



## Short communication

## Forest humus forms as a playground for studying aboveground-belowground relationships: Part 1, theoretical backgrounds

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## ABSTRACT

Within the context of soil biodiversity erosion and of soil recognition as a non-renewable resource *i.e.*, not recoverable within a human lifespan, we mix theoretical backgrounds from community ecology and functional ecology to address links between aboveground diversity and belowground diversity and their functional consequences for soil. We develop a working hypothesis, for future research, stating that the best performance of the soil-plant interface (*i.e.*, high organic matter recycling, low losses of biogenic elements, and plant productivity) is achieved when all communities (plant and soil biota) have reached a similar organizational pattern based on species assemblages, limiting functional traits similarity, and maximizing complementary traits. We conclude that the humus system is the best candidate for testing this hypothesis.

## 1. Introduction

Plant–soil feedback is becoming an important concept for explaining how the global performance of terrestrial ecosystems respond to global changes and has been the subject of numerous studies in the last several years (van der Putten et al., 2013). The study of aboveground-belowground relationships and their consequences for ecosystems functioning are not new but are an extension of an older, central issue in ecological research that began in the early 1990's: the search for relationships between biodiversity and ecosystem functioning (Hooper et al., 2005). Mainly fundamental at the beginning, the research efforts have turned toward applied finalities, such as conservation ecology or ecosystem management, thus highlighting the way biodiversity changes (in species composition or in species functional identity rather than only in species richness) could impede the provision of goods and services by ecosystems (Lavelle et al., 2006; Schwartz et al., 2000). Subsequent studies focused on potential direct links between vegetation and ecological processes such as primary productivity, organic matter decomposition, or nutrient cycling. The first experiments in manipulating plant species richness did not lead to a consensus about positive, negative, or idiosyncratic links between plant species richness and a given process (Hooper et al., 2005). However, they did highlight two main points: (1) the importance of considering species functional traits (*e.g.*, growth rate, litter quality, symbiotic N fixation) as the facilitators between biological communities and a given ecosystem process, and (2) the importance of considering the community the most proximal to the studied process (plant for primary productivity or soil biota for organic

matter recycling are examples). These works led to the development of functional trait databases for plants (*e.g.*, the LEDA database (Kleyer et al., 2008); the TRY database (Kattge et al., 2011; Kleyer et al., 2008)) and for soil fauna (the BETSI database (Pey et al., 2014a)). It also led to the use of multitaxonomic approaches for biodiversity manipulation experiments (Coulis et al., 2015; Hättenschwiler and Gasser, 2005; Hedde et al., 2010). Unfortunately, these multitaxonomic approaches remain relatively scarce to date, while ecological processes associated with organic matter recycling within humus systems require numerous taxa from bacteria to moles or rabbits, including nematodes, mites, collembola, isopods, and earthworms. Moreover, despite the increasing number of studies of soil biodiversity over these last decades, the biological trait framework proposed to improve the mechanistic understanding of biodiversity-functioning relationships has rarely been tested for organisms other than plants (Gagic et al., 2015). The result is that if plant diversity influences a wide range of ecosystem processes, (1) the underlying mechanisms remain poorly understood and (2) the links between plant diversity and belowground processes remain only fragmentarily explained (Lange et al., 2014).

Thus, the need is growing for an improved understanding of the mechanisms that structure soil biodiversity and for construction of a novel ecological theoretical framework to understand the relationships between soil biodiversity and soil functioning (Bardgett and van der Putten, 2014). Therefore, the aim of this chapter is twofold. We first summarize theories from both community ecology and functional ecology. Based on these theories, we thus propose a new working hypothesis linking aboveground diversity – belowground diversity –

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humus system functioning. The novelty of this hypothesis lies in the fact that (i) it considers the dynamic nature of the biodiversity – functioning relationships and (ii) it integrates the biological diversity both on the whole soil foodwebs and within trophic levels.

## 2. Framework from community ecology

As mentioned in the introduction, linking plant – soil functioning through a functional traits framework is not as simple as it appears. Species traits, which are expressed in a local community, are linked both to long- and short-term processes that have filtered biological traits, allowing the species occurrence independently of species themselves (see the concept of “trait-environment links” from [Keddy \(1992\)](#)). The new working hypothesis linking aboveground diversity – belowground diversity – humus system functioning we propose in this chapter is clearly mechanistic. We have been inspired by ecological concepts which consider the strong link between the history of a given region (*i.e.*, long term historical factors which have bequeathed the current regional species pools) and the diversity of species assemblages at the local scale (local biotic and abiotic factors) ([Ricklefs, 2004](#)). Passing from the regional scale to the local one involves different assembly processes such as limiting similarity ([Pacala and Tilman, 1994](#)) and habitat filtering ([Keddy, 1992](#)) that can be simultaneously at play ([Adler et al., 2013](#)). Among the two main diversity-maintaining mechanisms for community (equilibrium *versus* nonequilibrium), we mainly refer to equilibrium mechanisms that explain community composition based on differences among species in life-history strategy, in habitat affinity, in competitive ability or in pest or predator resistance (see [Chave et al. \(2002\)](#) and [Chesson \(2000\)](#)). Because of recent development ([Adler et al., 2013](#); [Taudiere and Violle, 2016](#)), we poorly address nonequilibrium mechanisms which explain community diversity as a balance between speciation (or immigration) and extinction based on Neutral theory ([Hubbell, 1979](#)) even if both kind of mechanisms have been shown to contribute to community diversity ([Chave et al., 2002](#)).

Practically, local species assemblages are established under the influence of two successive sets of factors: species pools and environmental constraints ([Fig. 1](#)). Environmental constraints restrict the development of species by filtering, from a regional total pool, the species that are least able to colonize suitable habitats (dispersal constraints) and to complete their life cycle within the abiotic conditions of these habitats (habitat constraints and local abiotic constraints). Dispersal, habitat, and local constraints represent a series of three environmental filters called “deletion rules” ([Belyea and Lancaster, 1999](#); [Diaz et al., 1998](#)). These deletion rules determine a pool of potential colonizers (the ecological pool) from which the constituent species of a given community will be selected. Selection is made on the basis of their ability to accommodate biotic interactions with other species, namely the “assembly rules” *sensu* [Belyea and Lancaster \(1999\)](#). The combined effects of the filters maximize the similarity of species’ ecological requirements (allowing accommodation of abiotic constraints) and minimize the similarity of biological traits (allowing species to accommodate biotic interactions—the less the species look alike, the more they can coexist ([Weiher et al., 1998](#); [Weiher and Keddy, 1995](#))).

Depending on the time elapsed since agricultural abandonment, ecosystems management, and/or natural disturbances ([Alard and Poudevigne, 2002](#)), a species turnover involves an interaction between the ecological pool and the expressed community, thus highlighting the dynamic nature of communities. As a result, by excluding species (with or without new recruitment from the ecological pool), a given community can spontaneously drift toward a state in which competitive interactions are limited ([Fig. 2](#)). An example of this is the biostatic phase described by [Oldeman \(1990\)](#) for forest ecosystems. In the biostatic stage, the variability of expressed biological traits can be the basis for a lasting species assembly that increases the collective performance for a given function in the ecosystem. This has been called the “complementarity effect” by [Loreau \(2000\)](#).

Mechanisms of competitive exclusion can sometimes lead to near monospecific assembly ([Paquette and Messier, 2011](#)), involving the dominance of extreme biological traits for a given function. Some of these plant traits can directly exert selection pressure on soil organisms, which will then preferentially recycle the organic matter of this dominant species at the expense of other co-occurring species (see the “home-field advantage concept” of [Vivanco and Austin \(2008\)](#)). Plant species can indeed select decomposer chains involved in their organic matter recycling. Species allocating a greater proportion of their C to growth and not to the synthesis of secondary metabolites often are characterized by litter with a high litter N/lignin ratio. Such easily degradable litter would select soil food webs based on dominant bacteria activity, whereas low growth species may allocate a large amount of their C to secondary metabolites, leading to poor quality litter (low N/lignin ratio) and the selection of fungal-based soil food webs ([Wardle et al., 2004](#)). Furthermore, long-lived plant species may change the physical and chemical properties of soils in the long term, even if they coexist with other species (see the “individual tree effect” of [Boettcher and Kalisz \(1990\)](#)) and, hence, indirectly switch the belowground compartment toward favourable abiotic or biotic conditions.

Disentangling and hierarchizing the influence of deletion rules *versus* assembly rules is actually a central issue in ecological research. First, recent critiques have emphasized that functional traits approaches are often insufficient to establish the role of abiotic *versus* biotic factors in determining the way communities match up ([Kraft et al., 2015](#)). Indeed, phenotypic convergence can result from a number of biotic processes aside from environmental filtering, such as plant-pollinator interactions or facilitation (see [Cavender-Bares et al. \(2009\)](#)). To the opposite, competition leading to community assembly based on phenotypic divergence, may also result in phenotypic convergence among community members if the phenotypes in question are associated with competitive dominance ([Godoy et al., 2014](#); [Kraft et al., 2015](#)). Thus, there is a clear need for additional studies mainly at largest scales, like continental or regional ones, as less than 10% of the studies addressing environmental filtering have worked at these scales (see [Kraft et al. \(2015\)](#)). And, to disentangle the impact of environmental filtering and species interactions on community assembly, there is a clearly need for new statistical tools sufficiently robust to work with (i) a variety of functional traits metrics, (ii) with both interspecific and intraspecific trait measures; (iii) with functional traits variation among different taxonomic levels and (iv) with functional traits variation among spatial scale ([Taudiere and Violle, 2016](#)).

## 3. Framework from functional ecology

All that has been mentioned above about biological traits and how species co-occur within a community can be applied to communities within each trophic level of soil food web (decomposer, detritivore, ecological engineer, and predator). Nevertheless, studies about belowground species co-occurrence under biotic interactions are scarce and focus on only a few emblematic taxonomic groups, such as earthworms ([Bell et al., 2010](#); [Decaëns et al., 2008](#); [Gao et al., 2014](#); [Jiménez et al., 2012](#); [Decaëns, 2010](#)). In addition, many studies have assessed the impacts of manipulating the diversity and the quality of the resources entering the soil (plant organic matter) on soil fauna – that is, studying the “bottom-up control” of soil food web – without assessing at the same time the impact of predatory organisms on the assembly rules of lower soil trophic levels (“top-down control”) (*e.g.*, [Henneron et al., 2017a](#); [Eisenhauer et al., 2011](#); [Wardle et al., 2006](#)) ([Fig. 3](#)). In the soil, the control of decomposer communities by predators may lead to great changes in the abundance of decomposers, thus affecting the recycling processes of organic matter ([Bardgett et al., 2005](#); [Mikola et al., 2003](#)). Nevertheless, the usual research approaches to trophic networks limit biotic interactions within food chains to these two types of controls (bottom-up and top-down) without considering the contributions of community ecology, *i.e.*, the balance between assembly rules and

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