



Humus macro-morphology and soil microbial community changes along a 130-yr-old *Fagus sylvatica* chronosequence

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ABSTRACT

We aimed to characterize humus macro-morphology and the associated soil microbial community within the unmodified litter (OL), the fragmented and humified layers (FH) and the organo-mineral (A) layer along a beech (*Fagus sylvatica* L.) forest chronosequence with four stand age-classes (15-, 65-, 95-, 130-yr-old) in Normandy, France. Humus macro-morphology was described with 36 quantitative and semi-quantitative variables. We measured microbial biomass N (N_{mic}), microbial N quotient ($N_{mic-to-N_t}$), fungal ergosterol, bacterial and fungal DNA using 16S and 18S rDNA real-time qPCR and evaluated the potential metabolic profile of heterotrophic bacteria within each soil layer and stand age-class. The log-transform ergosterol/fungal DNA ratio (EFR index) was used as an indicator related to active fungal biomass and the fungal/bacterial (F/B) ratio was calculated from qPCR results. There was a shift from mull (mainly dysmull) to moder humus forms along the chronosequence. While the N_{mic} did not change significantly, the $N_{mic-to-N_t}$ decreased along the chronosequence in the OL layer. Ergosterol content increased in FH and A layers and the F/B ratio increased in the FH layer with increasing beech forest age. The EFR index was significantly higher in the OL and A layers of the oldest stands, whereas the highest EFR index in the FH layer occurred in the 15-yr-old stands. The functional diversity of heterotrophic bacteria was greater within OL and FH layers of 130-yr-old stands, but highest in the A layer of 15-yr-old stands while the Average Well Color Development remained stable for all soil layers. We found significant correlations between macro-morphology and microbial variables, especially between FH-based morphology and fungal biomass. Our main results are that beech forest maturation is accompanied by (1) an increase in fungal biomass in the FH layers and, (2) an increase in heterotrophic bacteria functional diversity in the organic layers. We have identified key macro-morphology variables that are good predictors of the structural and functional profile of the soil microbial community during beech forest development.

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1. Introduction

The amount and structure of organic materials within the forest floor change greatly during temporal forest development in managed (Aubert et al., 2004; Chauvat et al., 2006) and semi-natural forest ecosystems (Bernier and Ponge, 1994; Ponge and Delhaye, 1995). Mull humus (thin organic and deep organo-mineral layers with clay–humus complexes) is dominant in early developmental stages, while moder (deep fragmented and humified layers with fine organic matter from fauna faeces, thin organo-mineral layer) is more frequently observed under older forest stands on acidic soils (Ponge, 2003; Salmon et al., 2006).

The shift from mull to moder humus forms with forest aging is usually accompanied by major changes in microbial processes (nutrient turnover) and soil acidification (Aubert et al., 2004; Zeller et al., 2007; Trap et al., 2009). For instance, a decrease in net nitrate production in forest chronosequences is frequently reported (Pedersen et al., 1999; Idol et al., 2003; Trap et al., 2009). This suggests a change in microbial community structure and functions within organic and organo-mineral soil layers associated with the development of deep fragmented and humified layers that characterize the shift from mull to moder humus forms (Idol et al., 2002).

Several studies have shown soil microflora changes along a forest chronosequence (Taylor et al., 1999; Idol et al., 2002; Chauvat et al., 2003, 2009; Jia et al., 2005; Smithwick et al., 2005) and between two stand age-classes (Bauhus et al., 1998; Tonon et al., 2005; Chatterjee et al., 2009). However, the reported

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changes in microbial communities are not consistently associated with the clear shifts in humus forms during forest development. For instance, the decline of soil microbial C within the forest floor with increasing stand age in southern boreal mixed forests recorded by Bauhus et al. (1998) was not observed by Chauvat et al. (2003) within the forest floor of a temperate spruce forest chronosequence (Germany). Furthermore, the fact that most studies evaluating soil microflora along forest chronosequences focused on the organo-mineral topsoil layer rather than forest floor may explain the lack of consensus about microbial community changes during forest development. Information about temperate forest aging and the associated changes in humus morphology on soil microflora within organic and organo-mineral soil layers along a whole silvicultural cycle will improve our understanding of long-term forest functioning.

In this study, we characterized (1) humus macro-morphology with many quantitative and semi-quantitative indicators and (2) microbial biomass (DNA, fungal ergosterol and chloroform-fumigation biomass N concentrations) and metabolic profiles (Biolog physiological profile) within the organic layers at different litter decay stages (i.e. unmodified dead leaves, fragmented litter and humified layer) and the organo-mineral layer along a 130-yr-old chronosequence of pure beech (*Fagus sylvatica*). We aimed to identify key morphological variables that could be used to infer microbial community shifts during forest development. We expected the development of the fragmentation and humification layers, with its high content of complex humic acids (Kanerva et al., 2008), to favor fungi since they are effective in the degradation of recalcitrant organic matter (Gobat et al., 2004), affecting hence bacterial biomass and functions.

2. Materials and methods

2.1. Study site

The study site was located in the Eawy state forest (France, Upper Normandy, 01°18' E; 49°44' N; 7200 ha). The climate is temperate oceanic with a mean annual temperature of +10 °C and a mean annual precipitation of 800 mm. A space-for-time substitution procedure (Pickett, 1989) was used to empirically reconstruct an even-aged forest chronosequence. Sixteen pure beech (*F. sylvatica* L.) stands were selected to represent four stand age-classes of different ages: 13–18 years (15YR), 65–66 years (65YR), 91–103 years (95YR) and 121–135 years (130YR) (Table 1). In each age-class, there were four replicated stands managed as even-aged full-grown forest by the French Forestry Service. All stands came from assisted natural regeneration (superficial topsoil scratching) without clear-cutting practices. We chose neighboring stands at the same altitude, on the same bedrock and with a similar topography (on a flat plateau, located 205 m a.s.l.). The soil was an endogleyic dystric Luvisol (FAO, 2006) developed on more than 80 cm of loess (lamellated silt) overlying clay with flint parent material. The understory vegetation was a characteristic Endymio-Fagetum according to phytosociological classification (Durin et al., 1967).

2.2. Humus macro-morphology

In each stand, a 16 m² plot (central plot) was designated away from vehicle tracks and as far as possible from tree trunks to avoid any disturbances and acidification due to organic matter accumulation (Beniamino et al., 1991). Macro-morphological descriptions of organic and organo-mineral layers were made in May 2007 within frames (25 cm × 25 cm) at three corners of the central plot according to the French nomenclature (Jabiol et al., 2007). Table 2 describes 36 macro-morphology variables assessed in the field. We distinguished mull (mainly dysmull) and moder (hemimoder + eumoder +

Table 1 General characteristics of beech (*F. sylvatica*) stands used to reconstruct the 130-yr-old pure beech chronosequence.

Stand age-classes	15-yr-old (15YR)				65-yr-old (65YR)				95-yr-old (95YR)				130-yr-old (130YR)			
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Age in 2009 (years)	15	20	2003	15	67	67	67	67	68	105	93	103	93	137	123	123
Last year cut	2004	2003	2003	2003	2003	2003	2003	2004	2004	2003	2004	2002	2004	2002	2003	2004
Area (ha)	14.52	8.03	4.57	4.45	10.84	9.46	9.46	9.46	12.1	4.52	16.48	18.06	13.47	3.56	13.81	16.25
Basal area (m ²)	15	21	22	17	26	30	30	30	30	20	29	30	22	20	23	20
% Beech (C/ha)	100	100	100	100	100	100	100	100	90	90	100	100	100	90	90	100
Humus forms ^a	Du	Du	H	Du	E	E	E	E	H	Do	E	E	H	E	Do	E
Vertical sequence ^b																
OlLn	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
OlV	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
OF	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
OH					x/(x) <1 cm	x/(x) <1 cm	x/(x) <1 cm	x/(x) <1 cm	x/(x) <1 cm	x >1 cm	x/(x) <1 cm	x/(x) <1 cm	x/(x) <1 cm	x/(x) <1 cm	x/(x) <1 cm	x/(x) <1 cm
A structure ^c	BM	BM	J	BM	J	J	J	J	J	J	J	J	J	J	J	J
Topsoil pH ^d	4.47	3.83	3.56	3.99	3.87	3.83	3.83	3.83	4.24	3.80	3.85	3.83	3.72	3.83	3.97	3.73
Topsoil C/N ^d	15.1	16.6	17.8	15.7	16.3	15.4	16.9	16.9	15.0	15.5	15.4	18.5	15.9	15.4	15.8	15.0
Topsoil P (g kg) ^d	0.13	0.23	0.18	0.16	0.18	0.12	0.10	0.10	0.20	0.18	0.21	0.22	0.23	0.48	0.12	0.12
Topsoil CEC (cmol + kg)	5.21	6.19	7.43	6.95	5.69	5.66	4.99	5.66	5.25	5.74	5.56	7.09	5.60	6.17	5.71	5.28

^a With Du: Dysmull; H: Hemimoder; E: Eumoder; Do: Dymoder (Jabiol et al., 2007).
^b With OlLn: unmodified leaves less than one year old, OlV: unmodified leaves more than one year old, OF: coarse plant fragments with fine organic matter (FOM), OH: more than 70% FOM, A: organo-mineral horizon according to Jabiol et al. (2007). x: continuous; (x): discontinuous.
^c BM: Biomacro-structured; J: Juxtaposition A (A with massive or single-grain structure but no biological or chemical structure).
^d Data are means (n = 3).

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