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Soil detritivore macro-invertebrate assemblages throughout a managed beech rotation

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Abstract – This work addresses the driving factors responsible for patterns in the detritivore macrofaunal communities of a managed beechwood chronosequence (28 to 197 years old, Normandy, France). We investigated the variation patterns of density, biomass and diversities of detritivore macrofauna throughout this rotation. Multivariate analyses were carried out to identify the main covariation patterns between species and some properties of their physical environment, and to describe the main ecological gradients constraining the macro-invertebrate community assembly. A total of 6 earthworm, 6 woodlouse and 7 millipede species were found in the whole data set. Density, biomass and diversity were profoundly influenced by forest ageing, mainly because of variation in humic epipedon spatial variability. Three groups of species were identified according to their environmental requirements. Some hypotheses regarding the external (related to management practices) or internal (related to inter-specific interactions) assembly rules behind species assemblages are proposed, an approach which has rarely been used in soil ecology. Finally, the impact of forestry practices on soil functioning through their impact on detritivore macro-invertebrate communities is discussed.

soil detritivore macrofauna / community ecology / assembly rules / humic epipedon / forest management

Résumé – Les assemblages de macro-invertébrés détritvires du sol d'une rotation de futaie de hêtre. Ce travail a pour but d'identifier les facteurs responsables des schémas de variation des communautés de la macrofaune detritivore d'une chronoséquence (28 à 197 ans) de futaie régulière de hêtre (Normandie, France). Les modèles de variation de la densité, la biomasse et la diversité ont été recherchés. Les modèles de covariation entre les espèces et certaines propriétés physiques du milieu ainsi que les gradients écologiques qui contraignent les assemblages de macro-détritivores ont été décrits à l'aide d'analyses multivariées. En tout, 6 espèces de vers de terre, 6 espèces d'isopodes et 7 espèces de diplopodes ont été identifiées. La maturation du peuplement de hêtre, principalement par les modifications de l'épisolum humifère, influence fortement les densité, biomasse et diversité. Trois groupes d'espèces sont identifiés sur la base de leurs exigences environnementales. Quelques hypothèses sont proposées quant aux règles externes (liées aux pratiques sylvicoles) et internes (liées aux relations interspécifiques) qui contraignent la composition des assemblages d'espèces, cette approche ayant jusqu'à présent été peu utilisée en écologie du sol. Enfin, l'impact des pratiques sylvicoles sur le fonctionnement du sol, au travers de leur impact sur les communautés de macro-détritivores, est discuté.

macrofaune detritivore du sol / écologie des communautés / règles d'assemblages / épisolum humifère / gestion forestière

1. INTRODUCTION

Soil invertebrates are recognized as having a high functional importance in soil processes and being responsible for the provision of ecosystem goods and services such as organic matter decomposition, water cycling or primary productivity [38]. These organisms are highly sensitive to natural disturbances and human practices [38]. Inadequate land use may dramatically decrease their level of activity and/or their community diversity, leading in some extreme cases to major soil dysfunctioning and ecosystem degradation [23]. In forest ecosystems, soil detritivores are considered an important group of organisms, involved in the comminution of fresh dead leaves and the stimulation of decomposer microflora, with consecutive impacts on organic matter mineralisation and humic epipedon functioning [45].

Based on observations in semi-natural forests, Ponge et al. [45] described the natural silvigenetic cycle as a two-step trajectory shifting from an autotrophic functional phase toward a heterotrophic one which markedly influences the availability of nutrients. In terms of ecosystem functioning, the autotrophic phase is characterised by a great influence of tree activity (photosynthesis, nutrient absorption) leading to the accumulation of organic matter on the forest floor (i.e. development of moder humus forms). The heterotrophic phase is characterized by an increase in soil-dwelling macro-invertebrate activity which promotes the rapid disappearance of fresh litter (i.e. development of mull humus forms). In mountain semi-natural spruce forests, parallel changes occur in vegetation, humus profiles and soil fauna communities [15, 16], e.g. in young stands, soil macro-invertebrate communities are dominated by epigeous taxa (many species of woodlice and millipedes) while old stands host numerous populations of earthworms. In the beech integral biological reserve of

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Table I. Description of the fifteen selected stands reconstituting a silvicultural rotation by the SFTS procedure.

Stand age (years)	Last cut year	Wood uptake (m ³ .ha ⁻¹ since 1980)	Silvicultural phase
28	1997	127.3	First thinning
28	1998	191.8	First thinning
30	1996	235.1	First thinning
61	1997	105.0	Refining
61	1997	112.6	Refining
65	1998	128.4	Refining
118	1998	138.7	Amelioration
127	1995	149.0	Amelioration
136	1995	162.4	Amelioration
147	1993	167.7	Amelioration
177	1996	255.3	Regeneration
179	1991	93.4	Regeneration
182	1998	127.1	Regeneration
197	1997	193.6	Regeneration
197	1997	115.8	Regeneration

Fontainebleau forest (France), Arpin et al. [4] described similar patterns and showed successional changes in humus, earthworm, nematode and vegetation communities as the result of forest dynamics.

The recent awareness of a global biodiversity crisis has underscored the urgent necessity of maintaining ecosystem integrity and functioning [36]. In forest ecosystems the conservation of biological diversity has been identified as a major goal of sustainable silvicultural management [39]. Intensively managed forests (e.g. planted, mono-specific, even-aged) are interesting models where vertical stratification of vegetation and tree composition are reduced to their simplest expression, making them about the most simplified forests [7]. In such systems, much attention has been paid to plant community diversity [5, 12] and most works on soil detritivore invertebrates in forest ecosystems were description of species composition [20, 26, 27] or comparative studies of communities across humus types [3, 47, 48]. To date, only few authors addressed successional pathways during forest rotation [22, 30, 52].

Hence, to identify sustainable management practices, it is now urgent to understand how soil invertebrate communities are assembled and how species assemblage diversity responds to human activities in intensively managed forests. In this context, the present paper aims at describing community patterns of detritivore macro-invertebrates (earthworms, woodlice and diplopods) in an even-aged beech forest rotation developed on loamy soil. Our research hypothesis was that changes in detritivore community occur and reflect the expected shift from autotrophic to heterotrophic functional phases. We addressed several aspects of community ecology: (i) patterns of variation in density and biomass, (ii) several dimensions of community diversity (structure, composition and organization) and (iii) relationships between species and environmental factors throughout this silvicultural cycle.

2. MATERIALS AND METHODS

2.1. Study sites

The study was carried out in even-aged pure beech stands of the “Forêt domaniale d’Eawy” (Haute-Normandie, France). The climate is temperate oceanic with a mean annual temperature of +10 °C and a mean annual precipitation of 800 mm [19]. All stands were located on a plateau with more than 80 cm of loess as parent material. Soils are LUVISOLS, according to the “Référentiel pédologique” [1] and equivalent to LUVISOLS in the world reference base [34]. Stands were managed by the French forestry service (ONF), essentially for beech timber harvesting.

In order to represent all phases of a silvicultural cycle, we used a space-for-time substitution procedure. Fifteen stands were chosen encompassing the following silvicultural phases: first thinning (Ft), refining (Rf), amelioration (Am) and regeneration (Rg) (Tab. I, mean ages are 29, 63, 132, and 186 years, respectively). The number of plot replicates per beech growth phase ranged from 3 to 5 and was a function of the specific duration of each phase (Tab. I). This set of stands was assumed to reconstitute the theoretical chronosequence that characterises a silvicultural cycle in the Eawy forest. The silvicultural phases were described by Aubert et al. [5].

2.2. Macro-invertebrate sampling

In April 2003, three samples were taken in each selected stand. Sampling points were 10 m apart from each other, and were located away from vehicle tracks and as far as possible from tree trunks to avoid any acidification due to organic matter accumulation [13]. The macrofauna was sampled at each point on a 1 m² area, the methodology comprised a combination of hand sorting and chemical extraction [9]:

1 – First, the holorganic layer was removed and brought to the laboratory to extract invertebrates by hand sorting after washing;

Table II. Coding for the fourteen environmental variables used in co-inertia analysis.

Environmental variable	Code	Environmental variable	Code
Total humus depth	Humusd	Total humus weight	Humusw
Minimum OL depth	minLd	Beechnut weight	BNw
Maximum OL depth	maxLd	Beech leaves litter weight	BLw
[OL]/[total humus]depth ratio	%Ld	Deadwood weight	DWw
Minimum OF+OH depth	maxFHd	Herbaceous layer litter weight	HLw
Maximum OF+OH depth	minFHd	Herbaceous layer biomass	HLb
[OF+OH]/[total humus]depth ratio	%FHd	Soil pH	Soil pH

2 – Then, 30 L of 4% formaldehyde were applied to the same area at the rate of 10 L every 15 min [29].

3 – Afterwards, a soil monolith of 25 × 25 × 30 cm was dug out in the middle of the area and hand sorted in the field. This was done to sample species or individuals less sensitive to formaldehyde and to calibrate the density and biomass data if necessary [40].

All extracted invertebrates were stored in 4% formaldehyde. Lumbricida, Isopoda and Diplopoda were identified to species level according to Bouché [18], Demange [31] and Hopkins [37], respectively. Invertebrates were counted and weighed to calculate species density and biomass at each sampling point. In this paper, litter invertebrates will refer to individuals sampled in holorganic layers and soil invertebrates to those found in the organo-mineral layer.

2.3. Descriptive variables of community

For each silvicultural phase, we calculated mean density, biomass and structural, compositional and organizational diversity indices. This enabled us to provide a model of variation pattern and to identify the main mechanisms of species co-existence throughout the silvicultural rotation [2, 10]. Four indices of diversity were calculated for each silvicultural phase:

(1) *SR*, the mean species richness per sample (i.e. the mean number of species identified per sampled area [43])

(2) *J'*, the mean Shannon Evenness index, a structural index which reflects the species dominance level [51]:

$$J' = \frac{H'}{H'_{\max}}$$

(3) *WPS*, the mean Within-Phase Similarity, a measure of compositional diversity which estimates pairwise similarity among all records of a silvicultural phase. It was computed using the Sørensen index [53]

$$\text{Sørensen index} = \frac{2c}{2c + a + b}$$

where *a* is the number of species found in sample A, *b* the number of species found in sample B and *c* the number of species that occur in both samples.

(4) *FD*, the conditional variance of records on the first two axes of Correspondence Analysis (see details in the statistical analysis section [24, 54]):

$$FD = \sum_{j=1}^i p_{j/i} [C_k(j) - L_k^{(i)}]^2$$

where $p_{j/i}$ is the conditional relative frequency of sample *i* for species *j*, $L_k^{(i)}$ the sample ordination on gradient by averaging, $C_k(j)$ the species ordination on gradient by weighted averaging. It assesses the degree of community organization by measuring species dispersion along correspondence analysis axes and thus reflects the coherence of species assemblages with reference to ecological gradients. As an example, high *FD* values indicate high species dispersion along the ecological gradient, i.e. low ecological coherence of species assemblages.

2.4. Description of environmental variables

Humus was described according to the French nomenclature at each sampling point before invertebrate extraction [1]. We thus distinguished mull (mesomull + oligomull), moder (eumoder + dysmoder) and intermediate mull-moder forms (dysmull + hemimoder). Fourteen parameters were also described at each point and used as environmental variables (Tab. II). Herbaceous vegetation biomass was sampled on 1 m² quadrats, oven-dried (40 °C) and weighed. Four soil cores (5 cm depth, 10 cm diameter) were sampled on the corners of the square meter and used to assess soil pH (1:2.5 soil/liquid mixture). After litter-invertebrate sampling by washing-sieving in the laboratory, remaining litter components (beechnuts, herbaceous litter, beech litter, dead wood) were separated, oven-dried at 40 °C and weighed.

2.5. Statistical analyses

Mean differences in density, biomass and diversity were tested using Tukey (HSD) test at the significant level of $p = 0.05$. Prior to analysis, data normality was tested using the Wilk-Shapiro test at the significance level of $p = 0.05$ and a logarithmic transformation was used to homogenize variances if necessary. These analyses were performed with R Software [46].

Density data were analysed by Correspondence Analysis (CA) to identify community gradients [24, 54]. Species occurring in less than 3% of the sampling points were removed from the data set, so the final matrix consisted of 45 lines (sampling points) and 14 columns (identified species retained after matrix screening). ‘Species habitat amplitudes’, i.e. the dispersion of records in which the considered species occurs, were calculated for each species on each interpretable CA axis.

Table III. List of detritivore macro-invertebrate species identified in the Eawy Forest rotation and their corresponding code.

Phylogenetic group	List of taxa	Code
Oligochaeta (Lumbricidae)	<i>Dendrodrilus rubidus</i> (Savigny, 1826)	Drub
	<i>Dendrobaena octaedra</i> (Savigny, 1826)	Doct
	<i>Lumbricus rubellus</i> Hoffmeister, 1843	Lrub
	<i>Lumbricus eiseni</i> Levinsen, 1884	Leis
	<i>Lumbricus castaneus</i> (Savigny, 1826)	Lcas
	<i>Octolasion cyaneum</i> (Savigny, 1826)	Ocya
Isopoda	<i>Trichoniscus pusillus</i> Brandt, 1883	Tpus
	<i>Oniscus asellus</i> Linnaeus, 1758	Oase
	<i>Philoscia muscorum</i> (Scopoli, 1763)	Pmus
	<i>Porcellio scaber</i> Latreille, 1804	Psca
	<i>Porcellio dilatatus</i> Brandt, 1833	Pdil
	<i>Trachelipus rathkei</i> (Brandt, 1833)	Trat
Diplopoda	<i>Glomeris marginata</i> (Villiers, 1789)	Gmar
	<i>Chordeuma sylvestre</i> C.L. Koch, 1847	Csyl
	<i>Polydesmus</i> sp. Latreille, 1802	Poly
	<i>Iulus scandinavicus</i> Latzel, 1884	Isca
	<i>Tachypodoiulus albipes</i> (C.L. Koch, 1838)	Talb
	<i>Cylindroiulus latestriatus</i> (Curtis, 1844)	Clate
	<i>Cylindroiulus nitidus</i> Verhoeff, 1891	Cnit

A co-inertia analysis (CoIA) was performed to explore co-variation patterns between community and environmental data. This statistical tool is described as the best way to couple two data tables (records \times species and records \times environmental variables). Environmental data were previously analysed with a principal component analysis (PCA) of a matrix containing 45 lines (sampling points) \times 14 columns (environmental variables). The co-inertia analysis was then run on the CA of faunal data and the PCA of environmental variables to (i) isolate new axes in both multidimensional spaces and (ii) create a factorial plane which distorts as little as possible the structure of each initial data set and enables their simultaneous ordination. The CoIA was validated by a Monte-Carlo permutation test ($n = 1000$, $p < 0.05$). Multivariate analyses and corresponding charts were performed using ade4 package for R [46,55].

3. RESULTS

3.1. Density and biomass patterns

A total of 19 species belonging to the investigated groups of detritivore macro-invertebrates were found in the whole sample set, including 6 earthworm, 6 woodlouse and 7 millipede species (Tab. III). Six species were sampled only in holorganic layers (*Trichoniscus pusillus*, *Trachelipus rathkei*, *Porcellio scaber*, *Cylindroiulus latestriatus*, *C. nitidus* and *Tachypodoiulus albipes*). No anecic earthworm species were sampled in these superficial layers and only one individual of endogeic earthworm species (*O. cyaneum*) was found. All other species were found in both holorganic and organo-mineral layers. Total density and biomass did not present significant differences between silvicultural phases. Density

and biomass of litter-dwelling communities significantly decreased from Ft to Rg stages (Fig. 1). Density and biomass of soil-dwelling communities (i.e. invertebrates sampled in organo-mineral layers) remained constant throughout the rotation. Density and biomass were significantly higher for litter-dwelling than for soil-dwelling species in Ft and Rf phases while no differences were found in Rg phase (Fig. 1).

3.2. Diversity patterns

Except for *Dendrodilus octaedra* which was not present in the amelioration phase, all species occurred at all silvicultural stages. This indicates that there was no species turn-over throughout the studied rotation. Mean *SR* of total and litter communities were lower in Rg when compared to other phases while no significant change was observed for soil-inhabiting invertebrates (Fig. 1). Except for Rg, mean *SR* was also significantly higher for litter-dwelling invertebrates than for soil-dwelling invertebrates. Mean *J'* was very high (> 0.80) and did not differ between silvicultural phases whatever the layer considered (Fig. 1), although it was higher in litter than in soil communities in Rf and Am. Mean *WPS* of the total litter-dwelling communities was higher in Rf and lower in Rg, while it remained constant for soil-dwelling invertebrates (Fig. 1). It was also higher for litter-dwelling than for soil-dwelling species in Ft and Rf phases (Fig. 1). The organizational dimension of diversity, measured by the mean *FD* of each phase, significantly increased from Ft and Rf to Rg along CA1. No differences appeared between stages for *FD* on CA2 (Fig. 1).

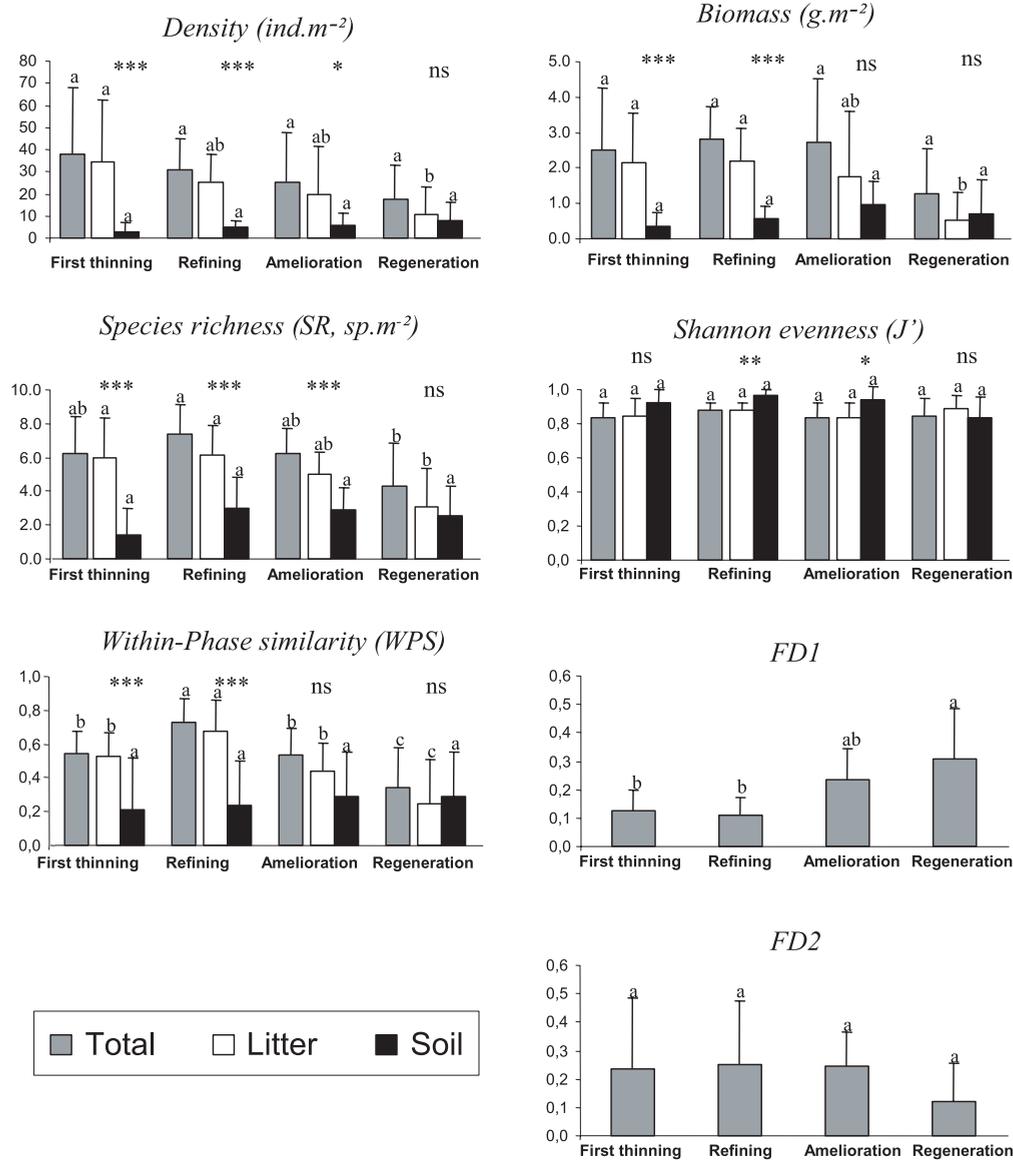


Figure 1. Mean values of community descriptors (bars are standard deviations) for total, litter- and soil-dwelling detritivore macro-invertebrate assemblages at each silvicultural phase. Different letters indicate significant differences at $p < 0.05$ (Tukey HSD test) between silvicultural stages. Asterisks indicate statistical differences between soil- and litter layer assemblages (*ns* not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

3.3. Correspondence analysis on total detritivore invertebrate densities

The first two axes of CA accounted for 48.4% of the total variance, with 29.5% and 18.9% for the first (CA1) and the second axes (CA2), respectively. The next axes displayed small eigenvalues and were not considered for the interpretation (Fig. 2a).

CA1 ordinated sampling points according to a gradient from Ft to Rg stands (Fig. 2b). Sampling points with negative scores on CA1 were mainly mull-moder and moder humus whilst those with positive scores were dominated by mull humus (Tab. IV). Species ordination and species 'habitat am-

plitudes' opposed: (a) a group of species with negative scores (i.e. *Philoscia muscorum*, *Glomeris marginata* and *Iulus scandinavicus*); to (b) two species with high positive scores (i.e. *Lumbricus eiseni* and *Dendrobaena octaedra*) (Figs. 2c and 2d). Most of the other taxa (e.g. *Chordeuma sylvestre*; *Oniscus asellus*; *Dendrodriulus rubidus*) were close to the origin, meaning that their contribution to this axis was low (Figs. 2c and 2d). CA1 was interpreted as the response of macro-invertebrate communities to the gradient of forest maturation.

Sampling point ordination along CA2 did not follow a simple and easily interpretable scheme as for CA1. Instead, samples with positive and negative coordinates on CA2 were found in all of the four silvicultural stages of the study

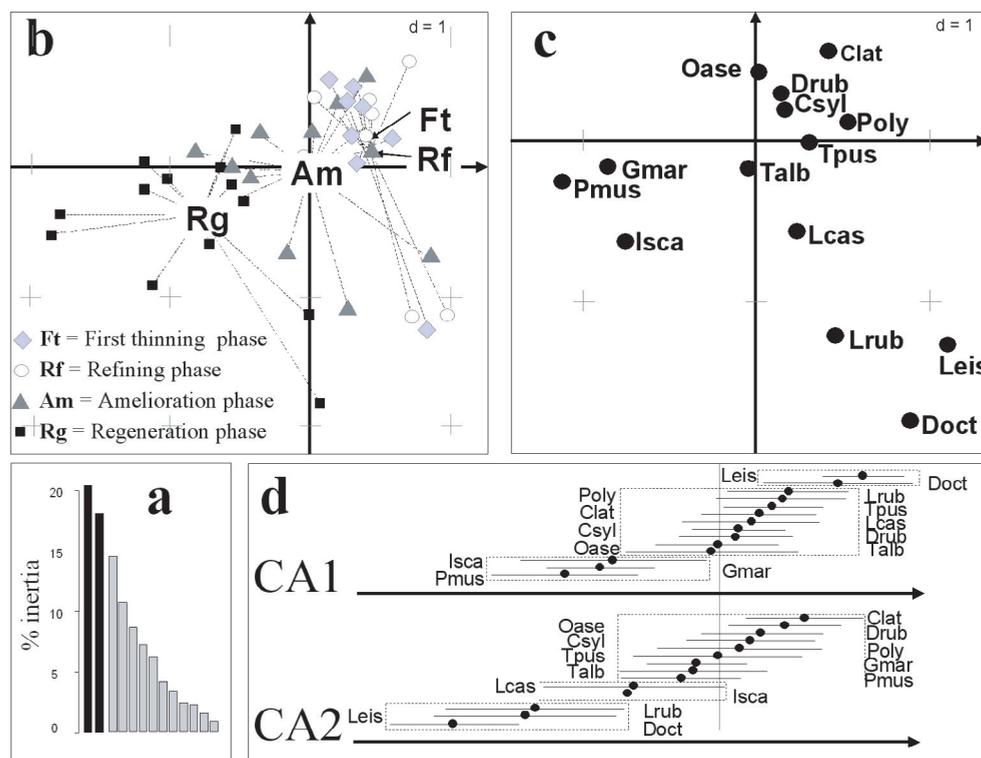


Figure 2. Results of Correspondence Analysis carried out on the matrix of detritivore macrofauna density (first factorial plane): (a) eigenvalue diagram; (b) site ordination with representation of the barycentres for each silvicultural phase; (c) species ordination; (d) species 'habitat amplitude' on the first two axis of the CA. Coding for species is given in Table III.

Table IV. Percentage of mull, mull-moder and moder humus forms in groups of points defined by their coordinates on the two first CA axes.

Points with:	Mull (%)	Mull-moder (%)	Moder (%)
Positive score on CA1	15.4	46.2	38.5
Negative score on CA1	73.7	10.5	15.8
Positive score on CA2	25.0	25.0	50.0
Negative score on CA2	57.1	38.1	4.2

(Fig. 2b). Sampling points with negative scores on CA2 were mainly mull humus while those with positive scores were preferentially moder humus (Tab. IV). Species ordination and species 'habitat amplitude' opposed 3 earthworms species with high negative scores (*L. rubellus*, *L. eiseni* and *D. octaedra*) to other species with low positive or negative coordinates, while *L. castaneus* and *I. scandinavicus* had as intermediate position (Figs. 2c and 2d). CA2 was assumed to reflect the effect of humus spatial variability on the presence of some earthworms species.

3.4. Species-environment relationships

The first two axes of the CoIA (CoIA1 and CoIA2) accounted for 60.6% and 18.1% of the total co-variance, respec-

tively (Fig. 3a). The first axes of both CA and PCA were highly correlated to CoIA1 while the second ones were opposed on CoIA2.

CoIA1 was interpreted as the effect of forest ageing on environmental parameters and detritivore macro-invertebrate communities. It opposed deadwood weight, beech litter weight and total humus depth and weight to herbaceous layer biomass and litter weight, soil pH and beechnut weight (Fig. 3b). Species such as *P. muscorum*, *G. marginata*, *I. scandinavicus* had strong negative contributions to this axis while most other species displayed low positive or negative coordinates (Fig. 3c).

CoIA2 was identified as the result of humus spatial variability. Minimum and maximum OL depth, total humus depth and OL/total humus depth ratio were opposed to total and beech litter weight, minimum OF+OH depth and OF+OH/total humus depth ratio (Fig. 3b). This axis opposed the woodlice *P. muscorum* (negative score) to a group of species with positive scores, mainly *L. eiseni*, *T. albipes*, *G. marginata* and *D. octaedra* (Fig. 3c).

4. DISCUSSION

4.1. Invertebrate-environment relationships

Multivariate analyses highlight the impact of forest stand ageing through modifications in the vertical and horizontal

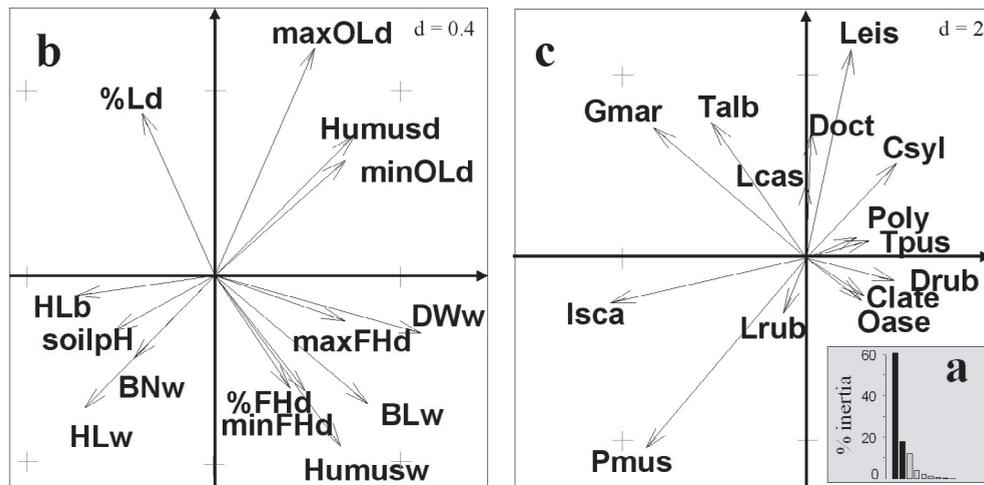


Figure 3. Results of Co-Inertia Analysis between density and environmental data sets (first factorial plane): (a) eigenvalue diagram; (b) environmental variable ordination; (c) species ordination. Coding for environmental variables is given in Table II, coding for species is given in Table III.

distribution of the resources of soil fauna [6]. Management practices may result in high environmental variability through e.g. local use of pesticides, canopy opening or soil disturbance [11, 14]. Local natural events such as storms may also be of importance [35, 41]. Coupling correspondence analysis with the co-inertia interpretation allows us to discriminate three groups of species with specific environmental requirements:

(1) The millipedes *C. sylvestre*, *C. latestriatus* and *Polydesmus* sp., the isopods *T. pusillus* and *O. asellus* and the earthworm *D. rubidus* dominated in young stands. These species were associated with deep OF+OH layers and abundant deadwood and beech leaf mass (Fig. 4). They were preferentially found in moder humus with moist, cool and buffered microclimate [17, 56], which dominated Eawy's closed-canopy stands (Tab. III).

(2) The millipedes *I. scandinavicus*, *T. albipes* and *G. marginata* and the woodlouse *P. muscorum* had the highest relative densities in old stands dominated by mull humus and were linked to high herbaceous biomass and litter weight even though they differ in horizon preference. While *P. muscorum* needed the development of OF layer, *G. marginata* and *I. scandinavicus* appeared to prefer mull-like humus (high OL/total depth ratio). These latter species are characterized by their ability to roll up and/or to burrow and by their exoskeleton impermeability, which confers them a high resistance to dry conditions. They are therefore particularly adapted to mull-like conditions with lower litter thickness, higher light intensity and higher soil dryness [17, 33].

(3) The earthworms *L. eiseni* and *D. octaedra* were opposed to the other detritivore species. This may be due to their strong preference for mull-like humus with deep OL layer whatever the silvicultural phase. On the other hand, *L. castaneus* and *L. rubellus*, presented weak relationships with environmental variables, even though they were preferentially located in mull-like conditions.

4.2. Factors that control detritivore invertebrate communities

The lack of change in species composition throughout the Eawy rotation may reflect the combined effect of some silvicultural practices which may have dramatic impacts on burrowing earthworms, e.g. the mono-culture of a soil-acidifying tree species on acidic soil, or the superficial tillage sometimes used to assist natural regeneration [11]. Moreover, Aubert et al. [5] showed a lack of pioneer and post-pioneer tree species (e.g. *Salix* sp., *Betula* sp., *Carpinus betulus*) at the junction between old and new beech generations. These litter-improving species favourably influence the quality of resources for detritivore invertebrates [8]. Hence, the composition of detritivore macro-invertebrate assemblages of Eawy forest rotation may be explained by a few habitat constraints linked to forest management.

On the other hand, the species richness was low, as reported by several authors in Western European forests (Tab. V). The species number of both woodlice and litter-dwelling earthworms is roughly about c.a. 4–5 species, while soil-dwelling earthworm and millipede species richness appears to be more variable. Species richness limitation in epigeic earthworms and woodlice suggests non-linear relationships between local and regional richness, a trend which is rarely observed in natural communities where local richness is usually determined by the size of the regional pool. This suggests that competition may reduce the number of coexisting species [21, 57]. More research is now needed to define how external factors and species interactions account for the observed community patterns. This will require larger data sets and the use of relevant statistical tools like e.g. null model analyses.

4.3. Mechanisms of community assembly

The patterns of community diversity described herein are relevant to exemplify assembly rules of detritivore

Table V. Species richness of earthworms (litter- and soil-dwelling), woodlice and millipedes in different western European forests.

Forest, Country	Parent rock	References	Management	Main tree species	Litter-dwelling earthworms	Soil-dwelling earthworms	Woodlice	Millipedes
Ardennes, Belgium	Limestone	[44]	Semi-natural	Beech	5	5	–	–
Ardennes, Belgium	Limestone	[20]	Not described	Oak and beech	–	–	5	11
Ardennes, Belgium	Schists and sandstones	[28]	Not described	Beech	4	2	4	6
Eawy, France	Loess	This work	Even-age	Beech	5	1	6	8
Eawy, France	Loess	[6]	Even-age	Beech	4	0	4	9
Fontainebleau, France	Schists and sandstones	[42]	Coppice with standard	Oak	–	–	5	–
Fougère, France	Vire granite	[30]	Even-age	Beech	4	1	–	–
Lyons, France	Loess	[6]	Even-age	Beech and hornbeam	5	0	4	9
Orléans, France	Sandstones	[26]	Not described	Oak	2	4	–	15
Orléans, France	Sandstones	[27]	Not described	Oak and beech	–	–	–	13
Orléans, France	Sandstones	[3]	Not described	Oak	–	–	–	6

macro-invertebrate communities [2, 10, 32]. These rules may be related either to factors external to the community (i.e. associated with habitat constraints acting as environmental filters) or to the internal community dynamics itself (i.e. associated with interspecific relationship constraints) [57]. Thus, species of detritivore macro-invertebrates may co-occur thanks to spatial segregation (i.e. without interspecific interactions) or co-exist through niche partitioning (e.g. variability in resources use) [50]. Three main stages of community assembly are highlighted by our results:

(1) First thinning and refining phases exhibited very similar high values of density, biomass and *SR*, except for *WPS* which was greater in Rf. The low *FD* with regard to the forest maturation gradient (CA1) indicated a high ecological coherence of these species assemblages. This may reflect *niche complementarity* in equilibrium conditions with regard to resource utilization. The low ecological coherence on CA2 emphasizes the role of the spatial variability of humus forms in community assembly. However, our results do not allow us to clearly separate the two underlying mechanisms: co-occurrence of species under environmental *micro-heterogeneity* or co-existence after ecological organization by *niche partitioning* (e.g. species specialization for a given litter horizon or a given organic particle size).

(2) Amelioration phase represented a transition between the first stage and regeneration. Although not always statistically significant, this phase was characterized by a decrease in all community indices but evenness and *FD*. A reasonable hypothesis is that past and current management locally (i.e. at the community scale) led to assemblages which contain species selected by habitat constraints (lower mean *SR*), whereas the humus variability at the silvicultural phase scale allowed a high number of species to occur. These results thus suggest that, in Am phase, many species co-occur because a mosaic of different humus forms results in a high spatial variability of resources and allows a high level of *species spatial segregation*.

(3) In regeneration phase, low values of community indices are probably due to changes in trophic and habitat resources caused by the shelterwood cut. Low values of *WPS* and low ecological coherence in species assemblages reveal an important variability in species assemblage composition in non-equilibrium conditions. Number of processes involved in regeneration practices present different spatio-temporal extent which may overlap leading to high spatial variability. This may explain why all species found in the whole rotation were present in this phase, each of them founding adequate environmental conditions for survival. We thus assumed species to co-occur under *spatial segregation*.

4.4. Implication for humic epipedon functioning and management practices

From a functional view-point, our results refute the hypothesis of Ponge et al. [45] which predicts community changes during forest rotations. In fact, no species turn-over was observed and no burrowing earthworms colonized the soil in the older stands of the rotation. Furthermore, detritivore invertebrate density and biomass decreased with stand ageing, conversely to the theory pattern. This forest rotation doesn't encompass any shift from litter-dweller-dominated community in young and mature stands (autotrophic phase), towards soil-dwelling-dominated communities in regeneration stands (heterotrophic phase). These results are important features as far as the implications for sustainable management are concerned. Eawy intensive beech rotation favours the detritivore species richness and composition similarity to the detriment of the expected shift in functional phases.

On the other hand, mull humus occurred in the old stands despite the absence of (i) soil-dwelling earthworms and (ii) early successional, litter-ameliorant tree species [5]. This result is of particular importance from a management view-point as changes in humus profile are considered a key factor

of tree renewal patterns in beech regeneration [25, 44]. Soil-dwelling earthworm activities enhance microbial decomposer functions (decomposition and mineralization of organic matter, see e.g. Scheu et al. [49]) and lead to a ‘functional’ mull humus [16, 45]. The presence of mull humus devoid of anecic earthworms suggests that forest management practices (mainly canopy opening and soil disturbance) may (i) decrease litterfall and (ii) activate organic matter mineralisation. These processes lead to the formation of a “practices-induced mull humus” with quite different functional features when compared to a “true functional mull humus”. For instance, the bio-macro-structured A horizon, which results from earthworm bioturbation and may favour tree seedling establishment was lacking in Eawy’s regeneration stands. Further research should now investigate if future stands coming from currently assisted natural regeneration will follow similar successional trends than stands coming from artificial plantations such as these used in our sampling design.

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