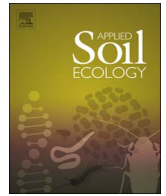




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Forest humus forms as a playground for studying aboveground-belowground relationships: Part 2, a case study along the dynamic of a broad lived plain forest ecosystem

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ABSTRACT

A set of research studies has been performed over a period of 10 years on the silvicultural cycle of an even-aged beech forest in Normandy, France. The striking results about both soil functioning (litter decomposition, N cycling, soil C stock) and soil biota (microorganisms, mesofauna, and macrofauna) are presented with the goal of developing an empirical model of the successional patterns of aboveground-belowground relationships in forests. Our purpose was to test the hypothesis stating that the best performance of this forest ecosystem, as high organic matter recycling and low biogenic element losses, is achieved in an ecological stage exhibiting limiting similarity in functional traits and maximizing traits complementary for both plant and soil communities. The present synthesis showed that this hypothesis seems to be confirmed for a late successional stage, *i.e.*, a mature even-aged forest with a closed canopy. The most organized communities, on the basis of ecological requirement similarity, were found in 130 year-old stands. These stands also support the greatest values in microbial functional diversity, in soil C stock and in nitrogen mineralization. Nitrogen losses were the lowest in 95 year-old stands. We also provide some methodological advices for using humus forms for the study of aboveground-belowground relationships in forest ecosystems.

1. Introduction

Humus has long been recognized as a system that fully integrates all environmental parameters that occur in a forest stand. Hence, humus form results from both abiotic parameters including climate (Aerts, 1997a; Ponge et al., 1998); parent materials and derived soil properties (Kindel and Garay, 2002) and geomorphology (Ettema and Wardle, 2002). It also includes biotic parameters such as litter quality (Aerts, 1997b; Loranger et al., 2002); soil biota (Chauvat et al., 2007; Loranger et al., 2002; Ponge, 2003) and anthropic factors *e.g.* forest management (Muys, 1995). The vertical morphological description of the humus form (Jabiol et al., 1995), is considered to be a great integrator of soil biological activity, conditioning the rate of decomposition and nutrient cycling (Gobat et al., 1998; Jabiol et al., 2009). From the description of humus forms, one can estimate the rate of organic matter turnover and, by extension, the site fertility for plant productivity. As an example, the gradient formed by the three main humus forms “mull-moder-mor” has long been considered to be a decreasing gradient of organic matter recycling, and then of a decreasing amount of mineral nitrogen (NH_4^+

and NO_3^-) available for plant growth (Andrianarisoa et al., 2009; Michalet et al., 2001).

Therefore, humus forms result from the balance between litter inputs and decomposition processes, a balance driven by plant–soil biota interactions. An increasing number of experimental and field studies show that, within the humipedon, the structure of soil detritus food webs can be considered as a controlling factor in decomposition and plant growth (Gessner et al., 2010; Handa et al., 2014; Lenoir et al., 2007). The humipedon is defined as the upper part of a soil made of organic and/or organic-mineral horizons (formerly named humic epipedon). The shift from mull toward moder humus forms is recognized as indicator of (1) a shift from bacterial-based soil food webs toward fungal-based ones and (2) the decreasing activity of anecic earthworms and the simultaneous increasing activities of epigeic macrofauna (epigeic earthworms, diplopodes, woodlice) and mesofauna (Ponge, 2003). Bacterial-based channels and associated fauna are synonymous with rapid nutrient turnover and productive ecosystem developed on fertile soils, whereas fungal-based channels refer to slow decomposition, slow nutrient turnover, and unproductive ecosystems developed on unfertile

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soils (Wardle et al., 2004). However, the control of plant–soil biota interactions over decomposition processes and nutrient losses have been poorly documented as a result of (1) the small number of multi-taxonomic approaches necessary to study soil food webs and (2) long-term studies required to determine the assembly rules mechanisms and organization of species communities cf. part 1, “theoretical background” (Aubert and Bureau, in press). Many studies assessed the bottom-up control of plant litter diversity, quality or quantity on decomposition processes (Eisenhauer et al., 2011; Henneron et al., 2017a; Wardle et al., 2006) without specifically addressing how biotic interactions among soil fauna can impact the relationships between litter diversity and litter decomposition rate. For example, interspecific competition is recognized as minimizing the similarity of biological traits among co-occurring species. The less the species look alike, the more they can accommodate biotic interactions and coexist (Weiher et al., 1998; Weiher and Keddy, 1995). Competitive interactions within decomposer communities may gradually lead to a community organization which maximizes the dissimilarity of biological traits for resource acquisition and their complementarity, limiting thus the competitive interaction. Complementary traits may allow a maximum exploitation of soil organic matter. Coulis et al. (2015) and Hedde et al. (2010) have shown that functional traits dissimilarity among detritivores communities was positively linked to organic matter decomposition and mineralisation thus highlighting the importance to consider it to explain the mechanisms which link litter diversity and litter decomposition.

Here, we present a review of 8 studies performed over a period of 10 years on a single French forest examining both soil functioning (litter decomposition, N cycling, and soil C stock) and soil biota (macrofauna, microorganisms, and mesofauna) (Aubert et al., 2003a, 2004; Chauvat et al., 2011; Hedde et al., 2007, 2008; Trap et al., 2011a, 2011b, 2011c). The main objective of this review is to develop an empirical model for the successional patterns of aboveground-belowground relationships based on the “one-armed bandit” hypothesis proposed in the part 1 “theoretical background” (Aubert and Bureau, in press) along the successional trajectory of a low dynamic system, such as forests, which has been poorly documented to date. Our purpose was to test the “One-Armed Bandit Hypothesis” developed in the previous chapter (Aubert and Bureau, in press). According to this hypothesis, the best performance of forest ecosystem, as high organic matter recycling and low biogenic element losses, is achieved in an ecological stage exhibiting limiting similarity in functional traits and maximizing traits complementarity for both plant and soil communities. We intend to demonstrate that (1) the humus system could be an ideal playground within which to focus on the sharp ecological mechanisms underlying the links between the communities occurring at the plant-soil interface and soil functioning, and (2) that low dynamic systems (such as a forest) are good partners to assess the impact of assembly rules mechanisms on soil functioning. We also take this opportunity to provide methodological advices for the use of humus forms in the study of aboveground-belowground relationships.

2. Materials and methods

2.1. Approach used when ecosystem dynamics proceed on a longer time than the scientists’ life span

Forest dynamics can occur over several hundreds of years, preventing diachronic monitoring and, therefore, imposing a space-for-time substitution approach to the study of successional processes along chronosequences (Oldeman, 1990; Walker et al., 2010). The main criticism of such an approach is that the resulting model of temporal patterns can diverge from the real pattern that would be obtained with diachronic monitoring (Aubert et al., 2003a). This discrepancy results mainly from factors such as environmental and historical variables that create confounding effects with the aging of forest stands. To minimize

these potential confounding effects, a selection of at least four independent forest stands of the same age is required for each age-class (Trap et al., 2011a). Replication stands provide a measure of the variance *within* each age class, allowing separation from the variances *between* age classes, and permitting identification of the forest aging effect. In the context of humus studies within forest ecosystems, specific precautions should be taken to ensure that between-age-class variance is mainly due to stand ageing. Selected stands should share the same topographic situation, similar soil type, and similar climatic conditions. Careful attention must be paid to the history of selected stands (ancient forest status), as specific species of ancient forest can strongly affect the functioning of the humus system see Hermy and Verheyen (2007). These forests can be primary or secondary forests, managed or not, but the forest land use must have been continuous for the longest possible period. Within such a context, recent forests must be excluded because past land-use – such as crop or grassland history – may affect young forest vegetation, soil biota, and soil functioning (Gossner et al., 2008; von Oheimb et al., 2008). The control of land use legacy to the earliest possible period is crucial because former occupations, even dating back as far as ancient Roman agricultural systems, still have an impact today on soil pH, soil available P, and plant community composition (Dambrine et al., 2007). Thus, the presence of archeological sites indicating such former human occupations should be checked. The study site should not be selected on the edges of forest, as edge-to-core gradients occur with respect to soil pH, soil N pool, and plant community composition. Indeed, the periphery of ancient forests is likely to be occupied by recent forests in which former agricultural practices have irreversibly modified topsoil properties (Bergès et al., 2013b). In addition, confounding effects can be limited by checking the legacy of land ownership, forest unit size, management intensity, and harvesting intensity (Bergès et al., 2013a). Next, assessing the patterns of biodiversity and ecosystem functioning throughout a silvigenetic cycle (for primary or natural forests) is not fundamentally a problem once all these previous recommendations are respected. Things are quite more difficult for silvicultural cycles (managed forest) because space-for-time substitution approach requires to select stands which have received the same management all along their growth. For instance, this implies to select old stands which have had, in their youth, similar characteristics to that of currently young stands e.g. diameter at breast height, basal area, height or volume of harvested trees. Scientist have thus to explore forest managers archives before finalizing a sampling design allowing them to disentangle the impact of forest ageing from that of management practices.

Finally, to avoid any short-term impact on soil fauna, selected stands should not have undergone selective thinning operations for at least the prior 3 years (Aubert et al., 2003b). Within stands, sampling points also should be located away from vehicle tracks, harvesting residues, and tree trunks, all of which are likely to affect humus forms, soil biota, and humus systems (Aubert et al., 2006; Beniamino et al., 1991).

Based on all of the foregoing criteria, we reconstituted an empirical silvicultural cycle from young stands toward regeneration phase of an ancient forest managed as even-aged, pure-beech forest, as described in Fig. 1. The studies were carried out in the Eawy forest (France, Normandy region, 7200 ha). The climate is temperate oceanic, with a mean annual temperature of +10 °C and a mean annual precipitation of 800 mm. All chosen stands were managed as even-aged forest by the French Forestry Service (ONF). All stands were situated on a flat topography (plateau). Soils were all endogleyic dystric Luvisol (FAO et al., 2006), developed on more than 80 cm of loess (lamellated silts) lying on clay with flint. Soil texture was similar among stands, with 13.5% of clay, 69.5% of silt, and 17% of sand. Understorey vegetation was defined as characteristic *Endymio-Fagetum* according to the phytosociological classification of Durin et al. (1967). Data were obtained between 2000 and 2010 see Aubert (2003); Hedde (2006) and Trap (2010), with some few differences in chronosequence length (with or

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