOM is intimately mixed with mineral matter within aggregates in a crumbly organo-mineral (A)
5 horizon, resulting from joint effects of root, animal and microbial excreta (Brêthes et al., 1995), the
6 humus form is called 'mull'. Mull is commonly associated with earthworm activity (earthworm mull),
7 but many other agents may contribute to the incorporation of organic matter to the mineral soil, i.e.
8 roots (Velasquez et al., 2007), white-rot fungi (Wilde, 1951), termites (Garnier-Sillam and Toutain,
9 1995), ants (Baxter and Hole, 1967), and although imperfectly from a biological/ecological point of
10 view, mechanical disturbances (Olchin et al., 2008). When SOM segregates from mineral matter,
11 forming an upper organic O horizon rich in fungal mycelia and faunal excrements of varying size,
12 overlying an A horizon made of mineral particles juxtaposed to faunal excrements, the humus form is
13 called 'moder' (Pawluk, 1987; Brêthes et al., 1995). When plant litter is slowly transformed and
14 accumulates, with a sharp transition to a purely mineral E horizon or to the parent rock, the humus
15 form is called 'mor' (Brêthes et al., 1995), showing analogies to sphagnum peat as in its original
16 description by Müller (1884). All three main humus forms have been subdivided in several variants,
17 according to classifications which still need to be harmonized worldwide (Green et al., 1993; Brêthes
18 et al., 1995; Broll et al., 2006; Zanella et al., 2011). Other less common humus forms, such as 'amphi'
19 and 'tangel', have been described, too (Kögel et al., 1988; Galvan et al., 2008; Tagger et al., 2008),
20 more especially on calcareous parent rocks under Mediterranean and subalpine climates, but the
21 present review will focus on the three well-known forms mull, moder, and mor, which spread out on a
22 gradient of decreasing contribution of soil fauna to humification processes (Ponge, 2003). Although
23 many humus forms have been described in the tropics (Garay et al., 1995; Loranger et al., 2003;
24 Kounda-Kiki et al., 2008) they are still in need to be compared and classified, but mention to tropical
25 soils will be made throughout the text when needed. However, it must be noticed at least provisionally
26 that, based on the present knowledge, most tropical humus forms can be considered as variants of
27 mull, moder and mor, which have been described for the first time with these names in temperate areas

1 (Hartmann, 1944). In particular, mull should not be considered as resulting only from earthworm
2 activity, as this is commonly observed in temperate biomes, since other animal groups may contribute
3 to the formation of a crumbly structure where mineral and organic matter are tightly assembled,
4 notably in dry climates where earthworms are disadvantaged, e.g. termites (Garnier-Sillam and
5 Toutain, 1995), tenebrionids (Peltier et al., 2001), or millipedes (Loranger et al., 2003).

6

7 *2.2. Humus forms as ecological attractors of plant-soil interactions*

8 Many authors associated humus forms to environmental factors such as climate, parent rock
9 (Garay et al., 1995; Ponge et al., 2011), and vegetation (Emmer, 1995; Chauvat et al., 2007; Salmon et
10 al., 2008a, b). Climate, parent rock and vegetation can be considered as distal factors setting the stage
11 for the formation of humus forms, of which plant roots, soil invertebrates and microbes are the agents.
12 In his pioneer work Handley (1954) explained mor formation under ericaceous heathland (as opposed
13 to mull in various ecosystems) by the tanning property of heather debris and the negative effect it
14 exerted on soil enzymic activity and nutrient availability. Read (1986, 1993) associated plant
15 communities (grassland, woodland, heathland) and their dominant mycorrhizal habits (resp. vesicular-
16 arbuscular, ectomycorrhizal, ericoid) along environmental gradients of decreasing nutrient availability,
17 exemplified by the transition from mull to mor. Ponge (2003) associated plant, microbial and soil
18 animal communities to humus forms, and hypothesized that mull, moder and mor could be three main
19 strategies which ecosystems evolved in the course of time, mull being characterized by complex
20 trophic networks, feed-backed to high levels of nutrient turnover, productivity and to high plant,
21 animal and microbial functional diversity, opposed to mor with much simpler plant-litter-fungal
22 trophic networks associated to low turnover rates and productivity, moder being in an intermediate
23 position along a gradient of decreasing bulk biological activity. In this concept, vegetation is involved
24 in feed-back loops with animals and microbes, the humus form being the seat of most interactions, and
25 climate and parent rocks the factors which attract (and select) interactions towards one or the other
26 'basin of attraction' (Beisner et al., 2003). This concept of a restricted set of ecosystem 'attractors' (as

1 opposed to a continuum), with the humus form as the seat of feed-back loops between plants, animals
2 and microbes, was based on commonly held views about nutrient cycling and productivity of
3 ecosystems (Flanagan and Van Cleve, 1983; Van Breemen, 1993; Wilson et al., 2001), in the frame of
4 Odum's concept of development of ecosystems (Odum, 1969), to which more modern knowledge
5 about positive and negative feed-back loops between compartments of the ecosystem was added
6 (reviewed in Ehrenfeld et al., 2005). The idea of selection acting on whole ecosystems rather than on
7 individual species is not new (Lovelock, 1979; Chapin, 1993) but it found renewed interest in the
8 study of microbial communities (Swenson et al., 2000; Williams and Lenton, 2007).

9 As mentioned above, humus forms are an association of organic and mineral matter, in
10 variable arrangement according to diagnostic O and A horizons (Brêthes et al., 1995). Soil organic
11 matter comes from the transformation into humus of dead parts and excreta of terrestrial plants,
12 microbes and animals (Pawluk, 1987; Johnston et al., 2004). Some soil animals, the so-called 'soil
13 engineers' (earthworms, termites, ants...), have a decisive influence on the control of SOM levels, in
14 particular in tropical biomes where humified organic matter is of paramount importance for the
15 sustainability of moisture and nutrients (reviewed in Wolters, 2000). Soil mineral matter comes from
16 the weathering of rocks, mediated by chemical and biological agents (Augusto et al., 2001; Carpenter
17 et al., 2007; Frey et al., 2010). Both organic and mineral matter transformations are under the control
18 of climate (De Deyn et al., 2008; Egli et al., 2010), and any variation in the quantity and quality of
19 mineral and organic inputs will influence the alimentary habits and way of life of organisms which
20 relies on them for growth, survival and reproduction (Sticht et al., 2008).

21

22 *2.3. How plants react to humus forms, and the reverse*

23 The quantity and quality of organic matter falling on the ground, or resulting from the death of
24 subterranean parts of plants, depend on the availability of:

- 25 • carbon dioxide in the atmosphere

- 1 • soil nutrients and throughfall
- 2 • sun, heat and water
- 3 • herbivory and various injuries

4 and is at least partly under genetic control, some species or genotypes having less exacting
 5 requirements than others. Any defect in plant requirements may stem in resistance forms such as
 6 sclerophylly, succulence, synthesis of secondary metabolites, evergreen foliage or prostrated life
 7 habits, which influence in turn litter amount and quality (Aerts 1995). In the frame of plant-soil
 8 relationships much has been said about the way by which any decrease in nutrient availability may
 9 make the foliage more resistant to decay (Fig. 1, path 1) through increased synthesis of secondary
 10 metabolites, in particular lignins, tannins or terpenes which:

- 11 • make litter components more recalcitrant or deterrents to herbivory and saprovoxy (Bernays et
 12 al., 1989; Bardgett et al., 1998; Hättenschwiler and Vitousek, 2000)
- 13 • control symbiotic associations through direct (Peters and Verma, 1990) and indirect
 14 associations (Jousset et al., 2008)
- 15 • interact negatively with other nutrients (Aerts, 1995; Hättenschwiler and Vitousek, 2000)

16 This process has been identified at:

- 17 • the community level in the form of species replacements along environmental gradients
 18 (Pastor et al., 1984) or in the course of succession (Wardle et al., 1997)
- 19 • the species level in the form of selection of better adapted suites of traits (Chapin et al., 1993;
 20 Northup et al., 1995a; Hättenschwiler et al., 2003) or acclimation through phenotypic
 21 plasticity (Glyphis and Puttick, 1989)

22 However, some interesting decoupling between foliage and litter quality has been demonstrated by
 23 Hättenschwiler et al. (2011): in tropical rain forests with rapid recycling of nutrients through a

1 superficial network of plagiotropic roots (St. John et al., 1983) and intense withdrawal before leaf
2 abscission (Hättenschwiler et al., 2008), nutrient-poor litter is not necessarily associated with nutrient-
3 poor foliage, contrary to what is currently observed in temperate forests (Niinemets and Tamm, 2005;
4 Hagen-Thorn et al., 2006). Other aspects of litter quality, such as synergetic effects of the diversity of
5 litter components available to decomposer communities, should not be neglected, too (McLaren and
6 Turkington, 2011; De Marco et al., 2011).

7 What effects can be expected from any increase in the recalcitrance of litter? First, a delay is
8 necessary for leaching or degrading tannins or terpenes (Kuiters and Sarink, 1986) and demasking
9 cellulose through lignin degradation (Austin and Ballaré, 2010) before litter components rich in
10 secondary metabolites can be consumed (and digested) by saprovores (Soma and Saitô, 1983; Sadaka-
11 Laulan & Ponge, 2000), stemming in increased litter thickness. Second, an increase in secondary
12 metabolites is often accompanied by a decrease in macro-nutrients other than carbon, such as N, P, Ca,
13 among others (Nicolai, 1988), all of them being needed in greater amounts by macro-saprophages,
14 which feed only on plant litter (David et al., 1991), than by micro-saprophages, which feed on nutrient
15 accumulators such as fungi and bacteria (Graustein et al. 1977; Clarholm 1985a; Van der Heijden et al.
16 2008). Animals of the latter group are given access to richer food, a strict requirement of their higher
17 metabolic rate (Reichle, 1968; Spaargaren, 1994). As a consequence, small-sized consumers will be
18 favoured against big-sized consumers, in other terms saprophagous micro-invertebrates (enchytraeids,
19 micro-arthropods) will be favoured against saprophagous macro-invertebrates (earthworms, molluscs,
20 woodlice, millipedes, insects). Beside this body size effect, which prevents bigger animals to reach
21 nutrient-rich microbial colonies, many macro-invertebrates need more nitrogen and calcium than
22 animals of smaller body size, because they excrete either mucus (earthworms, molluscs, termites) or a
23 thick carapace which has to be renewed, and thus is partly lost, during ecdysis (millipedes, woodlice,
24 insect larvae). These processes stem in a disadvantage for saprophagous macro-invertebrates when
25 feeding on nutrient-poor, recalcitrant litter (Fig. 1, path 2). This is currently avoided by selecting
26 nutrient-rich litter (Satchell and Lowe, 1967; Nicolai, 1988; Loranger-Merciris et al., 2008) and
27 vegetation patches under which to live in heterogeneous environments (Babel et al., 1992; Ponge et

1 al., 1999; Kounda-Kiki et al., 2009). This results in a litter-controlled shift from mull, dominated by
2 saprophagous macro-invertebrates, to moder, dominated by saprophagous micro-invertebrates (Van
3 der Drift, 1962; Schaefer and Schauer mann, 1990; Scheu and Falca, 2000). Ponge et al. (1997) showed
4 that mull and moder humus forms from 13 beech forests of the Belgian Ardennes differed mainly by
5 the contribution of saprophagous micro- and macro-invertebrates to the total soil fauna (microfauna
6 were not considered in this study). Mor is just an exacerbation of this litter control effect, the micro-
7 invertebrate transformation of litter being in turn disfavoured, turning to direct extraction by symbiotic
8 fungi of nutrients accumulated in dead plant parts (Abuzinadah et al., 1986; Näsholm et al., 1998).
9 Notable exceptions to this rule (bigger saprophages cannot feed on nutrient-poor food sources) are
10 patterns associated with social invertebrates such as ants and termites which collect and concentrate
11 plant remains in their nests, allowing these macro-invertebrates to live in nutrient-poor environments
12 (Brossard et al., 2007; Domisch et al., 2008). A parallel selection occurs in soil microbial
13 communities, the fungal/bacterial biomass ratio being driven by vegetation changes (Eskelinen et al.,
14 2009; Mitchell et al., 2010), suggesting the existence of fungal vs bacterial-based food webs (Hedlund
15 et al., 2004), which have been associated to mor/moder vs mull humus forms, respectively (Karroum
16 et al., 2005; Frouz and Nováková, 2005). Priming effects of macroorganisms (typical of mull humus
17 forms) on microflora have been suggested as driving factors of plant-bacterial associations (Lavelle
18 and Gilot 1994). Bradley and Fyles (1996) showed that root activity stimulated C and N cycling in
19 mull while it did not have any effect on it in mor soil, pointing on the existence of a 'mull' model
20 based on rapid and indirect N and C cycling, stimulated by both plant root and macrofaunal activity, as
21 opposed to a conservative 'mor' model based on slow and direct nutrient cycling (involving
22 mesofaunal activity in moder) in the organic matter accumulated by vegetation. The mull/mor contrast
23 is reminiscent of the contrast depicted in spodosols by Parmelee et al. (1993) between organic
24 horizons, where tree roots limit microbial activity, to mineral horizons, where microbial activity is
25 stimulated by root activity In tropical rainforests, the organic reservoir of moder and mor is replaced
26 by the tree biomass (including roots), where most nutrients accumulate and circulate with a poor
27 contribution of belowground food webs (Hilton, 1987; Johnson et al., 2001). In this sense the humus

1 forms can be considered as the showcase of the soil foodweb (Pimm et al. 1991), justifying its use as a
2 proxy of soil nutrient regime (Wilson et al., 2001; Ponge et al., 2002; Ponge and Chevalier, 2006) and
3 stand productivity (Delecour and Weissen, 1981; Ponge et al., 1997; Ponge and Chevalier, 2006).

4 Another, as yet neglected aspect of litter recalcitrance was recently raised by Berg et al.
5 (2010): the initial concentration of manganese in litter (and thus Mn availability in the soil) was shown
6 to exert a prominent influence on decomposition rates, although underlying mechanisms are still
7 poorly known, reinforcing views about the importance of this oligo-element in the genesis of humus
8 forms (Ponge et al., 1997).

9

10 *2.4. Some pending questions about the role of microbial communities in the genesis of humus forms*

11 Other aspects of plant-soil interactions are involved in the control of processes through which
12 organic matter accumulates or disintegrates in the topsoil and in the genesis or disappearance of
13 horizons, i.e. in the control of humus forms. In particular, stemming from abovementioned seminal
14 studies by Read and collaborators (Read et al., 1985; Read, 1986, 1991) and from older observations
15 on the key role of symbiotic fungi in plant-soil relationships (Handley, 1954; Meyer, 1964), the
16 importance of microbial communities associated to the rhizosphere has been recognized as pivotal to
17 the whole ecosystem (Van der Heijden et al., 2008; Schnitzer et al., 2011). Can these communities
18 influence durably their surrounding environment, hence modify or stabilize the humus form? That
19 plants-soil interactions influence the decomposition of organic matter via rhizosphere microbial
20 communities is now well-established experimentally (Sutton-Grier and Megonigal, 2011; Zhu and
21 Cheng, 2011; Robertson et al., 2011). However, the applicability of laboratory inoculation
22 experiments to field conditions has been recently questioned (Courtois and De Deyn, 2012) and we
23 may wonder whether rhizosphere bacterial and fungal communities are able, by themselves or under
24 vegetation control, to change their environment (exemplified by the humus form) in order to make it
25 more favourable to plant/microbial requirements. The best example of such durable action of a
26 rhizosphere micro-organism on the humus form is the ectomycorrhizal fungus *Cenococcum*

1 *geophilum*. This widespread ascomycete, known as dark sterile mycelia protruding from jet-black
 2 mycorrhiza, has been shown to be intimately associated with thick litter layers (Meyer, 1964; Ponge,
 3 1990), where it is able to take use of organic nitrogen for host and own requirements (Dannenmann et
 4 al., 2009). Given the poor palatability and degradability of its thick hyphal walls (Ponge, 1991), and its
 5 antibiotic activity, shown to be transferred from roots to tree foliage (Grand and Ward, 1969),
 6 *Cenococcum geophilum* acts as a sink for carbon and nitrogen, contributing to the accumulation of
 7 recalcitrant organic matter of microbial origin. Due to a higher tolerance of adverse conditions,
 8 compared to most other ectomycorrhizal fungi (Holopainen et al., 1996; di Pietro et al., 2007), its
 9 dominance in stressful environments, whether natural or man-made, may lead to irreversible changes
 10 in the topsoil, stemming in the passage from mull to mor according to a positive (self-reinforcing)
 11 feedback process.

12

13 **3. Are humus forms the frame of indirect feedbacks between plant and soil communities?**

14 *3.1. Symmetrical interactions between plant and soil communities are mediated by humus forms*

15 Indirect feedbacks between plant and soil communities are mediated by the environment
 16 common to both plant and soil organisms, i.e. by the part of the soil which is enriched in organic
 17 matter by the decomposer system which transform plant debris into available nutrients (mineralisation)
 18 and humus (humification).

19 If we consider the time required for nutrients present in litter to be recycled through the
 20 degradation of organic matter until its final mineralisation, any delay in this cycle, which may range
 21 from a few weeks to several years (Enriquez et al., 1993; Zhang et al., 2008), will impoverish the
 22 vegetation via a decrease in immediate nutrient availability. Exceptions are:

- 23 • the direct extraction of nutrients from rock and atmosphere by plant roots and their microbial
 24 associates (Arocena and Glowa, 2000; Landeweert et al., 2001; Lambers et al., 2009)

- 1 • man-made occasions such as fertilisation and atmospheric deposition (Falk et al., 2010)
- 2 • black carbon, originating from charcoal, as a source of stable humus able to retain nutrients in
- 3 tropical soils, as in the famous Amazonian ‘Terra preta de indio’ (Glaser et al., 2001)
- 4 In most cases the degradation of litter is necessary to ensure the normal growth of vegetation, because:
- 5 • the litter compartment contains most nutrients which vegetation needs (Vinton and Goergen,
- 6 2006)
- 7 • the rate at which litter is degraded controls the rate at which nutrients are taken up by
- 8 vegetation (Chapin et al., 1986; De Deyn et al., 2008)

9 This link between litter decomposition rate and nutrient availability (Fig. 1, path 3) generates a

10 positive feed-back loop: the richer the litter, the faster organic matter is degraded, the faster nutrients

11 are recycled through soil trophic networks, and the faster vegetation grows (Wedin and Tilman, 1990;

12 Northup et al., 1995b; Orwin et al., 2010). Limits to this feed-back loop between decomposition rate

13 and nutrient availability are cases where climate or soil features mask these effects. In tropical rain

14 forests, abundance of heat and moisture allows a rapid decomposition of litter whatever its nutrient

15 richness (Hättenschwiler et al., 2011). In the same way, waterlogging may impede the activity of

16 burrowing animals whatever litter quality (Valckx et al., 2010).

17 Within the abovementioned limits this succession of interconnected control processes results

18 in a selection of plant species and traits among vegetation, since more nutrient-exacting plant species

19 are those which contain nutrients in a higher amount, and thus those the litter of which will be

20 degraded more easily (Aerts, 1995; Northup et al., 1998; Orwin et al., 2010). Choices exerted by

21 saprophagous animals contribute to this selective process: if more palatable nutrient-rich litter species

22 (the ‘mull’ plant group) are preferred to nutrient-poor litter species (the ‘moder’ plant group), then

23 nutrients of the former group will be recycled (and thus transferred to vegetation) sooner than those

24 from the discarded group (Fig. 1, path 4). The discriminative power of litter-consuming animals

25 generates a bifurcation between two stable alternative states (Stone and Ezrati, 1996), exemplified by

1 mull (rapid recycling of nutrients through a variety of nutrient-exacting organisms, ‘dissipative
 2 pathway’, all signs switched to + on Fig. 1) and moder (slow recycling of nutrients through a few
 3 tolerant organisms, ‘conservative pathway’, all signs switched to – on Fig. 1). Thus plant litter controls
 4 soil animal and microbial communities, but it can also be said that soil organisms control plant
 5 communities (and thus litter) to the same extent (Bradford et al., 2002; Wurst et al., 2004; Van der
 6 Heijden et al., 2008; Eisenhauer et al. 2010), making rather obsolete basic assumptions about top-
 7 down versus bottom-up control in cascade models (Hunter and Price, 1992; Mikola and Setälä, 1998;
 8 Ponsard et al., 2000). Mull, moder and mor pathways are each characterized by a fine tuning between
 9 aboveground and belowground communities, humus forms (including litter) being the place where
 10 resonance between these communities takes place, both in functional and evolutionary sense. This fine
 11 tuning may breakdown (before being reconstructed on another template) under the influence of
 12 environmental degradation (Van Delft et al., 1999; Kiers et al., 2010), along ecotones (Goldberg,
 13 1982; Parmentier et al., 2005; Sarthou et al., 2010) and in the course of primary (Tilman, 1985;
 14 Emmer and Sevink, 1994; Hodkinson et al., 2004) and secondary succession (Ponge et al., 1998;
 15 Salmon et al., 2006). The present scheme is in accordance with:

- 16 • the non-stochastic component of community assembly (Drake, 1990; Weiher and Keddy,
 17 1995; Belya and Lancaster, 1999)
- 18 • the evolutionary model of Lambers et al. (2009) which associates plants, soils and microbes in
 19 self-stabilized mutualistic units of selection
- 20 • the concept of among-group selection developed by Wilson (2004)
- 21 • niche conservatism (Wiens et al., 2010)

22 It replaces mutualism in a wider environmental and evolutionary context than just friend-friend
 23 relationships (Boucher et al., 1982; Howe, 1984), replacing them by a network of commonly-evolved
 24 signalling (hormonal) processes linking plants, animals and microbes living in the same community
 25 (Canellas et al., 2002; Bonkowski and Brandt, 2002; Blouin et al., 2005). This vision, which is

1 growing in soil ecology (Lavelle et al., 2006) is strongly related to theories of self-organization
2 emergence, which have been successfully applied to ecology (Holling, 1973; Levin, 1998; Ponge,
3 2005) and social sciences (Garmestani et al., 2009; Moussaïd et al., 2011).

4

5 *3.2. A hierarchy of controlling factors*

6 Apart from these symmetrical interactions, which play a role at the inside of ecosystems, other
7 factors act asymmetrically, i.e. are not immediately under the control of feed-back processes between
8 plant and soils, at least if we restrain our scrutiny to the scale of, say, a forest stand or a meadow, and
9 over a few decades only (De Deyn et al., 2008). Climate, the action of which can be described in terms
10 of heat and water availability, increases or decreases the rate of most biotic and abiotic processes thus,
11 among others, rates of litter decomposition and mineral weathering (Ponge et al., 1998; De Deyn et al.,
12 2008). Similarly, the nature of the parent rock (in particular its mineralogical composition) controls the
13 rate at which nutrients included in rock minerals (P, Ca, Mn, Fe, Si, Al, etc.) can be transferred to the
14 ecosystem (Augusto et al., 2000). Despite the prominent role of vegetation and soil organisms in the
15 genesis of humus forms, earthworm mull, for instance, cannot be built when and where nutrients are
16 not in enough rates in the parent rock (Satchell, 1980). Climate has a decisive influence on the rate of
17 nutrient transfer from the parent rock to the ecosystem (White and Blum, 1995), and on the rate on
18 nutrient cycling and carbon sequestration within the ecosystem (Ponge et al., 1998; De Deyn et al.,
19 2008). The parent rock determines the total amount of weatherable minerals and the weathering rate
20 (Norton and von Blanckenburg, 2010), while the climate determines water and heat availability, with a
21 feed-back loop to antecedent soil conditions, pointing to the possible existence of climate ‘strategies’
22 (d’Odorico and Porporato, 2004). Correlations between climate and parent rock are often encountered,
23 in particular in mountain environments where geology, temperature and rainfall vary in parallel
24 according to altitude, acidic rocks and abundant precipitations being found at higher elevation
25 according to orogenic properties (Roe, 2005). That humus forms are distally controlled by climate and
26 geology has been demonstrated in the abovementioned study of 13 beech stands (Ponge et al., 1997)

1 and in a study embracing a wide variety of coniferous and deciduous forest stands covering the whole
2 French territory (Ponge et al., 2011). If humus forms are the stable, visible result of interactions
3 between plants, animals and microbes, and the place where most of these interactions take place, it
4 ensures that geology and climate will act more directly on them (as a habitat) than on organisms
5 themselves. This view corresponds to the hierarchy of determinants of litter decomposition proposed
6 by Lavelle et al. (1993), further supported by a global decomposition experiment embracing a wide
7 array of biogeographic domains (Wall et al., 2008). Given climate, geological and topographical
8 conditions, pronounced changes in humus forms follow variations in litter quality in time (Bernier and
9 Ponge, 1994) and space (Ponge et al., 1999).

10 It has been long time debated whether organisms which contribute to the degradation of
11 organic matter (decomposer microbes and animals) increase nutrient availability for plants or on the
12 contrary tend to immobilize nutrients in their biomass or excreta (Webb, 1977; Clarholm, 1985b).
13 Most experimentalists which concluded to the immobilisation of nutrients by microbial communities
14 were right in their conclusions when they considered only the net result of microbial loops
15 (Bonkowski, 2004) but wrong in their conclusions when they concluded on net nutrient availability
16 (Kooijman et al., 2008), because they did not take into account the mobilizing action of microbial
17 feeders (predation), which has been amply demonstrated by elsewhere (Ingham et al., 1985; Kuikman
18 et al., 1990; Bonkowski et al., 2000). This indicates a need to replace microcosm studies in a realistic
19 field framework as suggested by Bradford et al. (2002) and to take into account the whole array of
20 processes which ensure the stability of soil food webs, and thus of plant-soil relationships (Wardle and
21 Lavelle, 1997; Brussaard, 1998; Hedlund et al., 2004). Some examples are given below.

22 Martin (1991) showed that tropical earthworms increased SOM content when the soil was
23 poor in it and decreased SOM content in the opposite condition. Basker et al. (1994) showed that
24 European earthworms increased potassium availability when the soil was poor in it and the contrary in
25 soil richer in K. Similar stabilizing effects were observed with acid rains (Belotti and Babel, 1993;
26 Scheu and Wolters, 1991), which could be explained by buffering properties of mucus excreta

1 (Schrader, 1994). In all these cases earthworms generated negative feed-back loops, forcing the soil
2 (and thereby the ecosystem) to adapt itself to their own requirements, and creating a stable
3 environment. As a consequence, soil and vegetation degradation are currently associated with
4 earthworm disappearance, whether in temperate (Van Delft et al., 1999) or tropical environments
5 (Decaëns et al., 1999). Similar threats concern other mull-forming ecosystem engineers such as
6 termites (Jouquet et al., 2011). However, it must be noticed that earthworm activity has been thought
7 in some instances to be responsible for the degradation of the environment. This is the case in
8 temperate agricultural soils, where the casting activity of the endogeic earthworm *Allolobophora*
9 *chlorotica* was shown to decrease structural stability and increase soil compaction (Milleret et al.,
10 2009a, b). Similar processes are mediated in South America by *Pontoscolex corethrus* (Hallaire et
11 al., 2000) as well as by *Millsonia anomala* in Africa (Derouard et al., 1997), causing irreversible
12 pasture damage in the neotropics (Chauvel et al., 1999) where the compacting action of *P. corethrus*
13 cannot not counteracted by opposite effects of complementary species (Hallaire et al., 2000).
14 However, it should be noticed that detrimental effects of tropical earthworm species have been
15 registered only in areas which suffered from severe deforestation followed by permanent agricultural
16 landuse, known to decrease subterranean biodiversity (Jones et al., 2003; Rossi et al., 2010). Under
17 'slash-and-burn' agriculture, a traditional method of shifting cultivation using fire to create moderate
18 transitory openings, the same *P. corethrus* which is known to degrade permanent pastures (Chauvel
19 et al., 1999), was shown to initiate the mixing of finely divided charcoal with the topsoil mineral
20 matrix (Topoliantz and Ponge, 2005), a mechanism thought to have contributed to the formation of
21 black carbon and stable humus in the fertile Amazonian Dark Earths (Ponge et al., 2006).

22 Some other studies showed that litter adapts its decomposer communities to vegetation
23 requirements (Hansen, 1999). Studies on mor/moder adapted plants such as *Deschampsia flexuosa*
24 showed that in the presence of elevated amounts of monomeric aluminium, known to be associated
25 with strong acidity (Boudot et al., 1996) they excreted high amounts of organic acids, thereby
26 chelating Al^{3+} cations and thus decreasing aluminium toxicity (Schöttelndreier et al., 2001). Such
27 negative feed-back loops prevent the system to evolve toward another basin of attraction, and explain

1 its resilience (Bengtsson, 2002; Beisner et al., 2003; Scheffer and Carpenter, 2003). They are
2 complementary to positive feed-back loops which are driving forces of main changes taking place at
3 the ecosystem level (Bengtsson et al., 1996). Stabilising forces of biological nature act in parallel to
4 mineral buffers, the importance of which has been stressed by Ulrich (1986, 1994).

5

6 **4. What humus-lodged feedbacks imply for plant and soil biodiversity?**

7 *4.1. Humus forms and the aboveground-belowground debate*

8 Many studies tried to discern relationships between aboveground and belowground
9 biodiversity (Hooper et al., 2000; Loranger-Merciris et al., 2006; Rodríguez-Loinaz et al., 2008; Van
10 der Putten et al., 2009). There seems to be a consensus about a dominance of indirect above direct
11 relationships between these two compartments (Perry et al., 1989; Scheu et al., 1999; De Deyn et al.,
12 2003), if we except organisms which directly act on plant growth and nutrition and which co-evolved
13 with plants, such as symbiotic bacteria and fungi, herbivores, pathogens and parasites (Ehrenfeld et al.,
14 2005; Van der Heijden et al., 2008; Lambers et al., 2009; Van der Putten et al., 2009). Obviously, the
15 saprophagous (decomposer) compartment of the belowground community (and its predatory guild, i.e.
16 the decomposer system *sensu lato*) relies more on (i) quantity and quality of organic matter, and (ii)
17 physicochemical environment, both being exemplified by humus forms, than to vegetation itself (Paje
18 and Mossakowski, 1984; Eskelinen et al., 2009; Mitchell et al., 2010). However, some studies show
19 that signals are transmitted directly to the plant by soil saprophagous organisms (Bonkowski and
20 Brandt, 2002; Blouin et al., 2005), and the reverse (Peters and Verma, 1990; Jousset et al., 2008), and
21 that soil engineers may impact directly the soil seed bank (McRill and Sagar, 1973; Thompson et al.,
22 1994; Eisenhauer et al., 2009). Given the importance of the immediate environment (the humus form)
23 for the maintenance of soil biodiversity, and the existence of feedbacks between plant and soil
24 communities, the question can be shared in two parts, which in a first step can be treated separately, (i)
25 which relationships between humus forms and soil biodiversity, and (ii) which relationships between
26 humus forms and plant biodiversity.

1

2 *4.2. Humus forms and soil biodiversity*

3 The association of humus forms with particular features of soil animal and microbial
4 communities has been studied and debated for a long time. After Bornebusch (1930), Van der Drift
5 (1962) showed that mull was richer in invertebrates of a big size (earthworms, woodlice, millipedes)
6 compared to mor (moder being ignored or more often confused with mor in most biological studies).
7 Comparisons between forest stands of varied humus forms (often associated with varied canopy
8 composition) show that mull is richer in animal forms than moder, and saprophagous macro-
9 invertebrates make the difference (Schaefer and Schauer mann, 1990; Scheu and Falca, 2000). This
10 was verified in forest stands of the same canopy composition growing in a variety of environmental
11 conditions (David et al., 1993; Ponge et al., 1997; Salmon et al., 2008a) or in the course of primary
12 and secondary successions (Scheu, 1992; Kounda-Kiki et al., 2004; Salmon et al., 2006, 2008b),
13 stemming in the scheme drawn by Ponge (2003) of a gradient of increasing soil biodiversity from mor
14 to moder then to mull. When functional diversity is approached by classifying animals into families or
15 groups of a supra-specific taxonomic level mull is characterized by an increase in zoological richness
16 compared to moder and mor (Ponge et al., 1997; Popovici and Ciobanu, 2000). That there are more
17 animal groups (and thus more functions fulfilled) in humus forms dominated by earthworm activity, is
18 now beyond doubt (Loranger et al., 1998; Decaëns, 2010), a view justified by the existence of positive
19 asymmetrical interactions between macro- and micro-invertebrates (Wickenbrock and Heisler, 1997;
20 Salmon, 2004; Gutiérrez-López et al., 2011). Animals of a big size create locally micro-habitats, e.g.
21 casts, burrows, nests and middens (Szlavec z, 1985; Maraun et al., 1999; Decaëns et al., 1999) and
22 provide food resources, e.g. plant debris, mucus, urine, casts and other deposits (Salmon, 2001;
23 Lavelle, 2002) which are colonised by organisms of a smaller size feeding on or inhabiting them,
24 thereby increasing connection across scales (Peterson et al., 1998). This chain of interactions
25 (processing chain commensalism sensu Heard, 1994a, b) may explain how and why some important
26 functions (such as for example organic matter turnover or nitrogen mineralisation) are maximised

1 when different organisms are introduced in gnotobiotic experimental systems, the more when they are
2 complementary in function and ecological scale, making these artificial systems more reliable from a
3 field point of view (Coleman et al., 1978; Peterson et al., 1998; Heemsbergen et al., 2004; Eisenhauer
4 et al., 2010). A good example of processing chain commensalism can be observed between trees,
5 monkeys, dung beetles and earthworms in Guianan rain forests: red howler monkeys eat fleshy fruits
6 (mostly of pioneer tree species), defecate under resting canopies, their nutrient- and seed-rich dung is
7 rapidly buried by flying dung beetles then slowly incorporated to the mull profile by earthworms, this
8 processing chain generating places with locally higher nutrient availability, associated with higher
9 seedling and seed bank species richness (Pouville et al., 2008, 2009; Dos Santos Neves et al., 2010).
10 Other examples are given in a review by Jouquet et al. (2006), who show that social ecosystem
11 engineers (called 'extended phenotype engineers', e.g. termites and ants) benefit from positive feed-
12 backs from organisms which inhabit the long-lasting structures they create locally (nests, mounds). In
13 all these examples, nutrient availability (the result of functions such as mineralisation of organic
14 matter and predation on soil microflora) and thus ecosystem services increase with functional
15 complementarity of soil biota. This may explain in turn the observed relationships between
16 belowground biodiversity and primary productivity (Laakso and Setälä, 1999; Hooper et al., 2000).

17 Whether there is a symmetrical relationship (feedback loop) between belowground
18 biodiversity and primary productivity is still a matter of conjecture, but several studies threw light on
19 some important processes in which humus forms are involved. Doubling litter experiments and
20 fertilizing experiments did not demonstrate unequivocally that more carbon and nutrients given to the
21 soil system (a proxy of increasing plant productivity) allow the soil to harbour a higher amount and
22 variety of organisms, and thus may change the humus form (Judas, 1990; David et al., 1991; González
23 and Zou, 1999). However it was experimentally demonstrated that an increase in carbon input may
24 increase microbial biomass and soil respiration (Fontaine et al., 2004), pointing to a positive impact of
25 plant productivity on microbial communities, known for their ubiquity and fast rate of adaptation
26 (Macdonald, 1979; Loranger-Merciris et al., 2006). It may be suspected that soil invertebrate
27 biodiversity cannot reach equilibrium values within the duration of short-term experiments when

1 dispersal from possible colonisation sources is impossible or at a too low rate (Hedlund et al., 2004;
2 Ponge et al., 2006), while colonisation is readily observed at short scale (Auclerc et al., 2009), over
3 centuries (Hodkinson et al., 2004) or when long-range dispersal of soil animals occurs at flying stage
4 (Hövmeyer, 1992). Thus in the short-term any increase of soil habitat or food resources cannot do
5 anything else than stimulating species already present in the immediate environment (Garay and
6 Hafidi, 1990; Rundgren, 1994), a phenomenon which in some instances may put a constraint to further
7 colonisation by extraneous species (Belyea and Lancaster, 1999).

8

9 *4.3. Humus forms and plant biodiversity*

10 Clues on the relationship between humus form and plant biodiversity (more plants cohabit in
11 mull compared to moder and even mor, as claimed by Ponge, 2003) can be found in the relationship
12 between nutrient availability (or soil acidity) and plant biodiversity. By comparing broadleaf forest
13 stands of varying forest vegetation composition Lalanne et al. (2008, 2010) showed that there were
14 less flower plant species when passing from a good earthworm mull (eumull) to a dysmoder, and that
15 the observed decrease was a linear function of the Humus Index, a numerical expression of the humus
16 form along a gradient of increasing litter thickness (Ponge et al., 2002; Ponge and Chevalier, 2006).
17 Similar results, taking pH and nutrient levels as surrogates of humus forms, were obtained in forested
18 (Brunet et al., 1997; Koerner et al., 1997) and treeless environments (Roem and Berendse, 2000;
19 Michalet et al., 2002; De Graaf et al., 2009). These field observations conflict apparently with:

- 20 • theoretical views about the negative impact of high nutrient availability on plant biodiversity,
21 mediated by competition (Huston, 1979; Tilman, 1999)
- 22 • the negative impact of artificial nutrient enrichment on plant biodiversity (Tilman, 1996;
23 Vinton and Goergen, 2006)
- 24 • the conservational value of nutrient impoverishment (Niemeyer et al., 2007)

1 The well-known humped-back model of biodiversity-productivity, maximizing species richness at
2 intermediate stages of primary productivity (as revised by Grime, 1997) may at first sight reconcile
3 these views, if we consider that most studies on natural or near-natural environments are on the 'left
4 side' of the humped-back curve of species richness, while studies on artificially enriched or
5 impoverished environments are on the 'right side' of the same curve. However, a study recently
6 conducted by Adler et al. (2011) at local, regional and global scale showed that, when area was kept
7 constant (1 m²), no clear pattern was apparent in the relationship between plant species richness and
8 grassland productivity (a proxy of nutrient availability, De Schrijver et al., 2011), and concluded that
9 productivity was a poor predictor of diversity. A limit of this study is the lack of a wide array of soil
10 fertility levels, since heathland and other vegetation types established on poor soils were excluded
11 from such 'grassland' studies. Two arguments point to the existence of an increase in functional
12 biodiversity from mull to mor, in which plant biodiversity is involved, too.

13 First, it is a common tenet that heathland established on poor soils is richer in species than
14 grassland established on rich soils (Bakker and Berendse, 1999). However, if we take into account the
15 growth types typical of heathland or other related environments such as chaparrals and scrublands, i.e.
16 monospecific bushes of perennial plants which avoid competition through territoriality of their
17 aboveground and subterranean plant parts (Heath et al., 1938), species richness can be high over, say a
18 square kilometre, while it is poor over a square metre. On a rich soil, biodiversity will be high at the
19 metric scale while not increasing further with sampling area (Fig. 2). Several gradient studies
20 corroborated this point (Weiher, 1999; Michalet et al., 2006). When speaking of higher plant
21 biodiversity in mull humus, this means more especially higher functional diversity at the very local
22 level (e.g. multilayered forests) where interactions (positive as well as negative) among partners are
23 more expected to occur than at a more 'regional' level (Grubb, 1977; Zobel, 1997; Belyea and
24 Lancaster, 1999).

25 Second, it may be thought that the nutrient level, when experimentally increased (in particular
26 when in the form of ammonia or nitrate salts), may reach toxic values or be at least detrimental to

1 some plants and not to others according to attribute syndromes (Wedin and Tilman, 1993; Diekmann
2 and Falkengren-Grerup, 2002; Vinton and Goergen, 2006), in particular in the absence of enough time
3 for phenotypic adaptation (Wilson, 2004; Shimada et al., 2010). In this case the observed decrease in
4 plant species richness after fertilization (De Schrijver et al., 2011) may result, not (or not only) from
5 competition by a few nutrient-hungry species (Aerts and Berendse, 1988; Aerts, 1989; Falk et al.,
6 2010), but also from nutrient levels too high and eventually toxic for some species (Pearson and
7 Stewart, 1993; Berendse et al., 1994; Roem et al., 2002), resulting in a false interpretation of results of
8 multi-species studies except when single-species controls are included in the experiment (Aerts et al.,
9 1990).

10 Ponge (2003) developed the idea that mull humus forms are associated with highly productive
11 meadows and multilayered forests where the coexistence of many more organisms (plants included) is
12 possible due to rapid circulation and exchange of nutrients, and that moder and in a more pronounced
13 manner mor humus forms are associated with poorly productive forests and heathlands in which low
14 biodiversity at 'local' level keep pace with the conservation of nutrients in the accumulated organic
15 matter. Computer simulation of non-trophic relationships with a varying number of interacting species
16 supports the existence of a limited number of possible assemblages, resulting in two groups of
17 'efficient' and 'sub-efficient' communities, strongly resembling mull and moder-mor communities,
18 respectively (Arditi et al., 2005). As a result of coexistence, competition between species is high in
19 highly productive ecosystems (Del Moral et al., 1985; Berendse and Elberse, 1990) but it does not
20 necessarily result in the development of 'winners' to the detriment of 'losers', except in artificial
21 systems where space is limited and thus may lead to extinction. It is now accepted that plants
22 belonging to different species of the same community do not necessarily fight against each other
23 (Hunter and Aarssen, 1988; Grime, 1998), but rather take benefit of a common pool of shared
24 resources, for instances through mycorrhizal mycelia interconnecting different plant species (Francis
25 and Read, 1984; Simard et al., 1997; Hart et al., 2003), in the same manner as resources can be
26 transferred and exchanged through rhizomes of clonal species (Antos and Zobel, 1984; Hutchings and
27 Wijesinghe, 1997). In the presence of a notable pool of nutrients time can also be shared between

1 species (and thus allow more species to coexist) through the rapid recharge and discharge of reserve
 2 organs such as bulbs and tubercles of vernal plants (Tremblay and Laroque, 2001). The idea that more
 3 nutrients or more rapid nutrient cycling means less plant species (because most species are
 4 outcompeted by a few dominant species) was mostly supported by experimental studies in which
 5 nutrients were added to pre-existing nutrient-poor adapted communities (Heil and Bruggink, 1987;
 6 Aerts and Berendse, 1988; De Schrijver et al., 2011), but it has been shown elsewhere that resulting
 7 nutrient imbalances (such as between N and P) may overwhelm the effect of nutrient addition (Roem
 8 and Berendse, 2000; Roem et al., 2002). Discrepancies between observations on natural- or semi-
 9 natural environments and experimental plots to which nutrients are added can be explained by the long
 10 time taken to reach maximum biodiversity after disturbance, needing:

- 11 • evolution of a more favourable suite of traits
- 12 • arrival of diaspores of plants adapted to the created situation
- 13 • stabilisation of actively growing species (Chapin et al., 1993; Bakker and Berendse, 1999)

14 Negative effects of recently established earthworm communities on plant species richness (Hale et al.,
 15 2006), and nil effects of macrofaunal addition on vegetation biomass (Bradford et al., 2002) can
 16 probably be explained in the same manner. Long-term experiments such as the Park Grass
 17 Experiment, which has been conducted from 1856 to 2006 (Silvertown et al., 2006) seem to contradict
 18 the present view, but the authors themselves claim that the effect of uncontrolled external factors of
 19 recent influence cannot be ruled out, among which combined effects of acidification (decreasing
 20 species richness) and nitrogen deposition (increasing productivity) take probably a prominent role, as
 21 suggested by Thimonier et al. (1994).

22

23 *4.4. Humus forms as the seat of ecosystem selection?*

24 Present knowledge on feedbacks between plant and soil biodiversity give clues to humus

1 forms as the main seat of ecosystem selection which, for the moment, has been only demonstrated in
2 artificial microbial communities (Swenson et al., 2000; Williams and Lenton, 2007). However, several
3 lines of evidence point to a wider perspective for ecosystem selection, in which humus forms could be
4 involved. The study of phylogenetic trait variation within plant communities shows that plant
5 communities are strongly shaped by past and present interactions within lineages, pointing to non-
6 random selection of traits within communities (Prinzing et al., 2008): selection is thus strongly
7 context-dependent. Studies about early colonization of land (Selden and Edwards, 1989; Heckman et
8 al., 2001; Retallack, 2007) showed that symbiotic relationships between fungi and plants were
9 established from the beginning, and that trophic networks in which organic debris and mineral
10 particles were assembled and transformed by soil animals was the context. At last, competition
11 between ecosystems such as ericaceous heath and coniferous forest, when established simultaneously
12 and in similar environmental conditions, was shown to be reflected in corresponding changes in
13 humus forms (Ponge et al., 1998). In an evolutionary perspective, humus forms might well be the
14 ‘missing link’ between above ground and belowground biodiversity postulated by Wardle et al. (2004)
15 and De Deyn et al. (2008). Present-day debates about relationships between ecological similarity of
16 species and phylogenetic niche conservatism (Losos, 2008; Wiens et al., 2010) and on the
17 evolutionary importance of mutualisms (Kiers et al., 2010) are rich of perspectives in this respect.

18

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- 20

FIGURE CAPTIONS

1

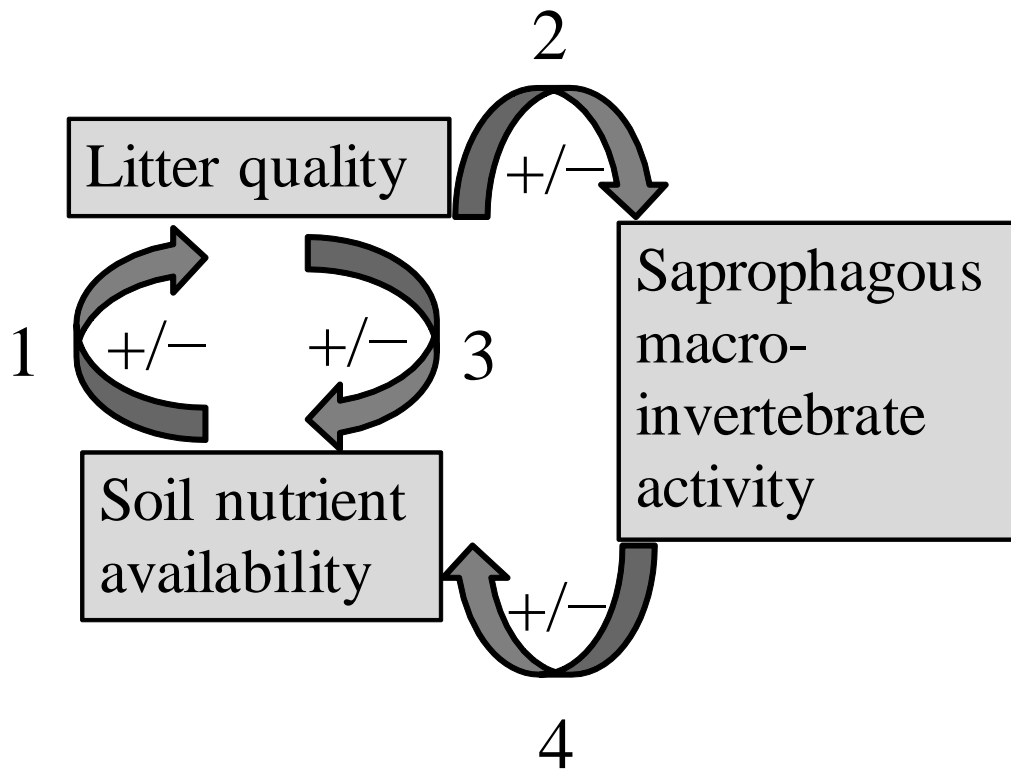
2 **Figure 1.** Feed-back relationships between litter quality, soil nutrient availability and saprophagous
3 macro-invertebrate activity. Plus and minus signs indicate the direction of change in humus
4 form dynamics (mor to mull and mull to mor, respectively) according to major positive (self-
5 stimulatory) feedbacks of the plant/soil system

6

7 **Figure 2.** Species-area relationships in a heathland on poor soil (mor) and a grassland on rich soil
8 (mull): according to sampling procedure, plant biodiversity in mor can be estimated to be
9 higher or lower than that of mull

10

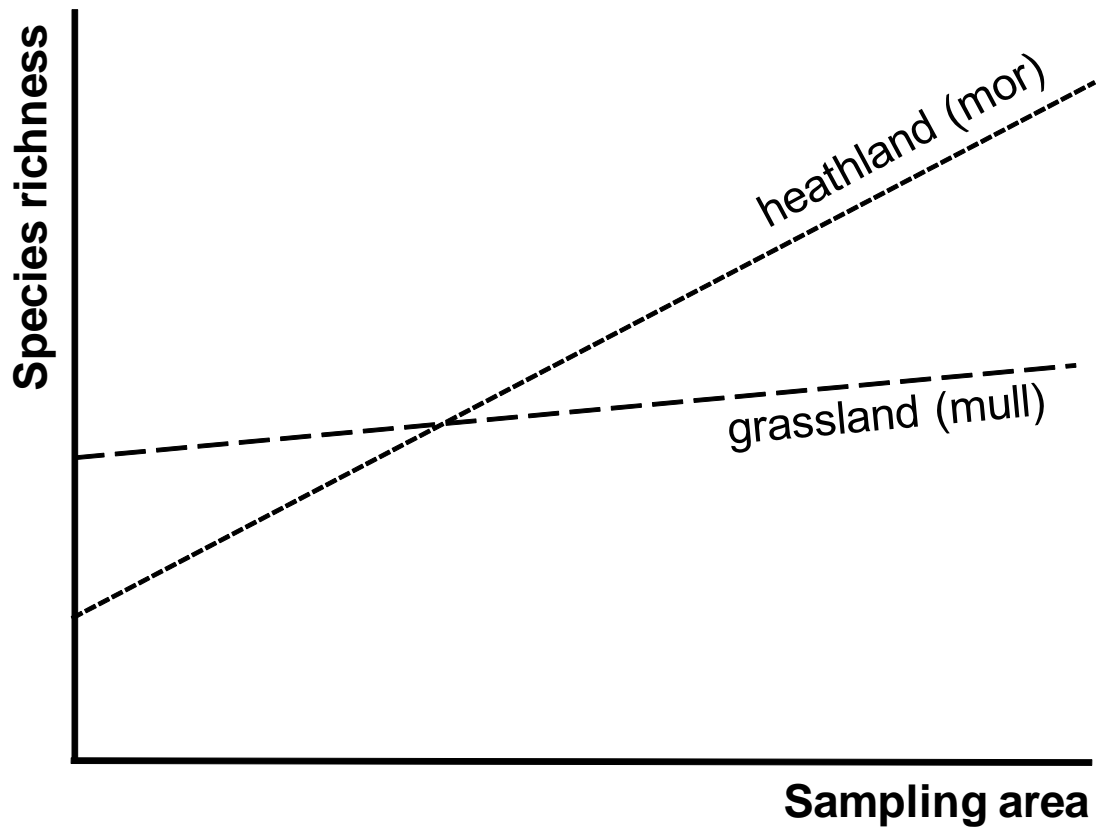
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1

2 Fig. 1

3



1

2 Fig. 2