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Assemblages of Collembola across a 130-year chronosequence of beech forest

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Abstract

Although microarthropods dominate forest floor faunas in both diversity and abundance, long-term aspects of forest cycles have been widely neglected in soil ecological research in the past. We studied which modifications occurred within collembolan assemblages during a typical beech forest cycle from the north-western part of France. We selected 16 sites representative for four age-classes: 15-year, 65-year, 90-year and 130-year-old stands. Strongly significant effects of the factor 'age class' reflect increasing collembolan abundance, biomass and mean species richness throughout the ageing of the forest. However, none of the species could be depicted as an indicator for a specific age-class. Nevertheless, shifts in the relative abundances of dominant or subdominant species were responsible for significant differences between communities of the four successional stages. Our results differ from previous studies, highlighting on the one hand the multiplicity of factors acting on soil invertebrates, and on the other hand the need for forest management aiming at combining productivity and biodiversity conservation to adapt to regional differences in tree species, soil, substrate and climatic conditions.

Keywords: Springtails, succession, forest management, soil fauna

1. Introduction

In Europe, wooded areas represent the predominant land-use type with a share of ca. 31% of the entire continental area. Microarthropods dominate forest floor faunas in both diversity and abundance (Wallwork 1976). Therefore, temporal changes in the structure of collembolan assemblages may significantly impact forest ecosystem processes. For example, alterations of the decomposition rate will inevitably affect the balance between the gain and loss of carbon (Schulze et al. 2000, Hooper et al. 2005).

However, long-term aspects of the forest cycle have been widely neglected in past research (Bengtsson et al. 2000, Chauvat et al. 2003). It has recently attracted new interest in the context of ecosystem-oriented approaches to forest management (Horwood & Butt 2000, Johnston & Crossley 2002, Peck & Niwa 2005, Chauvat et al. 2009, Siira-Pietikainen & Haimi 2009). Recent studies highlighted substantial modifications of soil collembolan assemblages and ecosystem processes during managed forest rotation (Chauvat et al. 2003, Salmon et al. 2006, Salamon et al. 2008, Salmon et al. 2008, Chauvat et al. 2009). Even if these studies acknowledged the role of different abiotic and biotic factors as structuring forces of springtail assemblages, we still lack the knowledge to be able to predict the long-term dynamics of soil collembolan assemblages throughout forest rotation. This is mainly due to the multiplicity of driving factors occurring in different forest types under different forest management schemes.

We decided, therefore, to study the fate of collembolan assemblages during a typical forest cycle from the north-western part of France.

In Normandy, beech (*Fagus sylvatica*) is the dominant tree species and largely cultivated in monoculture stands. Regeneration of beech forests on acid soils is usually carried out by natural processes. In practice the foresters, by selective cutting, choose which trees will bear fruits and give birth to the next generation. To facilitate the regeneration process, the soil is prepared by mechanically scraping the superficial layers and by using herbicides to limit competition with herbaceous plants (Lanier 1994).

We selected four beech silvicultural phases located in the Eawy forest (Normandy-France). The simultaneous availability of forest sites of different ages enabled us to apply the 'space-for-time substitution' approach as a surrogate for a long-term study on collembolan succession (Pickett 1989). Despite some methodological shortcomings, this approach is often considered to be the only way of determining long-term changes in forest ecosystems.

Due to the strong relationships between aboveground and belowground systems, we hypothesized that aboveground changes taking place during forest rotation (Aubert et al. 2003) impacted collembolan assemblages. In particular, post harvesting disturbances may significantly impoverished collembolan assemblages.

2. Materials and Methods

2.1. Site description

Within the Eawy forest (01°18'E, 49°44'N; 7200ha; 30 km NNE of Rouen; France), one of the largest forest districts in Normandy, site selection was constrained by three major filters. First by historical land-use (at least a complete beech monoculture rotation should have been already performed on the sites), second the management type (monoculture with assisted natural regeneration) and third the parent rock (endogleyic dystric Luvisol (FAO 2006) developed on more than 80 cm of loess lying on clay with flint). Then, within the reduced set of sites and after discussion with the French Forestry Service (ONF) in charge of the Eawy forest, we retained four age-classes forming a chronosequence: 15-, 65-, 95- and 130-year-old stands. In the following text these will be abbreviated to AGE 15, AGE 65, AGE 95, and AGE 130, respectively. The youngest age-class (AGE 15) represents the regeneration phase. All stands came from assisted natural regeneration (selective cutting and superficial topsoil scratching without clear-cutting practices). Selective but parsimonious thinning is then applied until the stand reaches 'maturity' between 115 and 130 years after the regeneration phase.

Within each age-class four replicate sites corresponding to the above mentioned filters were randomly chosen. The study was thus carried out at 16 secondary beech forest sites (*Fagus sylvatica* L.). All sites were situated in close proximity to each other in the Eawy forest (Fig. 1) and located on a flat topographic situation (plateau) with an elevation of about 205 m above sea level. Each site covered an area ranging from 4 to 18 ha. The climate is temperate oceanic with a mean annual precipitation of 800 mm and a mean annual temperature of +10 °C.

Understory vegetation was defined as a characteristic Endymio-Fagetum according to phytosociological classification (Durin et al. 1967). In early spring the soil was almost fully covered by an herbaceous layer dominated by *Endymion non-scripta*. Later in the growing season and depending on canopy gaps, *Millium effusum*, *Brachypodium sylvaticum*, *Dryopteris filix-mas* and *Carex pilulifera* dominated a less important herbaceous layer. A sparse shrub layer, increasing with stand age, was dominated by *Rubus fruticosus*, *Crataegus monogyna* and *Rosa sp*.

Humus forms according to the French classification (Brethes et al. 1995) varied between forest stages from dysmull at AGE 15 to dysmoder at AGE 130, which would correspond to a shift from leptomoder toward mormoder according to the Canadian classification (Green et al. 1993). The depth of the humus layer varied from 3.4 cm at AGE 15 to 4.0 cm at AGE 130 (data not shown). Water content and pH values of both organic and the first 5 cm of the A horizons did not significantly differ between stand age (data not shown). Within the organic horizon, mean pH value was of 4.9 and mean water content of 58.8% fresh weight. Within the A horizon, mean pH values were 3.9 and mean water content 36.4% fresh weight (data not shown). Furthermore, microbial N biomass either within the organic or the A horizons did not significantly differed between age-classes (Trap et al. 2011).

2.2. Sampling and identification of Collembola

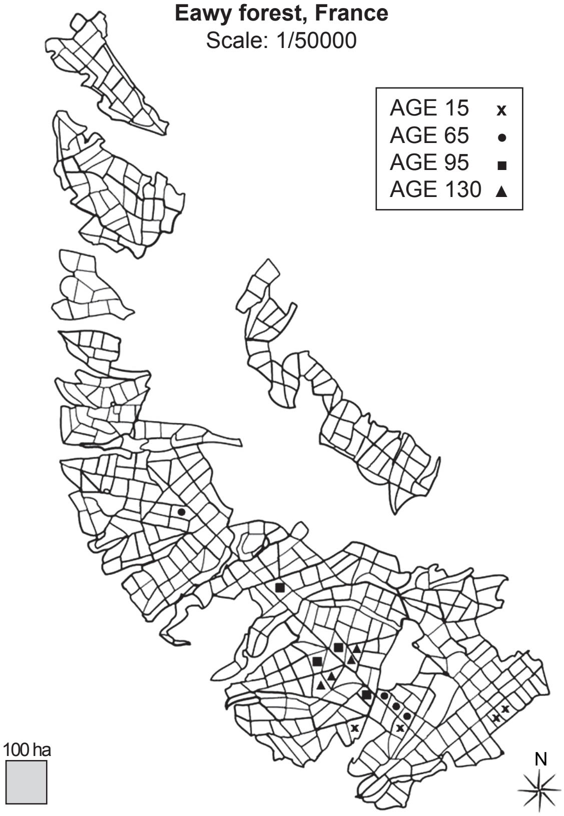

Fig. 1 Location of the 16 sampling sites (AGE 15 to AGE 130) in the Eawy forest, Normandy, France.

Two soil samples were collected at each of the 16 sites in November 2007, March 2008, June 2008 and September 2008 by means of soil corers (diameter: 5 cm). A single core included the organic layer and the top 5 cm of the mineral horizon. Collembola were extracted by means of the dry-funnel method. Identification to the species level followed standard identification keys (Gisin 1960, Zimdars & Dunger 1994, Pomorski 1998, Potapov 2001). A few juvenile specimens could only be identified with certainty to the genus level and were excluded in further analyses except for the computations of abundance and biomass.

2.3. Treatment of data and statistics

We calculated three measures of collembolan species richness: total number of species found at each age class, mean number of species found at each age-class and an estimated number of species richness per age-class based on the Chao1 nonparametric estimator (Magurran 1994). Furthermore, to determine whether the differences between age-classes in the number of sampled species were due to richness differences or to the unequal number of specimens collected, we used rarefaction curves (Magurran 1994). Chao1 and rarefaction curves were computed using EstimateS (Version 8.2, R. K. Colwell, http://purl.oclc.org/estimates).

Species richness of a site$_i$ at a particular sampling date was calculated by using the cumulative values of the two cores taken at the site$_i$. Abundance and biomass of a particular site$_i$ at a particular sampling date were calculated using mean values of the two cores taken at the site$_i$. Since seasonal variations were beyond the scope of this study, for each parameter we used the obtained mean values across the four sampling dates.

The biomass of a single collembolan species was calculated following the allometric function between length and dry weight (DW): Log Y = Log a+b Log l; where:

Y: dry weight (mg DW ind^{-1}), l: body length (mm). First, the average body length of each species was calculated by taking the mean of all length measurements given in the following determination keys (Gisin 1960, Palissa 1964, Fjellberg 1980, Zimdars & Dunger 1994, Fjellberg 1998, Pomorski 1998). The species-specific regression factors a and b were taken from the literature (Tanaka 1970, Petersen 1975, Persson & Lohm 1977, Pflug 2001). For species not mentioned in these publications, equation parameter values of species with a similar body shape of the same genus or family were used. The biomass of individuals identified only at the genus level was calculated by taking the mean biomass value of the respective genus. The biomass of juveniles was calculated by taking half of the body length of the respective adults.

The effect of the factor ‘age-class’ on collembolan parameters was tested by means of one-way ANOVAs. When necessary, data were transformed prior to analyses to ensure normal distribution of residuals and homogeneity of variances. Significant differences between means were tested at the 5% level using the Tukey HSD test. Anovas and post-hoc tests were performed using the Statistica software package (version 6.0, StatSoft Inc., Tulsa, StatSoft 2001).

The Simpson (1/D) index was used as an indicator of collembolan diversity (Magurran 1994) and the relative contribution of each species within an assemblage was described by the Simpson’s measure of evenness $E_{1/D}$ (Smith & Wilson 1996). Simpson index, Bray-Curtis index and Simpson’s evenness were calculated on the basis of composite means of abundance of all sites per age-class with the BIODIVERSITY PRO software (version 2, The Natural History Museum, UK, and the Scottish Association for Marine Science, Scotland 1997).

Non-metric multidimensional scaling (NMDS) was computed using Bray-Curtis similarity matrix based on square-root transformed species-abundance data to visualize the relationships between all sites. The optimal number of dimensions was determined by selecting the ordination with minimum ‘Stress’. Hypotheses of no assemblage difference between stages were tested using ANOSIM Global-R on square-root transformed species-abundance data (Clarke 1993). If two groups of sampling units are really different in their species composition, then compositional dissimilarities between the groups ought to be greater than those within the groups. The ANOSIM statistic R is based on the difference of mean ranks between groups and within groups. ANOSIM Global R-values are compared to a null distribution of rank distances generated by the random rearrangement of sites and species in order to estimate the probability of the same ordination, or Bray-Curtis distance configuration, occurring as a result of random chance. ANOSIM was performed with 10000 N permutations and Bonferroni’s correction was applied a posteriori. Similarity percentages (SIMPER) analyses were run to determine species contributions to the observed collembolan assemblage structure under the different stand ages (Clarke 1993). Only those species whose relative abundance was >0.1% of the total were included in the analyses. NMDS, ANOSIM and SIMPER were all performed with the free PAST software version 2.02 (Hammer et al. 2001).

3. Results

In total 7231 individuals were collected during this study: 1335 at AGE 15, 1394 at AGE 65, 1976 at AGE 95 and 2526 at AGE 130. The average abundance of Collembola ranged from 21271 ind. m^{-2} at AGE 15 to 40258 ind. m^{-2} at AGE 130 (Fig. 2). A strong significant effect of the factor ‘age class’ ($F = 15.85$, $p < 0.001$) mainly reflects increasing collembolan abundance throughout the ageing of the forest. AGE 130 carryed significantly more individuals than AGE 95 and AGE 95 significantly more than both AGE 65 and AGE 15 (Fig. 2). Similar increasing patterns with age was found for the biomass ($F = 3.96$, $p < 0.05$; Fig. 4). Across all sites, the total number of collembolan species determined was 40. Total species richness (ST) ranged from 23 species at AGE 15 to 26 at AGE 130 (Tab. 1). Rarefaction curves (figure not shown) showed differences between stands, on a basis of an equal number of individuals sampled, with a lower number of species in the first two stages (Tab. 1). However, the estimated total species richness (Chao1) produced comparable values between stages (Tab. 1).

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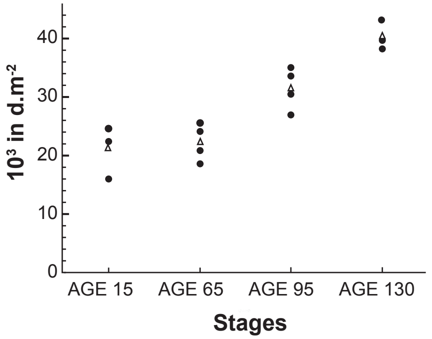

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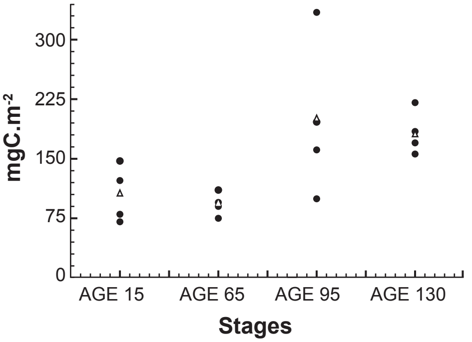

Fig. 2 Abundance of Collembolan assemblages in four stages of a beech chronosequence (AGE 15 to AGE 130) in the Eawy forest, France. Values of the 4 replicate sites per stage are given (black dots) as well as the mean (triangle).

Fig. 3 Biomass of Collembolan assemblages in four stages of a beech chronosequence (AGE 15 to AGE 130) in the Eawy forest, France. Values of the 4 replicate sites per stage are given (black dots) as well as the mean (triangle).

Nevertheless, mean species richness (SM) was significantly different between age-classes (F = 4.08; p <0.05). We did not observe a linear increase of SM with forest age, but SM at AGE 130 was significantly higher than at AGE 65, AGE 95 and AGE 15 having intermediate values (Fig. 4). The Simpson index (1/D) ranged from 4.7 (AGE 65) to 6.7 (AGE 15), with the two other age-classes being intermediate (Tab. 1). Simpson's evenness followed a similar pattern (Tab. 1). Species assemblages significantly differed between all stages except between AGE 15 and AGE 95, which however had a p-value under 0.06 (Tab. 2).

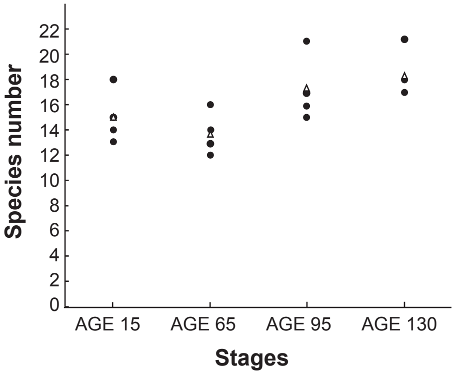

Fig. 4 Mean species richness of Collembolan assemblages in four age-classes of a beech chrono sequence (AGE 15 to AGE 130) in the Eawy forest, France. Values of the 4 replicate sites per stage are given (black dots) as well as the mean (triangle).

Tab. 1 Richness and diversity parameters of Collembola in four stages of a beech forest chronosequence (AGE 15 to AGE 130) in the Eawy forest, France. Standard deviations are given between brackets.

	AGE 15	**AGE 65**	**AGE 95**	**AGE 130**
Total species richness	23	23	26	26
Rarefaction	23	22.9 (0.35)	25.9 (0.36)	24.9 (0.84)
Estimated total species richness (Chao1)	26.1 (3.7)	30.5 (4.9)	30.1 (4.0)	29.0 (3.2)
Simpson s index (1/D)	6.3 (1.7)	4.7 (0.8)	5.4 (0.2)	6.0 (0.3)
Simpson's evenness ($E_{1/D}$)	0.41 (0.07)	0.32 (0.08)	0.33 (0.04)	0.33 (0.15)

Tab. 2 Results of ANOSIM analyses between collembolan communities inhabiting four stages of a beech forest rotation from young stands (AGE_15) to old stands (AGE_130) (Eawy forest, France). p-values and R-values (within brackets) are given.

	AGE 15	**AGE 65**	**AGE 95**	**AGE 130**
AGE 15	-	0.028 (0.52)	0.053 (0.48)	0.027 (0.66)
AGE 65		-	0.028 (0.66)	0.029 (0.78)
AGE 95			-	0.028 (0.46)
AGE 130				-

Tab. 3 Contribution of collembolan species to the dissimilarity between assemblages of four stages of a beech forest rotation from young stands (AGE 15) to old stands (AGE 130) (Eawyforest, France). For clarity only the first five discriminant species were shown. Cont: Contribution to dissimilarity; Cum %: Cumulative percentage of contribution to dissimilarity.

	AGE 15 to AGE 65			**AGE 65 to AGE 95**			**AGE 95 to AGE 130**			**AGE 130 to AGE 15**	
	Cont	**Cum %**		**Cont**	**Cum %**		**Cont**	**Cum %**		**Cont**	**Cum %**
Protaphorura subarmata	2.8	6.8	Parisotoma notabilis	3.2	9.1	*Ceratophysella denticulata*	2.1	6.7	*Folsomia quadrioculata*	3.3	8.0
Folsomia quadrioculata	2.5	13.0	Micranurida granulata	2.0	14.8	*Isotomiella minor*	1.8	12.5	*Micranurida granulata*	2.8	14.7
Sminthurinus signatus	2.4	18.8	Willemia denisi	2.0	20.4	*Sminthurinus signatus*	1.7	18	*Friesea truncata*	2.8	21.4
Isotomiella minor	1.9	23.5	Mesaphorura yosii	1.9	25.8	Folsomia quadrioculata	1.6	23.3	*Ceratophysella denticulata*	2.6	27.7
Friese truncata	1.9	28.1	Sminthurinus signatus	1.8	30.7	*Protaphorura sp.*	1.6	28.6	*Sminthurinus signatus*	2.3	33.3

According to the SIMPER results, dissimilarity of collembolan assemblages between stages decreased along forest maturation (Tab. 3). The overall difference between all stages (SIMPER, 37.2%) was mainly due to five species, namely *Folsomia quadrioculata, Willemia denisi*, *Friesea truncata*, *Simthurinus signatus* and *Parisotoma notabilis*. They explained over 26% of the total dissimilarity. *Folsomia quadrioculata* dominated all investigated age-classes with a relative abundance ranging from 26.9% at AGE 15 to 40.4% at AGE 65 (Tab. 4). Like this species, *Isotomiella minor* and *Parisotoma notabilis* were observed in all stages at high numbers. Other species were also present in all stages, but with an increasing abundance from AGE 15 to AGE 130 (e.g. *F. truncata*, *S. signatus* and *Mesaphorura yosii*). Several species were found only in young stands (e.g. *Allacma fusca* and *Proisotoma minuta*), while *Tomocerus minor* and *Pseudosinella mauli* were sampled only at AGE 130 (Tab. 4). From stage to stage, dissimilarities between assemblages structure were due to dominant but also to subdominant species (Tab. 3). For example *Ceratophysella denticulata* or *Micranurida granulata* strongly contributed to differences between assemblages (Tab. 3).

NMDS ordination of the 16 sites with a stress of 0.18 revealed a clear transition from AGE 15, on the left hand side of the graph, to AGE 130 on the right hand side. The dispersion of cluster points within age-classes was particularly high at AGE 15 and low at AGE 130 (dispersion of sites of a same age-class) (Fig. 5).

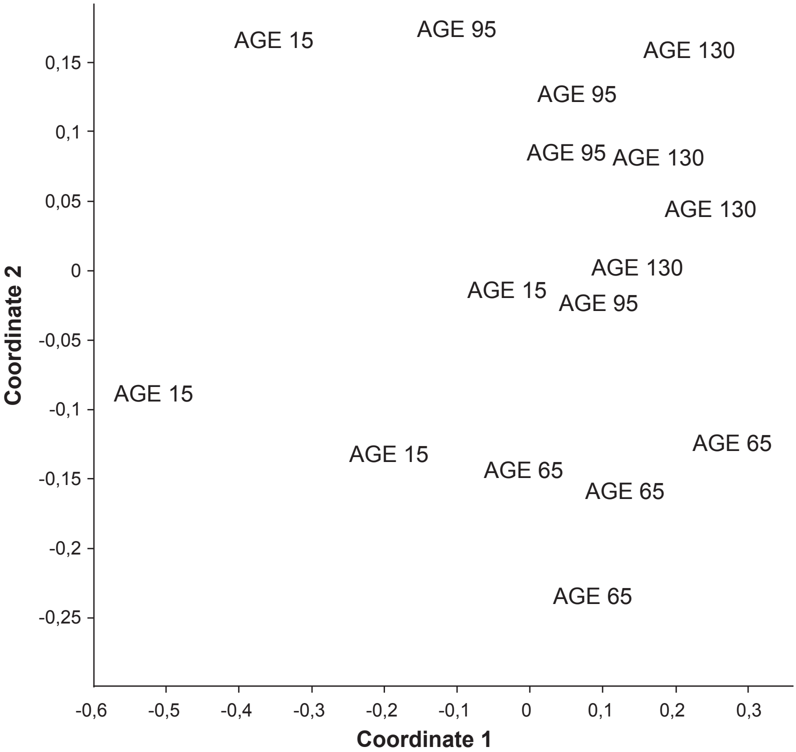

Fig. 5 Non-metric multidimensional scaling (MDS) plot based on Bray-Curtis dissimilarity measures derived from square-root transformed abundances of collembolan species recorded in four stages of a beech chronosequence (AGE 15 to AGE 130) in the Eawy forest, France.

Tab. 4 Species list, dominance structure (values in %) and total abundances of Collembola in four stages of a beech forest chronosequence (AGE 15 to AGE 130) in the Eawy forest, France.

	AGE 15	**AGE 65**	**AGE 95**	**AGE 130**
Folsomia quadrioculata (Tullberg, 1871)	26.9	40.4	34.2	31.2
Isotomiella minor (Schäffer, 1896)	22.3	16.7	15.4	21.6
Parisotoma notabilis (Schäffer, 1896)	11.7	6.7	16.4	7.5
Mesaphorura macrochaeta Rusek, 1976	7.0	5.3	3.3	3.3
Protaphorura subarmata (Gisin, 1957)	4.5	0.0	0.7	0.6
Sminthurinus signatus (Krausbauer, 1898)	3.4	7.7	4.4	5.8
Friesea truncata Cassagnau, 1958	2.6	4.0	5.8	6.6
Lepidocyrtus lanuginosus (Gmelin, 1788)	2.4	6.5	3.0	3.6
Mesaphorura yosii (Rusek, 1967)	2.3	0.4	2.7	1.5
Protaphorura armata (Tullberg, 1869)	2.3	0.6	1.1	0.0
Entomobrya multifasciata (Tullberg, 1871)	2.1	0.1	0.6	0.5
Willemia denisi Mills, 1932	2.0	0.7	2.3	3.4
Arrhopalites sericus Gisin, 1947	1.8	0.1	0.7	0.3
Proisotoma minuta (Tullberg, 1871)	1.7	0.0	0.0	0.0
Protaphorura sp.	1.6	0.0	0.0	2.3
Protaphorura eichhorni (Gisin, 1954)	1.4	0.0	1.1	0.6
Megalothorax minimus Willem, 1900	1.3	1.3	0.7	1.7
Paratullbergia callipygos (Börner, 1902)	1.2	2.4	1.1	1.5
Allacma fusca (Linné, 1758)	0.6	0.0	0.0	0.0
Supraphorura furcifera (Börner, 1901)	0.5	0.0	0.0	0.0
Neanura muscorum (Templeton, 1835)	0.2	0.0	0.4	0.2
Stenaphorurella denisi (Bagnall, 1935)	0.2	0.0	0.0	0.0
Metaphorura affinis (Börner, 1902)	0.2	0.0	0.0	0.0
Ceratophysella denticulata (Bagnall, 1941)	-	1.5	0.2	2.4
Desoria violacea (Tullberg, 1876)	-	0.0	0.3	0.3
Dicyrtoma fusca (Lubbock, 1873)	-	0.0	0.2	0.4
Lepidocyrtus curvicollis Bourlet, 1839	-	-	0.6	-
Mesaphorura sp1	-	-	-	0.5
Mesaphorura sp2	-	1.3	-	0.6
Mesaphorura sylvatica (Rusek, 1971)	-	0.3	-	-
Micranurida granulata (Agrell, 1943)	-	0.3	2.1	2.7
Micranurida pygmaea Börner, 1901	-	0.7	1.1	0.1
Neelus murinus Folsom, 1896	-	0.3	-	-
Orchesella villosa (Geoffroy, 1762)	-	-	0.3	-
Pogonognathellus flavescens (Tullberg, 1871)	-	-	0.8	-
Pseudosinella mauli Stomp, 1972	-	-	-	0.3
Sphaeridia pumilis (Krausbauer, 1898)	-	0.1	0.5	-
Tomocerus minor (Lubbock, 1862)	-	-	-	0.6
Xenylla boerneri Axelson, 1905	-	1.9	-	-
Xenyllodes armatus Axelson, 1903	-	0.4	-	-
Total abundance per m-2 (without juveniles)	**20761**	**21548**	**30239**	**39557**

4. Discussion

Our study revealed significant changes of the structure of collembolan assemblages during forest rotation. The three coarse collembolan parameters (biomass, abundance and mean species richness) had their highest values in old growth stands (AGE 130). Furthermore, rarefaction curves indicated that differences in species number between stages were not simply due to differences in total number of individuals collected. However, computing species richness estimators indicated that the species pool might in fact not differ in terms of numbers between age-classes. Therefore, we cannot exclude the possibility that our results are partly biased by our sampling design, specifically by taking a low number of cores per site and per sampling occasion. However we tried to minimize this by increasing sampling occasions within a single year to deal with species phenology.

The enrichment of collembolan assemblages both in terms of abundance or species richness during forest maturation is far from being a rule. Other authors equally reported a higher abundance of Collembola beneath old spruce stands (>160 years) (Hågvar 1982, Addison et al. 2003). But, in other studies higher densities of Collembola occurred in regeneration stands of spruce forests on both acidic and calcareous substrates (Salmon et al. 2006, Salmon et al. 2008), or densities did not vary between stand stages of either spruce or beech forests on acidic or calcareous bedrocks, respectively (Chauvat et al. 2003, Chauvat et al. 2009). Contrasting observations were also made regarding biomass, species richness or diversity (Sterzynska 1995, Chauvat et al. 2003, Salmon et al. 2008). All these studies were performed on forests growing with different site conditions and under different management schemes.

It is particularly difficult to partition or distinguish the effects of such parameters as they may drive numerous underlying abiotic and biotic factors. For example, responses of Collembola to regeneration methods (e.g. clear-cutting or prescribed burning) seem site dependent. Their abundances can increase, decrease or remain unchanged after the treatments (Huhta et al. 1967, Huhta 1976, Sterzynska 1995, Addison et al. 1998, Marra & Edmonds 1998, Siira-Pietikäinen et al. 2001, Addison et al. 2003, Malmström et al. 2008). The time passed since harvesting and environmental conditions such as soil moisture (Marra & Edmonds 1998, Chauvat et al. 2003, Siira-Pietikainen & Haimi 2009) and site productivity (Bengtsson et al. 1998) are often considered to be driving factors.

In our study, the natural regeneration strongly minimized disturbances associated to, for example, burning or clear-cutting. Abiotic (soil pH, water content) and biotic factors (microbial biomass) were not significantly different between our sites. Both the high diversity and evenness values of collembolan community recorded at AGE 15 support this assertion. However, the harvesting of the old stands and the following regeneration management significantly changed the collembolan assemblages (between AGE 130 and AGE 15) by reducing the dominance of *F. quadrioculata* in favour of deep-dwelling collembolan species like *Protaphorura subarmata* or *M. macrochaeta.*

Low disturbances of the soil and litter biotic assemblages during forest rotation indicate benefits for tree growth. Nutrient release for plants would become more stabilized, and the soil conditions would become more suitable for root growth and plant water uptake. Keeping a certain degree of ecosystem integrity is central to maintaining site productivity for sustainable timber production. Both production of wood and protection of natural resources (e.g. species diversity or water) are objectives of modern forestry aimed fulfilling societal demands (Thomas & Packham 2007).

The ANOSIM results tend to agree with the time-frame for recovery of soil collembolans suggested by other studies (Addison et al. 2003, Chauvat et al. 2003). Even at AGE 95, 95 years after stand initiation, the collembolan assemblage could still be distinguished from that at AGE 130. The significant dissimilarity reflects changes in the abundances of dominant species, rather than the elimination or addition of species to the assemblages. This may partly be due to our sampling design which favoured the collection of dominant species. Furthermore, NMDS results tend to prove a separation between AGE 15 and the other age-classes. However, AGE 15 and AGE 95 were not different in terms of Collembolan communities. Dissimilarities between assemblages decreased as trees grew. Within-age-class dissimilarity also diminished (NMDS), which may indicate a maturation of the assemblage during forest rotation.

Few species were found at a single age-class: *P. mauli* and *T. minor* at AGE 130 for example or *A. fusca* and *P. minuta* at AGE 15. It is difficult to consider them either old-growth or regeneration specialists as they have low abundances. Moreover, in a previous study *A. fusca* were also found in intermediate stages of a spruce chronosequence (Chauvat et al. 2003). Our inability to find indicator species of old growth forest is not surprising as research in other disciplines has generally found only a few species of vertebrates and plants that were unique to old forest (Carey 1998). In our study dominant species at all age-classes were ubiquitous species with a large ecological spectrum.

Focusing on subdominant species revealed that several of them showed increasing (e.g. *F. truncata* or *S. signatus*) or decreasing abundances during forest maturation (e.g. *M. macrochaeta* or *P. subarmata*). These subdominant species also significantly contributed to the observed differences between age-classes. This may highlight the potential use of subdominant species as indicator of forest stages for example. In the literature, *S. signatus*, also preferred old stands in forest system (Chauvat et al. 2003). One reason may be the preference of *S. signatus* for habitats offering a high amount of litter (Ponge et al. 1993). However, in the literature, *M. yosii* for example rather preferred young stands to old ones (Chauvat et al. 2003, Salamon et al. 2008) contrary to our results. These contrasting results may reveal the importance of local biotic and abiotic factors as filters for collembolan assemblages. In general, too few studies have investigated this indicator question on a species level in forest system.

In conclusion, the abundance, biomass ahe structure of collembolan assemblages differed significantly between stages of a beech forest chronosequence on acid soil. However, changes in diversity were moderate and only shifts in relative abundance of dominant to subdominant species were depicted. Despite the fact that several studies have also described modifications of collembolan assemblages during forest rotation, we still lack a general model. In this context, the contrasting findings between several studies highlight the need for forest management aimed at combining productivity and biodiversity conservation to adapt to regional differences in tree species, soil, substrate and climatic conditions.

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