DIVERSITY, STRUCTURE AND ENDEMICITY
OF EARTHWORM AND SPRINGTAIL COMMUNITIES
OF A SOFTLY MANAGED BEECH FOREST IN THE PYRENEES (FRANCE)

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Résumé.— *Diversité, structure et endémicité des communautés de vers de terre et de collemboles dans une hêtraie peu aménagée des Pyrénées (France).*— Nous avons évalué et comparé les patrons de biodiversité et la composition de deux communautés d'invertébrés du sol (collemboles et lombrics) dans trois parcelles peu aménagées d'une hêtraie-sapinière dans les Pyrénées françaises. Ces parcelles sont gérées selon trois modalités différentes: une futaie régulière (REG), une futaie irrégulière fermée (NAT) et une futaie irrégulière ouverte (IRR). À chaque point d'échantillonnage les vers de terre et les collemboles ont été collectés dans la litière, le sol et au moyen de pièges Barber, et neuf paramètres édaphiques et environnementaux ont été mesurés. La faune récoltée était riche en espèces ainsi qu'en taxons rares et endémiques. Aucune différence marquée de la richesse spécifique n'est apparue entre les parcelles. Néanmoins (1) le site le moins perturbé, *i.e.* NAT, hébergeait un nombre légèrement plus élevé d'espèces endémiques et rares que IRR et REG; (2) la structure des deux communautés différait significativement entre NAT, REG et IRR selon l'altitude du site et la teneur en azote organique (plus forte dans NAT), la température à la surface du sol et le pH du sol (plus élevés dans IRR), ainsi que l'indice d'humus et la teneur en eau du sol (plus élevés en REG). Ces facteurs, à l'exception de l'altitude, peuvent s'expliquer par l'ouverture de la canopée partiellement contrôlée par les pratiques de gestion; (3) un à-côté de cette étude est d'avoir montré que l'exhaustivité de l'échantillonnage requiert plus d'efforts pour le sol que pour la litière, et plus pour les lombrics que pour les collemboles. Dans un contexte plus large, le cas traité dans cette étude suggère que des pratiques de gestion avec un éclaircissement limité du couvert forestier n'affectent que légèrement la biodiversité du sol, ce qui contraste fortement avec l'effondrement de la biodiversité endémique qu'induit la reforestation.

Summary.— We assessed and compared patterns of biodiversity and the composition of two soil invertebrate communities (Collembola and Lumbricidae) in three slightly managed plots in a beech forest of the French Pyrenees. The plots were managed in three different ways: an even-aged (REG), a closed uneven-aged stand (NAT), and an open uneven-aged full-grown stand (IRR). At each sampling point, earthworms and Collembola from litter, soil, and pitfall traps were collected, and nine edaphic and environmental parameters were measured. The fauna collected was rich in species, and endemic and rare taxa. No clear-cut differences in species richness appeared between plots. Nevertheless, (1) the less disturbed plot, i.e. NAT, hosted a slightly larger number of endemic and rare species than IRR and REG; (2) the structure of both communities in NAT, REG and IRR differed significantly depending on the site elevation and organic nitrogen content (higher in NAT), soil surface temperature and soil pH level (higher in IRR), and humus index and soil water content (higher in REG). Those factors, except elevation, may be explained by the canopy opening partly controlled by management practices; (3) a side aspect of the study was to show that sampling exhaustiveness required more sampling effort for soil than for litter, and more for Lumbricidae than for Collembola. In a broader context, the case documented in this study suggests that management practices with limited clearing of forest cover affect soil biodiversity only slightly, which is in sharp contrast with the collapse in endemic biodiversity induced by reafforestation.

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The composition of invertebrate communities changes under anthropogenic activities (Kasprzak, 1987; Ponge *et al.,* 2003). Forest management in particular has been repeatedly shown to influence the composition of soil fauna communities at various degrees through modifications of many interacting factors (Baguette & Gérard, 1993; Lauga-Reyrel & Deconchat, 1999; Cassagne *et al.*, 2006; Matlack, 2001; Jabin *et al.*, 2004; Pontégnie *et al.,* 2005). Forest management encompasses a large range of practices. Deforestation, over-exploitation and reforestation, which concern huge surfaces in Europe, are the most harmful for biodiversity (Deharveng, 1996; Schulze *et al.*, 2004; Cassagne *et. al.,* 2006). They may strongly deplete soil biodiversity in Atlantic forest (Deharveng, 1996), but even more contrasted effects are reported from forest stands of the Mediterranean region (Gama *et al.*, 2003). Most management practices are less destructive. Nevertheless, they influence the soil fauna in various ways (e.g., biomass, population size, density of taxonomic groups), through selective harvesting, high density of exploitation trails, soil compaction, canopy opening and periodical increase of wooden material on the soil surface (Pontégnie *et al.*, 2005; Jabin *et al.*, 2004; Jordan *et al.,* 1999). However data about changes in biodiversity linked to such soft management practices are often unavailable (e.g. mentioned in inaccessible local reports), and reliable data on invertebrate communities remain scarce (Werner & Raffa, 2000). Moreover, changes in biodiversity also depend on endemism since endemic species are particularly well adapted to their habitat, thus supposed to be more affected by management practices and to respond differently from common species, which is not really documented.

Most studies of the impact of forest management to date have focused on particular faunal species, or members of species assemblages (e.g. guilds), and sometimes on a whole taxonomic group, with the aim to select the best indicators (Lindenmayer *et al.,* 2000; Cassagne *et al.*, 2006). Studies comparing the pattern of biodiversity of several taxonomic groups are extremely scarce (Schulze *et. al.*, 2004), although testing relationships between the responses of several taxa to forest ecosystem changes is a prerequisite to estimating the sustainability of forest management practices (Lindenmayer *et al.*, 2000; Ferris & Humphrey, 1999). We may hypothesize, as it has been shown in tropical forests (Schulze *et al.*, 2004), that changes in biodiversity with management practices depend on the initial composition of the fauna, as different groups do not react in the same way to the same management practices. Earthworms, springtails and mites represent functionally the most important components of the forest soil meso- and macro-fauna (Coleman *et al.*, 2004). Their response to forest management practices has been studied, mostly in terms of abundance or biomass (Jordan *et al.*, 1999). Changes in their diversity are much less documented (Cassagne *et al.*, 2003).

The selected taxa are readily identifiable, widespread and well diversified in soils, fulfilling the conditions for a meaningful assessment of biodiversity (Ferris & Humphrey, 1999). They are also easy to collect in a standardized way, allowing adequate sampling protocols for our purpose. We examined here the species assemblages of Collembola and Lumbricidae in three plots located in a large beech forest of the pre-Pyrenean range, and managed in three slightly different ways. We aimed at exploring patterns in order to answer three questions:

(1) Are there significant variations in biodiversity, endemism, and community composition among the studied plots with slightly different management practices?

(2) Is there a correlation between diversity or community composition and biologically important environmental parameters?

(3) What is the level of soil invertebrate biodiversity in slightly managed forests compared to that in forests subjected to extreme management practices, and do changes in biodiversity follow similar trends in the two model soil-faunal groups across the three management treatments?

MATERIAL AND METHODS

SITES AND SILVICULTURAL PRACTICES

The study was carried out in the fir-beech forest of Gar-Cagire (42°96'N, 0°69'E) near Saint-Gaudens (Haute-Garonne, France). The mean annual temperature is 11.1 °C, and the annual rainfall 1137 mm at the foot of the massif (Arbas). The soil was a brown calcareous clay soil on limestone. The humus form varied from eumull to amphimull according to the sampling points. Three plots of about 2500 m^2 and 300 m apart, corresponding to three modalities of forest management were selected. All stands were situated on 30-50 % slopes with North-West exposure. They were issued from natural regeneration, and were exploited since at least 19th century. The largest trees were 120-130 years old. The three plots were:

- NAT: in a closed uneven-aged full-grown stand at 1310-1340 m a.s.l., characterized by a high number of dead fallen trees, a high tree density and a shallow soil because of the stand location on a crest with lapies.
- REG: in an even-aged full-grown stand, located in a depression with limestone outcrops at 1265-1300 m a.s.l.
- IRR: in an open uneven-aged full-grown stand, located on a slope at 1225-1260 m a.s.l., with a lower tree density resulting from successive cuttings.

Management of full-grown stands (REG, IRR) began in 1895 with a large cut in 1919 in the three stands, and two and five harvestings of windfall wood from 1906 to 1967 in REG-NAT and IRR respectively. The last cut in REG and NAT occurred in 1958 while IRR was subjected to another large cut in 1991 and a smaller one in 1996. Management practices were consequently similar in REG and NAT except the "standardization" cut in REG with lesser extent compared to IRR. The vegetation of the plots under study was characterized as follows (most frequent species listed):

- NAT: *Fagus sylvatica, Abies alba, Cardamine heptaphylla, Dryopteris affinis* subsp. *affinis, Galium odoratum, Polystichum setiferum*; total species richness: 18; herb and tree cover: 30 % and 70 %, respectively; basal area: 35.5.
- REG: *Fagus sylvatica, Abies alba, Alliaria petiolata, Athyrium filix-femina, Circea lutetiana, Dryopteris affinis* subsp. *affinis, Epilobium montanum, Galium odoratum, Polystichum setiferum*; total species richness: 20; herb and tree cover: 10 % and 90 %, respectively; basal area: 26.
- IRR: *Fagus sylvatica, Abies alba, Brachypodium sylvaticum, Carex flacca, Carex sylvatica, Circea lutetiana, Epilobium montanum, Festuca heterophylla, Fragaria vesca, Galium odoratum, Geranium robertianum, Milium effusum, Poa trivialis, Potentilla sterilis, Urtica dioica*; total species richness: 45, herb and tree cover: 90 % and 55 %, basal area: 25.5.

SAMPLING DESIGN

Six sampling points were selected at random in each of the three study stands. Sampling points with soil less deep than 30 cm were discarded and replaced by another sampling point randomly selected. At each point, we used four sampling techniques targeting different invertebrate communities: litter, soil and pitfall sampling for collecting Collembola from litter, soil and surface; soil digging associated to formalin solution for collecting earthworms.

Litter, soil and pitfall sampling for soil Collembola

At each point a pitfall trap of 1 cm opening, filled with 95 % ethanol, was placed for two days. When collecting the pitfall, we sampled 250 cm^3 of litter nearby, and 250 cm^3 of the soil (non-figured organic matter, organo-mineral layer A and mineral layer B) beneath it to the depth of 5 cm. All samples were taken over a same period of three days. Litter and soil cores were brought to the laboratory for faunal extraction in Berlese funnel. They were let for 8-10 days in a dry room, till complete desiccation. The identification of Collembola was made at the species level.

Earthworm sampling

Earthworms were extracted by the formalin method (Raw, 1959) completed by hand-sorting (Coleman *et al.*, 2004). Sampling was carried out over a total surface of 1.5 m^2 per plot, made of six circular areas 0.25 m^2 each. Litter and aerial parts of ground vegetation were examined for the presence of epigeic earthworms before being removed. Three waterings (5 liters per replicate) were applied every fifteen minutes with 3, 4 and 5 ‰ diluted formalin, respectively. When no earthworms emerged at the soil surface after the first application (3 ‰ formalin solution), the two following waterings were not carried out. Expelled earthworms were collected and kept in 90 % ethanol. The soil underneath was then dig out to 30 cm depth to collect remaining endogeic earthworms by hand. Earthworms were identified at the species level according to Bouché (1972), Sims & Gerard (1985) and Lainez & Jordana (1987). We referred to Qiu & Bouché (1998) and Zicsi & Csuzdi (1999) for species name updating. Some immature individuals were classified to the genus level. Earthworm species were classified into ecological categories (epigeic, endogeic, anecic) according to Bouché (1972). The total of adult and immature individuals was used to estimate earthworm densities per unit surface.

ENVIRONMENTAL PARAMETERS AND SOIL FEATURES

Temperature was recorded at soil level of each point using a digital recorder (one measure every two hours from 18 May 2006 to 16 October 2006). The mean temperature was calculated for each point.

Carbon mineralization was measured through the soil respiration. At each sampling point, a soil core was extracted using a rectangular 4.2 x 8.3 x 11.3 cm (depth) crystal polystyrene box. The boxes, which contained each a soil core, were open by a 5 mm hole at the inferior face and by a wide aperture on the top (covered with a nylon gauze of 35 μm mesh to prevent invertebrates from escaping) enabling gas exchanges between soil cores and the surrounding air. Carbon mineralization in the soil cores was assessed by measuring CO_2 release with an analyser based on the infrared method (ADC MGA-3000 SERIES MULTI-GAS Analyser). Each box containing the soil core was placed in a tight-air enclosure with fresh air injection to obtain approximately the same basal CO_2 concentration (around 350 ppm). An initial measure of CO_2 concentration was recorded immediately (beginning of the incubation), followed by the second measure after 4h of incubation (Salmon *et al.*, 2008). The amount of mineralized C released by each soil core (CO_2-C) was calculated from the measured CO_2 concentrations. Mineralization activity (CO_2-C/C) was obtained by calculating the ratio of CO_2-C to the soil organic carbon content (see below).

Each humus form at each sampling point was classified and given humus index value by examining the soil profile and measuring humus layer thickness (Brêthes *et al.*, 1995; Ponge *et al.*, 2002). Humus index is a number varying from one (Eumull) to seven (Dysmoder) and attributed to humus forms on the basis of the thickness and number of organic layers, which allows to process humus forms as numerical data (Ponge *et al.*, 2002).

Water content was obtained by weighting soil cores before and after soil drying at 40 °C for 15 days. Soil pH-H_2O was measured using dried soil cores mixed with deionized water (soil:water 1:5 v/v) for 5 min, pH being measured 3 h after this procedure (Anonymous, 1999).

Soil organic carbon and total nitrogen analyses were carried out in the Laboratory of Soil Analysis of the National Institute of Agronomic Research (Arras, France) according to ISO 10694 and ISO 13878 standards (Anonymous, 1995, 1998), respectively. Soil samples were dried, ground to pass a 250 μm sieve and homogenized. A 50 mg fraction was then heated to convert total organic carbon and nitrogen to CO_2 and N_2 respectively, which were measured with an analyser.

Multivariate analyses

Distance-based redundancy analysis (db-RDA, Legendre & Anderson, 1999) was used to test the relationships between environmental factors (quantitative variables – pH, water content, etc., and plots separately) and collembolan and earthworm communities. For Collembola, abundances in litter, soil and pitfall traps were pooled together in order to obtain one value per species. Although data from pitfall depend on the activity of collembolan species, they complement data from soil and litter samples and may be used in a comparative study of abundance since the number and the area of pitfall were similar in the three plots. Db-RDA used sample and species scores resulting from a principal coordinates analysis (PCoA) as input data for redundancy analysis (RDA). In the present study, the PCoA was run using the program PrCoord included as a part of the CANOCO® software package (Version 4.5. ter Braak & Šmilauer, 2002) with the distance matrix calculated using Hellinger's distance measure (Legendre & Gallagher, 2001). The redundancy analysis was performed using CANOCO. The impact of two sets of environmental variables (environmental parameters and plots), was successively tested on the distribution of invertebrate species using Monte Carlo analysis with 499 permutations. Variables with variance inflation factor higher than 10 were arbitrarily removed from the analysis. A db-RDA with the automatic forward selection option was performed in order to select a minimal set of environmental variables that explain the greater part of the species ordination. Only the minimal set of environmental variables was used in the final ordination of species scores by db-RDA. A fourth db-RDA was run to test the differences of earthworm and Collembola communities between three plots under study (REG, IRR and NAT).

Species diversity and abundance

Cumulative plots were used to visualize both the ratio species richness per sample/species increase with increasing sampling effort, and the expected number of species using Jack1 estimate (hence an estimate of sampling exhaustiveness when compared to the observed number of species). Jack1, the first order jackknife estimate of total species richness, was computed as: $S = S_{obs} + L ((n-1) / n)$, where S_{obs} is the number of observed species in the set of samples, L the number of species which occurred in one sample only, and n the number of samples (Colwell & Coddington, 1994).

Correlations between species richness and environmental variables were tested using Pearson´s correlation coefficient (Sokal & Rohlf, 1995).

Variation in the total abundance and mean species richness of Collembola and Lumbricidae among the plots were tested by ANOVA (one-way ANOVA, six replicates). ANOVAs were performed by Statbox-pro.5® and correlation measures by XLSTAT 2006.5® software.

Similarity between the assemblages

The similarity between sample assemblages was measured by two indices (Magurran, 1988):
- Jaccard's coefficient: j / (a + b - j)
- Morisita's index: $2*\sum (ani*bni) / [(da + db)*aN*bN]$ with $da = \sum ani^2 / aN^2$ and $db = \sum bni^2 / bN^2$

where j = number of species present in both samples A and B; a = number of species in sample A; b = number of species in sample B; ani, bni = number of individuals of species i in sample A and sample B, respectively; aN = total number of individuals in sample A; bN = total number of individuals in sample B.

Jaccard's coefficient weights mismatches versus matches in species composition (Krebs, 1989). Morisita's index takes into account species abundance thus better reflecting ecological similarity between the compared samples, giving lower weight to rare species. Similarity indices, diversity indices, Jack1 and values for species accumulation curves were calculated in the database Ecobase (Deharveng & Bedos, 1995).

RESULTS

Overview of the fauna

Eleven Lumbricidae species belonging to ten genera were found (Tab. I) among 213 specimens. The identification of the *Prosellodrilus* species remains doubtful because most characters and its distribution match those of *Prosellodrilus idealis* Bouché, 1972 (restricted in Haute-Garonne department), as confirmed by R. Jordana & D. Diaz Cosin (unpublished observations 2006), but the form and location of its *tubercula pubertatis* and *clitellum* are closer to those described in *Prosellodrilus pyrenaicus* (Cognetti, 1904), more largely distributed but also located in the Pyrenean mountains and parapatric with *P. idealis*. Both species are Pyrenean endemics. *Dendrobaena octaedra* also displayed variations in the form and location of its *tubercula pubertatis* (gutter in segments 30-33 instead of band in segments 31-33) compared to the type species.

TABLE I

Species code (abbreviated name) of Figure 2 and mean abundance of Lumbricidae species (± standard error) in the three forest management types

Lumbricidae species	Code	NAT		REG		IRR	
Aporrectodea icterica (Savigny, 1826)	*Aic*	0.17	(0.17)	0.00	-	0.00	-
Aporrectodea rosea (Savigny, 1826)	*Aro*	0.00	-	0.67	(0.67)	0.00	-
Bimastos eiseni (Levinsen, 1884)	*Bei*	0.17	(0.17)	0.00	-	0.00	-
Dendrobaena octaedra (Savigny, 1826)	*Doc*	1.83	(0.70)	2.83	(0.79)	2.17	(1.08)
Dendrobaena pygmaea cognettii (Michaelsen, 1903)	*Dpy*	0.50	(0.34)	0.00	-	0.00	-
Dendrobaena immature	*Dim*	0.83	(0.31)	1.67	(0.42)	1.17	(0.79)
Lumbricus friendi Cognetti, 1904	*Lfr*	0.00	-	0.33	(0.21)	0.33	(0.21)
Lumbricus immature	*Lim*	0.17	(0.17)	0.00	-	1.00	(0.63)
Murchieona muldali (Omodeo, 1956)	*Mmu*	0.00	-	2.17	(1.42)	2.33	(1.48)
Octolasion cyaneum (Savigny, 1826)	*Ocy*	0.83	(0.65)	0.00	-	0.50	(0.22)
Octolasion immature	*Oim*	0.00	-	0.67	(0.42)	0.33	(0.21)
Proctodrilus antipai (Michaelsen, 1891)	*Pan*	0.00	-	0.17	(0.17)	0.00	-
Prosellodrilus cf *idealis* Bouché, 1972	*Psp*	0.33	(0.33)	0.00	-	0.00	-
Scherotheca savignyi (Guerne and Horst, 1893)	*Sss*	0.00	-	0.33	(0.33)	0.00	-
Unidentified immature	*Imm*	4.50	(1.95)	3.83	(1.17)	5.67	(1.56)

Totally, 7506 individuals belonging to 64 species and 49 genera of Collembola were collected (Tab. II & III). Among the most abundant species *Isotomiella* cf. *minor* and *Pseudisotoma* sp.1 are probably new for science, as well as three rarer species (*Lepidocyrtus* cf. *lignorum*, *Orchesella* cf. *orientalis*, *Pseudisotoma* sp.2).

Sampling exhaustiveness

Species accumulation curves did not reach a maximum in spite of a strongly decreasing steepness of the slope in their distal part (Fig. 1). Seventeen additional species (+ 24 %) could be expected according to Jack 1 estimate of total richness. The number of rare species (present in a single sample) reached a maximum at 28-30 samples with subsequent slow decrease. The

TABLE II

*Species code (abbreviated name) of Figure 2 and mean abundance of Collembola species (± standard error)
in the three forest management types*

Collembola species	Code	NAT		REG		IRR	
Allacma cf. *gallica* (Carl, 1899)	Aga	1.67	(1.67)	1.17	(0.83)	0.00	-
Arrhopalites sp.	Asp	1.00	(0.82)	0.33	(0.21)	1.00	(0.37)
Bourletiellidae sp.	Bsp	0.00	-	0.50	(0.34)	0.00	-
Caprainea sp.	Ca	0.00	-	0.00	-	0.17	(0.17)
Ceratophysella cf. *armata* (Nicolet, 1842)	Car	17.50	(6.92)	4.33	(1.89)	14.17	(2.34)
Ceratophysella ind.		1.83	(1.33)	4.17	(3.39)	0.50	(0.34)
Ceratophysella sp.	Csp	0.00	-	0.17	(0.17)	0.17	(0.17)
Ceratophysella tuberculata Cassagnau, 1959	Ctu	0.33	(0.33)	0.00	-	0.67	(0.67)
Coloburella zangherii (Denis, 1925)	Cza	0.00	-	0.00	-	15.50	(15.50)
Proisotomodes debilis (Cassagnau, 1959)	Cde	261.00	(42.73)	126.67	(32.69)	159.00	(28.60)
Deuteraphorura cf. *insubraria* (Gisin, 1952)	Din	0.00	-	0.33	(0.21)	0.17	(0.17)
Deutonura deficiens deficiens Deharveng, 1979	Ddede	0.17	(0.17)	0.00	-	0.50	(0.34)
Deutonura deficiens sylvatica Deharveng, 1982	Ddesy	0.17	(0.17)	0.17	(0.17)	0.00	-
Deutonura monticola (Cassagnau, 1954)	Dmon	0.17	(0.17)	0.17	(0.17)	0.17	(0.17)
Dicyrtoma fusca (Lubbock, 1873)	Dfu	1.33	(0.76)	0.00	-	0.00	-
Dicyrtomina minuta (Fabricius, 1783)	Dmi	0.00	-	0.00	-	0.17	(0.17)
Entomobryidae ind.		0.17	(0.17)	0.17	(0.17)	0.00	-
Folsomia manolachei Bagnall, 1939	Fma	55.83	(21.22)	38.50	(8.19)	39.00	(11.13)
Folsomia pyrenaea Cassagnau, 1954	Fpy	10.17	(4.80)	6.33	(2.38)	4.00	(3.42)
Folsomia quadrioculata (Tullberg, 1871)	Fqu	4.83	(3.19)	20.50	(12.36)	20.33	(6.40)
Friesea subterranea Cassagnau, 1958	Fsu	1.33	(0.33)	1.17	(0.65)	1.17	(0.65)
Heteromurus major (Moniez, 1889)	Hma	0.00	-	0.17	(0.17)	0.33	(0.21)
Hypogastrura elevata Cassagnau, 1959	Hel	3.50	(2.23)	0.00	-	15.67	(15.27)
Isotomidae ind.		0.00	-	0.33	(0.33)	0.00	-
Isotomiella cf. *minor* (Schäffer, 1896)	Imi	29.50	(5.03)	14.17	(3.69)	27.00	(6.82)
Isotomurus sp.	Isp	0.00	-	0.33	(0.33)	0.00	-
Lepidocyrtus cf. *lignorum* (Fabricius, 1793)	Lli2	0.50	(0.50)	0.33	(0.33)	0.00	-
Lepidocyrtus cyaneus Tullberg, 1871	Lcy	1.00	(0.26)	0.33	(0.21)	0.33	(0.33)
Lepidocyrtus lignorum (Fabricius, 1793)	Lli1	0.33	(0.21)	1.67	(0.61)	30.50	(9.24)
Lipothrix lubbocki (Tullberg, 1872)	Llu	3.67	(1.28)	1.00	(0.45)	3.33	(0.56)
Megalothorax sp.	Megsp	10.83	(2.82)	15.50	(4.88)	19.83	(8.68)
Mesaphorura ind.		0.00	-	0.17	(0.17)	0.17	(0.17)
Mesaphorura macrochaeta Rusek, 1976	Mma	5.67	(5.47)	0.00	-	0.00	-
Mesaphorura sp.	Msp	0.17	(0.17)	0.00	-	0.50	(0.34)
Micranurida candida Cassagnau, 1952	Mca	0.33	(0.21)	0.67	(0.33)	0.33	(0.21)
Micranurida pygmaea Börner, 1901	Mpy	0.17	(0.17)	0.00	-	0.00	-
Microgastrura ind.		0.00	-	0.17	(0.17)	0.00	-
Microgastrura minutissima (Mills, 1934)	Mmi	0.33	(0.33)	0.00	-	0.17	(0.17)
Micronychiurus cf. *cassagnaui* (Gers, 1980)	Mca	4.50	(1.18)	0.17	(0.17)	2.83	(1.40)
Monobella pyrenaica (Deharveng, 1979)	Mpy	0.00	-	0.17	(0.17)	0.00	-
Mucrella acuminata (Cassagnau, 1952)	Mac	0.33	(0.33)	0.83	(0.48)	0.50	(0.22)
Neelus murinus Folsom, 1896	Nmi	0.00	-	0.00	-	0.17	(0.17)
Oncopodura crassicornis Shoebotham, 1911	Ocr	14.83	(3.88)	1.00	(0.45)	8.83	(2.33)
Onychiuroides pseudogranulosus (Gisin, 1951)	Ops	0.50	(0.50)	0.00	-	1.17	(0.79)

TABLE II

Species code (abbreviated name) of Figure 2 and mean abundance of Collembola species (± standard error) in the three forest management types

Collembola species	Code	NAT		REG		IRR	
Orchesella cf. *orientalis* Stach, 1960	Oor	0.50	(0.50)	0.17	(0.17)	0.00	-
Paratullbergia callipygos (Börner, 1902)	Pca	2.50	(0.76)	0.67	(0.49)	0.67	(0.49)
Parisotoma notabilis (Schäffer, 1896)	Pno	0.83	(0.54)	1.50	(1.31)	3.67	(1.43)
Protachorutes pyrenaeus Cassagnau, 1955	Ppy	0.17	(0.17)	0.67	(0.33)	0.17	(0.17)
Protaphorura sp.	Prsp	9.67	(1.71)	12.83	(2.65)	7.17	(1.38)
Pseudachorutes palmiensis Börner, 1903	Ppa	0.17	(0.17)	0.00	-	0.00	-
Pseudachorutes parvulus Börner, 1901	Ppar	2.17	(2.17)	0.67	(0.49)	0.67	(0.67)
Pseudanurophorus binoculatus Kseneman, 1934	Pbi	0.50	(0.50)	0.00	-	0.00	-
Pseudisotoma sp.1	Psp	21.33	(5.25)	29.17	(7.19)	18.50	(5.32)
Pseudisotoma sp.2	Psp2	0.50	(0.34)	0.00	-	0.67	(0.67)
Pseudosinella alba (Packard, 1873)	Pal	2.33	(0.80)	4.67	(3.72)	1.17	(0.65)
Pseudosinella duodecimoculata Handschin, 1929	Pdu	0.50	(0.22)	3.00	(1.65)	4.17	(1.62)
Rusekella peyrei (Cassagnau, 1955)	Rpe	10.83	(9.10)	4.83	(2.76)	7.50	(5.54)
Sminthurides sp.	Smsp	0.17	(0.17)	0.50	(0.50)	0.17	(0.17)
Sminthurinus niger (Lubbock, 1867)	Sni	1.33	(0.88)	3.17	(2.02)	2.33	(2.14)
Sminthurinus signatus (Krausbauer, 1898)	Ssi	2.33	(1.23)	3.33	(0.56)	23.33	(6.78)
Superodontella sp.	Ssp	0.17	(0.17)	0.00	-	0.00	-
Symphypleona gen. sp.	Sgensp	0.00	-	0.17	(0.17)	0.00	-
Symphypleona ind.		0.00	-	0.33	(0.21)	0.00	-
Tetracanthella cf. *recta* Deharveng, 1987	Tre	0.00	-	0.00	-	0.67	(0.49)
Tetracanthella orbaicetensis Cassagnau, 1959	Tor	0.33	(0.33)	0.00	-	0.00	-
Tomocerus ind.		0.67	(0.42)	0.00	-	1.00	(0.37)
Tomocerus minor (Lubbock, 1862)	Tmi	0.00	-	1.00	(1.00)	2.17	(0.98)
Triacanthella perfecta Denis, 1926	Tpe	0.33	(0.21)	0.00	-	6.00	(5.80)
Willemia anophthalma Börner, 1901	Wan	0.50	(0.34)	1.50	(1.50)	0.50	(0.34)
Willowsia platani (Nicolet, 1842)	Wpl	0.00	-	0.17	(0.17)	0.00	-
Xenylla sp.	Xen	0.33	(0.33)	0.17	(0.17)	0.17	(0.17)

TABLE III

*Mean and total species richness, and mean and total abundance of earthworms and Collembola in the three forest managements (mean per sample of 6 values ± standard error); *: including one species represented by immature specimens, but sole representative of its genus in the stations. ANOVA did not indicate significant differences between means*

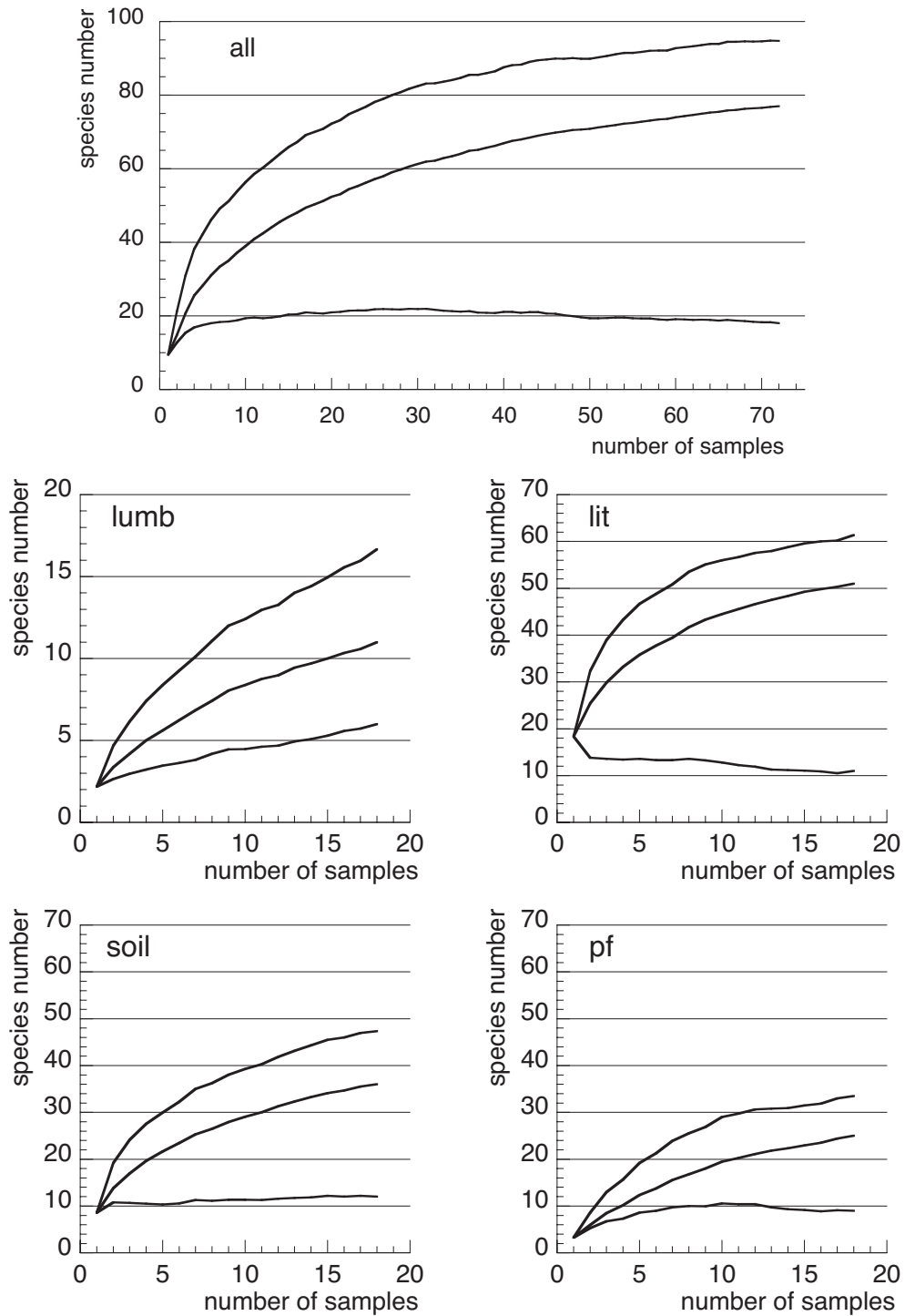|		NAT		REG		IRR	
Species richness of earthworms	Mean Total	2.50 7*	(0.43)	4.00 7*	(0.58)	3.50 4	(0.81)
Species richness of Collembola	Mean Total	23.5 50	(1.28)	20.5 44	(1.41)	24.5 48	(4.09)
Species richness of Collembola+earthworms	Mean Total	26.0 57	(1.4)	24.8 51	(1.3)	27.8 52	(4.8)
Abundance of earthworms	Mean Total	9.33 56	(1.38)	12.67 76	(3.06)	13.50 81	(4.68)
Abundance of Collembola	Mean Total	489.2 2935	(62.9)	304.8 1829	(41.5)	447.3 2684	(50.2)

Figure 1.— Cumulative plots of species richness for Lumbricidae + Collembola (all), Lumbricidae (lumb), litter Collembola (lit), soil Collembola (soil), Collembola of the surface of the litter caught by pitfall traps (pf) (50 iterations). Curves: upper, Jack1 estimate of total species richness; middle, observed species richness; lower, number of rare (= single-sample) species. Unidentified specimens are not included in the analysis.

expected number of additional species for additional sampling effort is + 50 % for earthworms (with almost no inflexion of the accumulation curve), + 48 % for pitfall, + 31 % for soil, and + 20 % for litter Collembola. The sampling of Collembola in litter was the most efficient since 80 % of its fauna has been collected.

STRUCTURE OF COMMUNITIES

A first db-RDA computed with ten environmental variables (elevation, soil pH, content of nitrogen and organic carbon, temperature, CO_2-C, CO_2-C/C, C/N, humus index and water content) indicated a high inflation factor for organic carbon. This variable was thus eliminated from further db-RDA. The db-RDA with the automatic forward selection option allowed us to select a minimal set of seven variables that explain the greater part of the ordination of species: elevation, temperature, humus index, CO_2-C/C, soil organic nitrogen, water content and pH (ordered by decreasing contribution to species ordination). The four canonical axes representing the effect of involved environmental variables explain significantly (p = 0.020) 50.1 % of the species ordination. The two first factorial axes explained 18.8 % and 12.4 % respectively of the total variance of collembolan and earthworm species (Fig. 2). Axis 1 separates earthworm and collembolan species of NAT plot on one side, and REG and IRR plots on the other. The axis displays a gradient of decreasing elevation and organic nitrogen and of increasing soil water content from NAT to REG. NAT is characterized by earthworm species with low abundance (Tab. I), i.e. *Prosellodrilus* cf. *idealis* and *Dendrobaena pygmaea* limited to this plot, and the collembolans *Proisotomodes debilis, Dicyrtoma fusca, Folsomia pyrenaea, Lepidocyrtus cyaneus, Paratullbergia callipygos* and *Superodontella* sp. The earthworms *Dendrobaena*
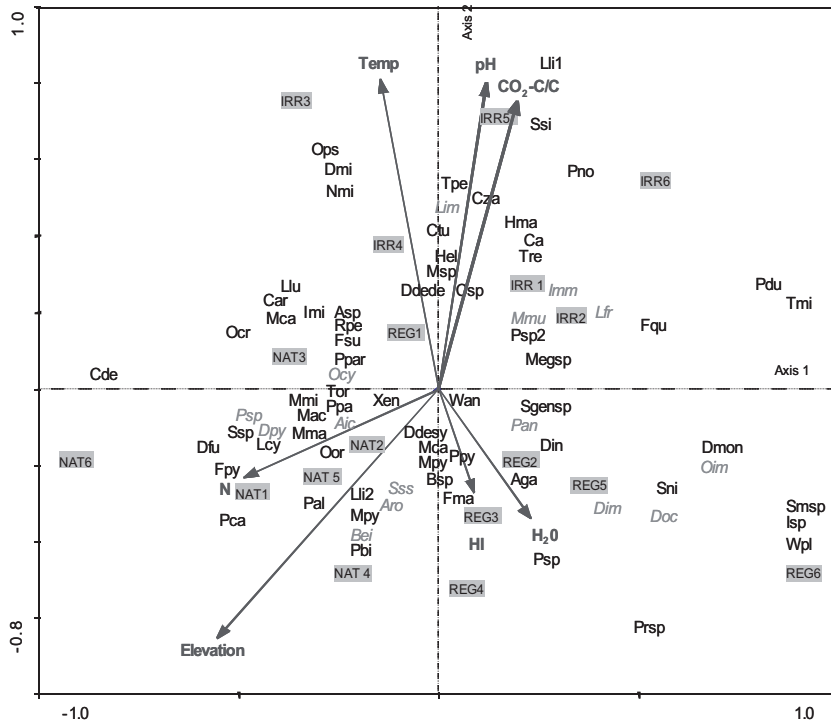

Figure 2.— Db-RDA triplot showing the ordination of collembolan (dark letters) and Lumbricidae (grey letters in italic) species scores constrained by seven environmental and soil variables (arrows), and samples from the three plots NAT, REG, and IRR (letters with grey shading), along canonical axes 1 and 2. For abbreviations of earthworm and collembolan species see Tables I and II, respectively.

octaedra and immature *Octolasion* sp., and the collembolan *Deuteraphorura insubraria, Isotomurus* sp., *Protaphorura* sp., *Pseudisotoma* sp.1, *Sminthurinus niger, Sminthurides* sp., and *Willowsia platani* were more abundant or exclusively present in REG. Axis 2 emphasizes differences in earthworm and collembolan communities between IRR and REG-NAT. Axis 2 is explained by a gradient of increasing temperature, soil pH and CO_2-C/C, which were higher in IRR, and a reverse gradient of decreasing elevation, humus index and soil water content, which were higher in REG and NAT (Fig. 2, Tab. IV). As indicated by humus index, the thickness of litter and humus layer was higher in NAT and REG compared to IRR (Tab. IV).

TABLE IV

Soil and environmental parameters (mean of 6 measures ± standard error except for temperature) and code (abbreviated name) of Figure 2

	Code	NAT	REG	IRR
Humus index	HI	5.1 (0.4)	4.3 (0.6)	3.6 (0.5)
Soil organic carbon (g.kg-1)		134.0 (31.9)	97.2 (15.2)	94.6 (10.9)
Soil nitrogen (g.kg-1)	N	8.4 (1.6)	6.6 (0.7)	6.1 (0.6)
C/N ratio		15.2 (0.8)	14.4 (0.6)	15.4 (0.6)
CO_2-C (mg)		3.75 (0.30)	4.74 (0.43)	6.42 (0.44)
CO_2-C/C ratio	CO_2-C/C	0.0427 (0.0068)	0.0421 (0.0057)	0.0707 (0.0063)
Soil pH	pH	5.81 (0.23)	5.77 (0.16)	6.78 (0.12)
Water content (%)	H_2O	42.42 (2.94)	46.26 (3.10)	41.96 (2.46)
Temperature (C°)	Temp	13.5 (0.2)	13.4 (0.2)	13.9 (0.2)

IRR was characterized by *Murchieona muldali* and *Lumbricus friendi*, and the collembolans *Coloburella zangherii, Dicyrtomina minuta, Lepidocyrtus lignorum, Neelus minutus, Onychiuroides pseudogranulosus, Parisotoma notabilis, Pseudosinella duodecimoculata, Sminthurinus signatus, Tomocerus minor* and *Triacanthella perfecta* (Fig. 2).

The fourth db-RDA measured the impact of plots in the structure of communities, and confirmed that earthworm and collembolan species assemblages differed significantly (p = 0.002) in NAT, REG, and IRR; plots being responsible for 21.4 % of the variation of the species ordination. The graph resulting from this analysis is not showed here since the distribution of species is similar to that obtained under the constraint of environmental variables (see above).

Jaccard's index of similarity differed between plots, with lowest values for pitfall and highest values for litter Collembola (Tab. V). Morisita's index was in all cases but one (NAT-REG for pitfall) higher than Jaccard values, indicating that the communities are more similar in their most abundant species than in their least abundant ones. In particular, the high values of Morisita's index for litter reflect a relative homogeneity of community structure in these habitats.

TABLE V

Similarity indices (Jaccard/Morisita) between the faunal assemblages on the different plots for Collembola from litter, soil and pitfall traps, earthworms and total species number

	Litter	Soil	Pitfall	Earthworms	Total
IRR-NAT	0.70/0.91	0.52/0.74	0.47/0.35	0.25/0.64	0.61/0.89
IRR-REG	0.60/0.96	0.47/0.54	0.18/0.75	0.43/0.95	0.59/0.94
NAT-REG	0.60/0.95	0.45/0.55	0.27/0.31	0.09/0.67	0.52/0.95

The spatial rate of species turnover derived from sample species richness, and the number of additional species which can be expected from increased sampling effort are illustrated by the cumulative species plots of Fig. 3. Clearly, NAT has the highest between-sample diversity, the highest overall richness and the highest potential for further species discoveries. It is also the only plot where the number of rare single-sample species continues to increase in the distal part of the curve. On the other hand, IRR and REG are quite similar for all these biodiversity parameters, and appear globally less diverse than NAT.

Comparison tests did not detect significant differences in the total abundance and mean species richness of Lumbricidae and Collembola, although the number of Collembola tended to be higher in NAT compared to the two other stands ($p = 0.058$) (Tab. III). The total species richness of Collembola and lumbricids was the highest in NAT, and NAT and REG, respectively (Tab. III). NAT and REG hosted four and three Lumbricid species respectively, which were exclusively found in these two plots while all species collected in IRR also occurred in REG or NAT. None of the environmental and soil parameters tested was correlated either to Collembola, or to earthworm species richness.

DISCUSSION

BIODIVERSITY AND ENDEMIC SPECIES LEVEL

As in other weakly disturbed forests of the Pyrenees (Deharveng, 1996), the fauna collected in the studied forest beech stands was rich in species as well as in endemic taxa of the two studied soil-faunal groups. The number of collected earthworms was relatively low compared to densities observed in plain oak forest, suggesting that the role of earthworms in soil structuring may be less dominant in mountain compared to lowland soils. Nevertheless, species richness (11 species in 10 genera) exceeded the range of 4-8 species usually found in oak forests that are more hospitable to earthworms compared to beech forests (David, 1999; Salmon, 2001). The abundance of collected earthworms falls into the usual range from 0 to 60 ind. / m^2 for beech forests. Species number was among the highest observed in lowland beech forests (Phillipson *et al.*, 1978; Staaf, 1987; Römbke, 1987; Ponge *et al.*, 1997, 1999; Deleporte *et al.*, 2001), and these values appear remarkable for a site 1300 m in altitude (Bouché, 1972). The unexpectedly high local diversity and abundance of earthworms call for further exploration of this macrofaunal group in the Pyrenean range. High soil water content and soil pH levels of the study sites may explain such values of community parameters (Pop, 1997). They may also result from the mineral content of beech leaf litter and soil, which are probably rich in calcium because of the presence of limestone at low depth (Staaf, 1987; Ponge *et al.*, 1997, 1999). This assumption is supported by the number of neutrophilous and hygrophilous earthworm species (seven and six respectively) found in our study (Bouché, 1972; Muys & Granval, 1997).

Among the eleven earthworm species, six are widespread and common in Europe while two are endemic of the Pyrenean mountains (*Scherotheca savignyi savignyi*, and *Prosellodrilus* cf. *idealis*) and three of them have a wider distribution but are rather rare. *Proctodrilus antipai* and *Bimastos eiseni* are even recorded for the first time in the Pyrenees (Bouché, 1972; Pop, 1997; Ponge *et al.*, 1999). *B. eiseni*, exclusively collected in NAT, is strictly litter-dwelling and corticolous species, characteristic of non-anthropic forests (Bouché, 1972; Omodeo *et al.*, 2003). This species, not very frequent despite a wide distribution over Eurasia, could be a good indicator of the "natural" character of NAT. *Murchieona muldali* represents another rare taxon, typical of calcareous clay soils inhabiting deep layers of compacted soil. Although mull humus form at the study sites resulted from the activity of anecic and endogeic earthworms (Bernier & Ponge, 1994), the biomacro-structured layer was often restricted to few centimetres and surmounted by an OH layer in NAT and partly in REG, while underlying horizons were compact, particularly in NAT.
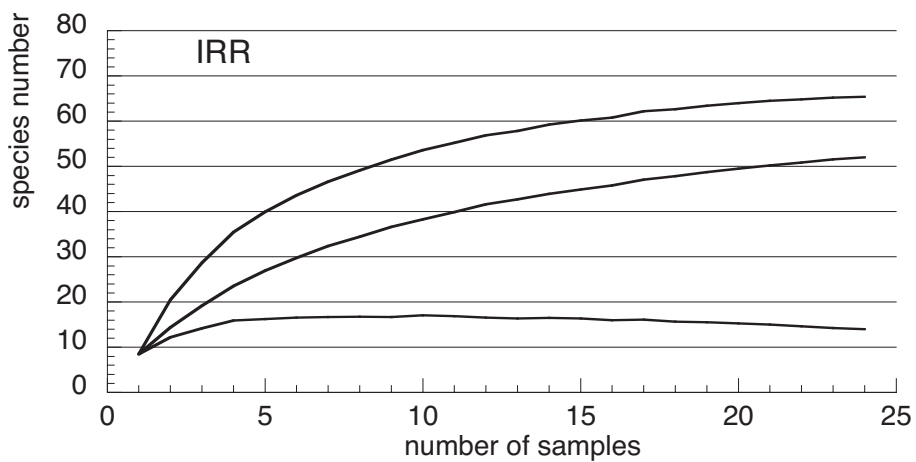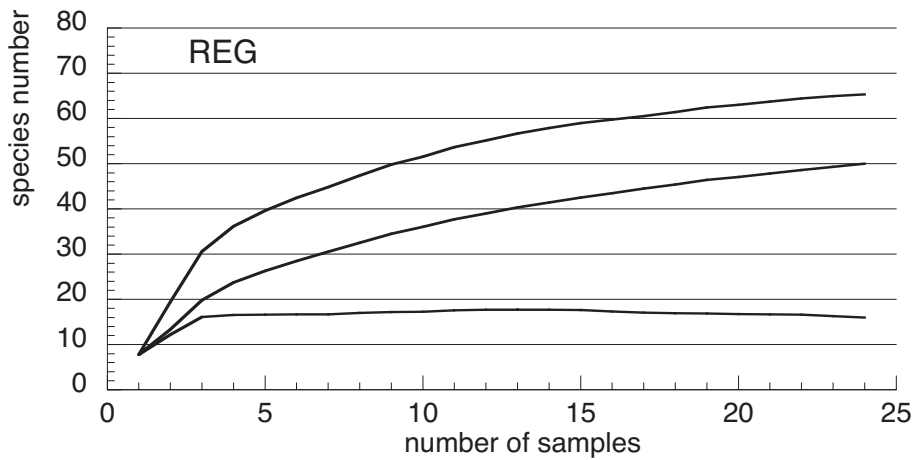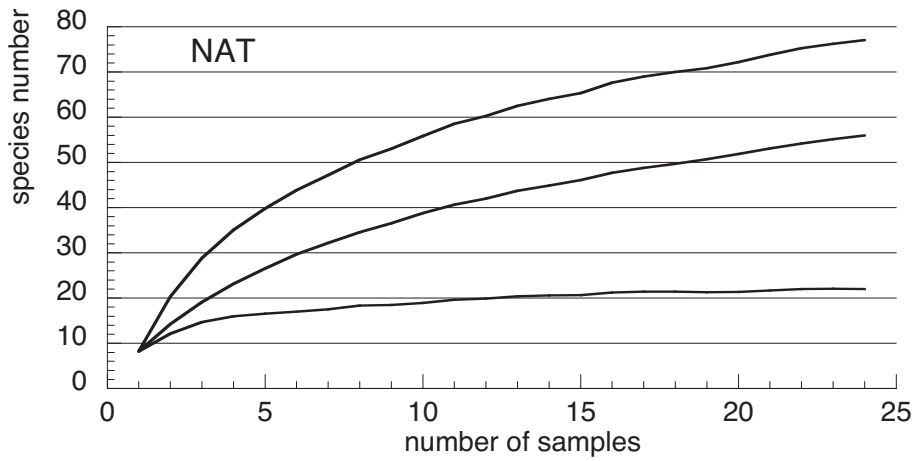
Figure 3.— Cumulative plots of (Lumbricidae+Collembola) species richness in the forest stands (30 iterations). Upper: Jack1 estimate of total species richness; middle: observed species richness; lower: number of rare (= single-sample) species.

Collembolan species richness (64 species for 7506 specimens) was higher than those of other Pyrenean beech forests for a similar sampling effort: 5131 specimens and 52 species in the Arize forest (Ariège, Deharveng, 1996), 11 832 specimens and 57 species in Orlu (eastern Ariège, unpubl.). At least fifteen (23 %) of the collected species are Pyrenean or Pyreneo-cantabric endemics (*Ceratophysella tuberculata, Deutonura deficiens deficiens, D. deficiens sylvatica, Folsomia pyrenaea, Friesea subterranea, Hypogastrura elevata, Micronychiurus* cf. *cassagnaui, Monobella pyrenaica, Orchesella* cf. *orientalis, Protachorutes pyrenaeus, Pseudisotoma* sp. 1, *P.* sp. 2, *Rusekella peyrei, Tetracanthella orbaicetensis, T.* cf. *recta*). Thirteen of these endemics were present in NAT, where only *M. pyrenaica* and *T.* cf. *recta* were absent, 9 in REG (*C. tuberculata, D. d. deficiens, H. elevata, P.* sp. 2, *T. orbaicetensis* and *T.* cf. *recta* absent), 11 in IRR (*D. deficiens sylvatica, M. pyrenaica, O.* cf. *orientalis* and *T. orbaicetensis* absent). One species, *Microgastrura minutissima*, described from Northern America and reported from Spain (Thibaud *et al.*, 2004), is a new record for France. The species indicated as 'cf.' and 'sp.' may correspond to new taxa. After Potapov (unpubl.), the Pyrenean *Orchesella orientalis*, a species originally described from Caucasus, actually corresponds to an undescribed species endemic of the Pyrenees where it is not common.

On the whole, species richness of earthworms and Collembola observed in the present study are among the highest reported in France.

IMPACT OF ENVIRONMENTAL FACTORS ON COMMUNITIES AND DIVERSITY

Although we studied one site per management modality and our sampling-points may be considered as pseudo-replicates as regards the impact of management modalities, the study of the impact of environmental factors, especially edaphic factors, remains pertinent since they could vary within a management modality, and overlap between management modalities. Moreover, we tried to minimize the bias caused by pseudoreplication by selecting contiguous plots, which then shared the same microclimatic and geological features (Oksanen, 2004). At least, we basically agree with Oksanen (2001), that concern about pseudoreplication in ecological studies has led to 'unwarranted stigmatisation of a reasonable way to test predictions referring to large-scale systems'.

The db-RDA indicated that the distribution or the abundance of several Collembola and earthworm species differed between the three plots. Nevertheless, similarity indices show that communities of Collembola from litter, whose sampling was the most exhaustive, as well as communities of pooled faunal groups (Lumbricidae and Collembola from litter, soil and pitfall traps) did not differ greatly among the three plots. They differed essentially by their least abundant species including mostly endemics, as illustrated by the large differences between Morisita's and Jaccard's indices.

Db-RDA also emphasized that the composition of both faunal communities was influenced by the following environmental and soil parameters: elevation, temperature, humus index, C mineralization activity (CO_2-C/C), soil organic nitrogen, water content and pH. Although the greatest mean variation of elevation was only 83 m (from NAT to IRR), elevation was the most pronounced factor. As the elevation range of each plot differed markedly without overlapping, we may assume that this parameter expressed the combined influence of several ecological characteristics of the plots under study. Elevation may especially express the impact of soil depth, which was the lowest in NAT because of the location of this plot on a crest. Nevertheless, Catterall *et al.* (2001) observed that a variation of 15-35 m elevation could affect the structure of invertebrate communities through aspect. Humus index was the lowest in IRR thus reflecting low thickness and high transformation degree of organic matter layers at this plot. The presence of *D. pygmea* and *B. eiseni* in NAT may be explained by a thicker and undisturbed organic layer probably due to a greater tree density and a lower abundance of particularly anecic and endogeic earthworms in this plot. Soil pH probably also contributed to the absence or lower abundance of acidophilous earthworms *B. eiseni* and *D. octaedra,* and the collembolan *Micranurida pygmaea* (Ponge, 1993; Muys & Granval, 1997) in IRR. Conversely, the higher abundance of the collembolans *Onychiurides granulosus* and *Parisotoma notabilis* in IRR may be explained by higher soil pH (Hågvar & Abrahamsen, 1980; Ponge, 1993). Some

Collembola (*Deutonura monticola, Folsomia quadrioculata, Isotomurus* sp., *Pseudosinella duodecimoculata, Sminthurides* sp., *Tomocerus minor*) and the earthworm *Murchieona muldali* occurring in REG and in the moist samples of IRR plots (on the positive part of the db-RDA biplot along axis 1) are hygrophilous species (Muys & Granval, 1987; Ponge, 1993). This supports the importance of soil moisture for earthworm and collembolan community structure and suggests that the accompanying species *Protaphorura* sp. probably corresponds as well to an hygrophilous form of the *P. armata* complex. Other accompanying species include *Willowsia platani* and *Sminthurinus niger*. The former, collected as a single specimen is accidental as the species is unambiguously xerophilous. The latter, usually considered as xerophilous, actually encompasses hygrophilous populations which may correspond to unnoticed species. Epigeic collembolan species *Dicyrtoma fusca, Sminthurinus niger, Sminthurides* sp. and *Willowsia platani* (Gisin, 1948; Ponge, 1993; Hopkin, 1997) were more abundant in REG and NAT compared to IRR, which is also true for earthworms (Bouché, 1972). Such a pattern could be explained by the opening of habitat (indicated by the percentage of tree cover) which could (1) directly affect epigeic collembolan species typical of forest habitat and (2) favour hemiedaphic / euedaphic species by increasing their living space in IRR through a thicker bio-macrostructured organo-mineral horizon (A horizon of mull) created by earthworms and a higher percentage of herb cover (Materna, 2004; Salmon, 2004). Forest opening, which seems to impact either directly or indirectly Collembola and earthworm communities, was also the main structuring factor for carabid communities (Baguette & Gérard, 1993) in spruce plantations of increasing age.

None of the studied parameters strongly affected local species richness and abundance of Collembola and earthworms. Only the trend towards a higher abundance of lumbricids in IRR may be explained by the higher soil pH and the herbaceous cover resulting from the greater openings created by thinning (Paoletti, 1999). When considering the total species richness in each management modality (instead of species richness per sample point), NAT cumulated the highest species number of both Collembola and lumbricids, while the species richness pattern differed in IRR and REG between earthworms and Collembola. IRR accommodated less species, and less rare and endemic species of earthworms than the two other plots. A higher anthropogenic pressure in IRR (cutting, soil compaction during wood harvesting, etc.) results in less favourable or less diversified habitats (Jordan *et al.,* 1999; Yamamoto *et al.,* 2001). Kasprzak (1987) and Cassagne *et al.* (2006) reported a decrease in specialized or endemic species and an increase in density of eurytopic earthworm or collembolan species related to anthropogenic disturbance. The higher collembolan richness in NAT may also be due to thicker litter layer that offered a larger living space, though at this scale no relationships between litter structure and diversity has been demonstrated so far. Nevertheless data are not conclusive, and diversity levels remain relatively similar in the three plots for litter, which was the most exhaustively sampled habitat. These results are in agreement with other authors (Werner & Raffa, 2000; Yi & Moldenke, 2005) who observed no changes in the species richness of ground-dwelling macro-arthropods (beetles, ants, spiders, millipedes and camel-crickets) among forest management regimes including either even-aged, uneven-aged and unmanaged northern hardwoods, or various thinning treatments. This stability under soft disturbance contrasts with the sharp decline in the species richness of various invertebrate taxa induced by extreme management practices such as deforestation and/or reafforestation with exotic tree species (Deharveng, 1996; Cassagne *et al.*, 2004, 2006; Grgič & Kos, 2005; Finch, 2005; Sousa *et al.*, 2006).

SAMPLING

This study brought to light a methodological problem. When comparing the biodiversity of faunal assemblages, similarity between plots was found to be related to sampling exhaustiveness, as illustrated in accumulation curves: similarity was higher for better sampled habitats. Implications of this observation are important for the meaningfulness of the results, and must be taken into consideration in further investigations. It is likely that this kind of bias may apply to most studies of communities ecology based on the comparison of different faunal assemblages where sampling exhaustiveness has not been evaluated. The simplest way to avoid

this problem is to have a large number of replicates, or to work in several steps, adjusting the number of replicates to the kind of faunal assemblage sampled. Theoretically, only Collembola from litter were sufficiently sampled as 80 % of its fauna were contacted. The weak sampling exhaustiveness of pitfall Collembola, as well as soil Collembola and earthworm collections, characterized by a large difference between expected and observed species numbers, could be the result of lower population density of the species, lower efficiency in species catching, and for earthworm high proportion of immature unidentifiable specimens. The low exhaustiveness of earthworm sampling estimated by Jack1 was also probably biased by two behavioural traits: their highly contagious distribution and the importance of mutual exclusion of some species by others, which imply a lower number of species per sample (Baker, 1999; Jimenez *et al.*, 2001). The overestimation of the earthworm richness by Jack 1 is also supported by the fact that the highest Lumbricidae species number recorded in approximately the same surface of forest area in Europe does not exceed eleven species (see citations above), rending unrealistic an estimated number of 22 species. Further investigations at different sampling intensity are being developed to test this intriguing observation.

CONCLUSIONS

The structure of earthworm and Collembola communities differed slightly but significantly between the three plots, essentially by their least abundant taxa, which include most endemic species. Assemblages of collembolan species from litter, whose sampling was the most exhaustive, did not differ greatly among the three plots. Changes in the distribution or the abundance of several Collembola and earthworm species are explained by variations of seven environmental and soil parameters. Although we studied only one plot per management modality, which does not allow, from this dataset alone, to assert that management practices directly impacted the structure of communities, our results corroborate the few data available in the literature (see above) on two essential points. Firstly, part of the changes in soil species assemblage results (indirectly through the thickness of humus layer, temperature, soil pH and nitrogen) from the forest opening induced by management practices and secondly, weak between-plot differences in soil biodiversity are probably explained by the softness of forest management practices.

Species richness and rate of endemism were high in all plots, without clear-cut differences in species richness between plots under different management modalities. This raises several points of concern for biodiversity conservation. (1) Reforestation with dense stand of allochtonous conifers at the expense of native beech forest has been shown to provoke a severe collapse of endemic taxa diversity in northern Pyrenees (Deharveng, 1996; Cassagne *et al.*, 2003, 2006). Conversely, none of the soft management practices used in the three plots studied here was strongly harmful or beneficial for Collembola, which were relatively diverse everywhere. It could be therefore assumed that manipulation of beech forest ecosystem without tree species replacement or strong changes in tree density is not or weakly detrimental to soil biodiversity. (2) Weak differences in biodiversity level between plots were however evident from different indicators, i.e. number of endemic and rare species, or number of species expected from further sampling. Considering both Collembola and earthworms, the less disturbed plot, i.e. NAT, hosted more species, including more endemic and rare species, and more potential (i.e. not yet contacted) species than the more disturbed plots IRR and REG. (3) Variations in soil parameters among the three plots, induced (temperature, soil pH, humus index) or not (elevation, water content) by forest opening, were not reflected in species richness. In other words, predicting species richness by environmental parameters may not be straightforward when compared habitats are rather similar. (4) The pattern of total species richness was slightly different between Collembola and earthworms since the highest biodiversity of both was observed in NAT but the lowest one either in IRR (earthworms) or in REG (Collembola). It implies that species richness measured from a single taxonomical or functional group is not necessarily a surrogate of global richness in fauna. (5) Surprisingly, canopy opening did not affect diversity in litter in greater extent compared to the soil, but as expected, it reduced the

abundance of epigeic species. The three plots had similar composition for litter Collembola, while soil (and also surface communities) exhibited more contrasted patterns. This led us to re-examine our data with respect to sampling exhaustiveness of the different target habitats. The ratio of observed versus expected species was much higher in litter than in soil or on litter surface, introducing a bias of uncertain magnitude. In any case, sampling effort would have to be strongly increased for non-litter habitats to provide level of sampling exhaustiveness similar to that of litter habitat.

Beyond the various improvements which remain to be achieved for better accuracy of sampling and biodiversity analyses, there is a major gap to fill in our knowledge: between the very harmful effect of reforestation and the weak effect of soft management practices, what is the level of disturbance at which the biodiversity of soil fauna begins to be significantly impacted? Can we efficiently monitor forest biodiversity – of which soil fauna is a major component - without answering such a basic question? We suspect that canopy opening, which largely depends on forest management practices, is the prime environmental factor that controls forest soil biodiversity. Understanding in what way and to what extent it operates, through soil and soil faunal studies in large range of canopy opening, would provide the necessary background for monitoring forest biodiversity.

ACKNOWLEDGEMENTS

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