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Diversity within the Collembola community in fragmented coppice forests in south-western France

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Abstract – In order to assess major characteristics of Collembola community diversity in fragmented coppice forests, a total of eighty soil samples were collected in sixteen plots that were representative of oak forest management practices, vegetation development after logging, and fragmentation in south-western France. Forty-seven species were recorded, but the community was dominated by two generalist species (*Folsomia quadrioculata* and *Isotoma notabilis*). The ecological classification of the species showed a dominance of forest generalist species. Forest specialist species were scarce, with open habitat species being less frequent and less abundant than might have been expected from this large area of forest frequently disturbed by clear-cuts. Correspondence factor analysis revealed that the communities were loosely structured. The three first factors were analysed: factor 1 was correlated with euedaphic habitats and extreme habitats; factor 2 was correlated with water content of habitats; and factor 3 was correlated with logging methods. However, a hierarchical classification showed that the majority of plots were structurally similar and could be considered as representative of this community. The recurrent disturbances caused by logging and fragmentation have standardised the communities by eliminating forest specialist species, which are more vulnerable to alteration of habitats. © 2000 Éditions scientifiques et médicales Elsevier SAS

Biodiversity / Collembola / coppice forest

Résumé – Diversité de la communauté des collemboles dans des forêts fragmentées de taillis du sud-ouest de la France. Pour évaluer les principales caractéristiques des communautés de collemboles dans des forêts fragmentées gérées en taillis, un total de 80 échantillons de litière ont été prélevés dans seize placettes représentatives des pratiques de gestion forestière en taillis de chêne, du développement de la végétation après les coupes et de la fragmentation des forêts du sud-ouest de la France. Quarante-sept espèces ont été recensées mais la communauté collemboologique était dominée par deux espèces généralistes (*Folsomia quadrioculata* et *Isotoma notabilis*). Les espèces forestières spécialistes étaient rares et celles d'habitat ouvert étaient peu représentées ce qui est surprenant dans des forêts où les coupes rases sont fréquentes. L'analyse factorielle des correspondances révèle que les communautés étaient peu structurées. Le facteur 1 était associé aux habitats euédaphiques et aux habitats extrêmes et le facteur 2 était associé au niveau de saturation en eau des habitats ; le facteur 3 était associé aux pratiques d'exploitation forestière. Cependant une classification hiérarchique a montré que la majorité des placettes avait une structure similaire qui peut être considérée comme représentative de cette communauté. Les perturbations récurrentes liées à l'exploitation et à la fragmentation forestières ont homogénéisé les communautés de collemboles par la raréfaction des espèces forestières spécialistes qui sont les plus vulnérables aux modifications des habitats. © 2000 Éditions scientifiques et médicales Elsevier SAS

Biodiversité / collemboles / taillis

1. INTRODUCTION

The development of agriculture and intensive logging in temperate zones has led to forest fragmenta-

tion, especially in western Europe [27]. This type of forest is often called farm forest or farm woodland because of its strong relationships with agricultural activities and dynamics [4, 78]. Fragmentation is con-

sidered world-wide to be one of the principal factors behind the reduction of biodiversity, and is therefore a topic of utmost importance in ecological research [38]. These forests differ from the larger northern forests which are more often studied [3, 56, 57, 61–63]. They are characterised by relatively small surface areas, frequent disturbances (every 15 to 30 years) through logging of small patches, noticeable influence of the neighbouring agricultural landscape and several edge effects. The effects of these characteristics have been studied principally in birds [43, 44, 51], plants [76], small mammals [7] and insects [46, 64, 65]. Results have indicated that communities in fragmented forests can be rich, but have few specialised and many ubiquitous or ruderal species [22]. Conservation matters, ecosystem dynamics and sustainability are often discussed in the light of these results.

Collembola could provide new insights into fragmented forest biodiversity and the effects of human activities and related disturbance regimes. Collembolan are particularly sensitive to microclimate changes such as those found in logging areas [17]. Numerous studies have shown that Collembola are sensitive to environmental parameters such as aspect [9, 10, 20], altitude [16], temperature [42], soil chemistry [36], moisture [25, 55, 77], litter accumulation [3, 41] and plant community composition [1, 57, 59–62, 67, 68]. They also show marked differences between open habitats and closed habitats such as forests [11, 12]. Collembola species indicate biological activity in soil and could therefore provide data on biological processes in soil which are important for forest ecosystem dynamics and stand productivity [2, 14, 37, 40, 41, 52, 57, 58].

Numerous studies in forests provide data on the influence of natural or human disturbance on the Collembola community. Afforestation with allochthonous species has been proven to reduce diversity [18, 54, 69], possibly endangering endemic species [24]. Logging can reduce Collembola density to 24% 8 years after clear-cutting [8], and whole-tree harvesting has been shown to reduce the abundance of species even up to 15 years later [6]. Similar results, showing effects of logging and forest management on Collembola communities, have been showed in various regions [15, 67, 70], but none of these was obtained in farm forests or in similar conditions, although this forest type is very common in western Europe [4].

It should be possible to identify the effects of forest fragmentation and logging regime within the Collembola community characteristics. Describing the community associated with farm forests might provide references that are currently missing. These could be used to give a precise assessment of the effects of short-term changes in human activities, such as logging practices. This type of diagnosis will be very valuable in the context of forest ecocertification [23, 48].

In this paper, an initial approach is presented for characterising top soil Collembola communities in

farm forests for their species composition, diversity, abundance, frequency, distribution and structure. The relative importance of the different status of species is assessed: taxonomical, biological, ecological and biogeographical. This descriptive study is a necessary step as an evaluation of the variability within communities which are not well studied, and before a more detailed analysis of the factors affecting Collembola communities in those forests can be performed.

2. MATERIALS AND METHODS

2.1. Study areas

The two areas studied are located in south-western France, near Toulouse (43° N, 1° E, *figure 1*). The main climatic influence is Atlantic, from the west, with less marked Mediterranean and mountain influences from the east and the south, respectively. Summers are dry and hot, with frequent periods of drought. Winters are mild and wet. The mean annual temperature is about 11 °C, and precipitation is 800 mm·year⁻¹. The meteorological conditions for the 3 months before sampling were 195 mm total rainfall and an average temperature of 7 °C.

The main substratum (called molasses) is the result of the high erosion of the Pyrenees mountains during the Tertiary period. South to north valleys cut the substratum sharply, creating foothills (altitude: 200–400 m) with steep (50%) slopes, where most forests

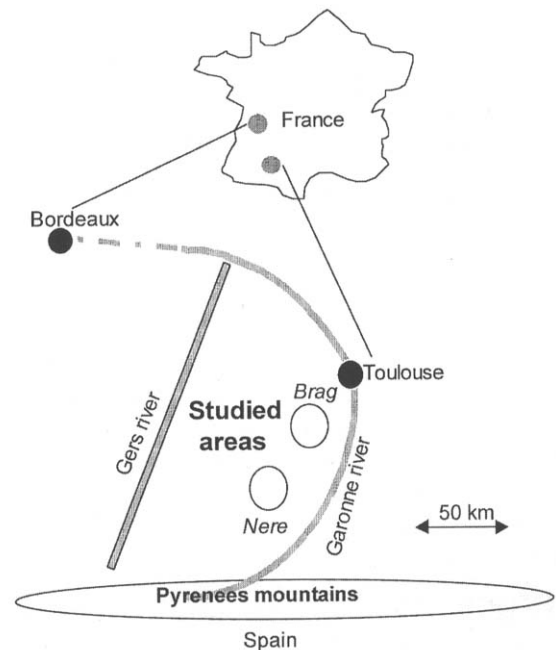


Figure 1. Location of the two study areas, Brag and Nere, in south-western France.

have developed. Soils on slopes are brown soils, with calcareous and frequent strata with pebbles. Variations in acidity level (5 to 7) might explain the main differences between soils, which should influence vegetation composition. Humus is mull, with poorly developed layers, because tree density is low and provides little organic matter, mainly chestnuts and oak leaves, which degrade very rapidly (2 years).

The main tree species in the area are oak (*Quercus robur* L., *Q. petraea* (Mattus.) Liebl, and *Q. pubescens* Willd.), often in association with chestnut (*Castanea sativa* Mill.) in coppice, cherry (*Prunus avium* L.) and wildservice trees (*Sorbus torminalis* (L.) Crantz). Flora can be considered as medio-European, with Atlantic and Mediterranean components. *Rubus* gr. *fruticosus* L., *Lonicera periclymenum* L., *Rubia peregrina* L., *Ruscus aculeatus* L., *Tamus communis* L. and *Hedera helix* L. are some of the most common plant species in the forest [21].

Forest represents 20 % of the area, with a high level of fragmentation, the remaining surface area is dominated by agricultural activities. Forest management is closely linked to agricultural activities, both physically, due to the prevalence of edges, and historically, through an interdependent evolution [4, 5, 35]. The most common silvicultural system is coppice, with standard trees retained to produce high-quality wood for timber. Coppice is used for fuel and pulp in a mill located near the study area.

The area, called Nere in this paper, is located 30 km south of the area called Brag, and is closer (100 km) to the Pyrenees. Nere is more influenced by the Pyrenees mountains and is wetter than Brag. Soil tend to be slightly deeper in Nere, and pebblier in Brag. Each area is a 5 × 5 km square. Forest fragmentation is higher in Brag than in Nere, where there are two large forests (> 400 ha) which have been in place for a long time (probably several centuries), with a continuous management. In the smaller forests, in each zone, the history of management has often been more chaotic. Some forests may have been created by natural afforestation in the last 70 years.

2.2. Sampling

In each area, plots were selected in order to be representative of the diversity of farm forest features in the studied area. We were careful to include the diversity of forest development stages after logging (0 to 50 years), the main types of forest management (coppice with or without standards), and different levels of forest fragmentation.

A total of eighty samples were collected in sixteen forest plots (five samples in each plot taken at the centre and extremities of a 2-m radius cross). Samples were mainly of heavy litter, humus and superficial ground. Particular habitats were removed, such as dead

wood and large moss shelter where Collembola are more influenced by micro-habitat than by meso-habitat parameters. Superficial leaves were removed in order to exclude the mobile species which are not associated with substratum. This sampling was not exhaustive but corresponded to an ecological functional compartment, the soil, which is of primary importance for forestry. For each sample, a volume of 250 cm³ substrate was taken from the 5-cm top soil. Collembola fauna was extracted slowly, to avoid mortality, using Berlese-Tullgren apparatus for 7 to 10 d at the Toulouse laboratory. Collembola were collected in ethanol, cleared in lactic acid and mounted in gum arabic for identification. Sampling was conducted over 2 d in the early spring of 1996. We collected forty-five samples in nine plots in the Brag area and thirty-five samples in seven plots in the Nere area.

Several variables were collected at the sample or plot level: botanical composition, humus, stratification of the vegetation, pH of the soil, age of the last cutting, silvicultural treatment, distance to the nearest edge. These variables were not directly used in the following analysis and will be integrated in further work dealing more precisely with ecological factors.

2.3. Identification and status of species

A total of forty-six species were found (*table I*), forty-four were determined easily [28–30, 34, 39, 71], but two species at a young stage were identified at genus level only (*Arrhopalites* sp. and *Onychiurus* sp.). For each species, all individuals included each development stage. The species were classified according to their taxonomical, biological, biogeographical and ecological status (*table I*).

Five taxonomical status were used: Poduromorpha (P), Isotomidae (I), Entomobryidae (E), Symphypleone (S) and Neelipleone (N).

The Gisin [33] morphological classification was used, developed by Tischler [75] and analysed by Delamare-Deboutville [26] to define four biological status of species: atmophilic (A) for species living in superficial litter, hemiedaphic (H) for species living in heavy litter and humus, euedaphic (E) for species living in soil and hemiedaphic-euedaphic (HE) for less specialised species.

Biogeographical knowledge about Collembola is fragmentary. Three biogeographical status have been defined [16]: cosmopolitan (C), European (E), holarctic and palearctic (H).

Ecological status was defined from the synthesis of several studies [11, 12, 25, 42, 56, 58]. Four ecological status were specified: open habitat species (O), generalist forest species (GF), specialist forest species (SF) and indifferent species (I). Specifying ecological status is difficult; it is rather indicative but not absolute.

Table I. List of species. See the text for explanation of species status. Farm forest: 28 species which were selected as the basic fauna of farm forests in the studied area.

Species	Abbr.	Taxonomical status	Biological status	Ecological status	Geographical status	Abundance	Frequency (%)	Farm forest
<i>Allacma fusca</i> (Linné, 1758)	AllFus	S	A	GF	E	229	53	O
<i>Arrhopalites</i> sp.	ArrSpe	S	E	GF	E	46	18	O
<i>Brachystomella parvula</i> (Schaeffer, 1896)	BraPar	P	H	O	C	2	1	
<i>Ceratophysella armata</i> (Nicolet, 1841)	CerArm	P	H	SF	C	553	64	O
<i>C. denticulata</i>	CerDen	P	H	O	C	63	13	
<i>Coloburella zangherii</i> (Denis, 1924)	ColZan	I	H	GF	E	3	4	
<i>Desoria tigrina</i> (Nicolet, 1841)	DesTig	I	H	I	E	13	5	
<i>Dicyrtoma ornata</i> (Fabricius, 1783)	DicOrn	S	A	SF	E	14	15	O
<i>Entomobrya nivalis</i> (Linné, 1758)	EntNiv	E	A	I	E	7	8	O
<i>Folsomia decemculata</i> (Stach, 1946)	FolDec	I	H	SF	E	26	10	O
<i>F. quadrioculata</i> (Tullberg, 1980)	FolQua	I	H	GF	C	4 803	71	O
<i>F. sensibilis</i> (Ksenerman, 1936)	FolSen	I	E	SF	E	11	3	
<i>Friesea truncata</i> (Cassagnau, 1958)	FriTru	P	HE	I	E	12	8	O
<i>Heteromurus major</i> (Moniez, 1889)	HetMaj	E	H	GF	E	72	20	
<i>Isotoma notabilis</i> (Schäffer, 1896)	IsoNot	I	H	GF	C	3 645	86	O
<i>Isotomiella minor</i> (Schaeffer, 1896)	IsoMin	I	E	GF	C	1 276	75	O
<i>Isotomurus maculatus</i> (Börner, 1901)	IsoMac	I	H	O	C	26	6	
<i>I. prasinus</i> (Reuter, 1891)	IsoPra	I	H	O	C	716	48	
<i>I. unifasciatus</i> (Boerner, 1901)	IsoUni	I	H	I	C	139	19	O
<i>Lepidocyrtus curvicollis</i> (Bourlet, 1839)	LepCur	E	H	SF	E	55	20	O
<i>L. cyaneus</i> (Tullberg, 1872)	LepCya	E	H	GF	C	1 018	75	O
<i>L. lignorum</i> (Fabricius, 1781)	LepLig	E	H	GF	H	509	83	O
<i>Lipothrix lubbocki</i> (Tullberg, 1872)	LipLub	S	H	SF	E	12	9	
<i>Megalothorax minimus</i> (Willem, 1900)	MegMin	N	E	GF	C	351	61	O
<i>Mesaphorura krausbaueri</i> (Börner, 1901)	MesKra	P	E	GF	C	141	30	O
<i>Micranurida candida</i> (Cassagnau, 1952)	MicCan	P	E	I	H	19	8	O
<i>M. pygmaea</i> (Börner, 1901)	MicPyg	P	HE	I	H	8	4	O
<i>Monobella grassei</i> (Denis, 1923)	MonGra	P	H	SF	E	32	16	O
<i>Neanura muscorum</i> (Templeton, 1835)	NeaMus	P	H	GF	H	89	38	
<i>Oligaphorura absoloni</i> (Börner, 1901)	OliAbs	P	E	GF	E	30	5	O
<i>Onychiurus</i> sp.	OnySpe	P	E	GF	E	448	14	
<i>Protaphorura armata</i> (Tullberg, 1869)	ProArm	P	E	I	C	368	20	
<i>Pseudachorutes palmiensis</i> (Börner, 1903)	PsePal	P	H	SF	E	23	20	
<i>P. parvulus</i> (Denis, 1934)	PsePar	P	H	SF	E	177	50	O
<i>Pseudosinella alba</i> (Packard, 1873)	PseAlb	P	H	SF	C	259	58	
<i>P. suboculata</i> (Bonet, 1931)	PseSub	E	H	SF	E	31	9	O
<i>Sminthurides schoetti</i> (Axelson, 1903)	SmiSch	S	H	I	E	150	23	
<i>Sminthurinus signatus</i> (Krausbauer, 1898)	SmiSig	S	H	GF	E	505	76	O
<i>Sphaeridia pumilis</i> (Krausbauer, 1898)	SphPum	S	H	O	C	146	31	O
<i>Stenognathellus denisi</i> (Cassagnau, 1953)	SteDen	S	H	GF	E	123	36	O
<i>Tomocerus minor</i> (Lubbock, 1862)	TomMin	E	H	GF	C	82	28	O
<i>Tullbergia callipygos</i> (Börner, 1903)	TulCal	P	E	O	E	80	25	O
<i>Vertagopus westerlundii</i> (Reuter, 1897)	VerWes	I	H	SF	E	15	9	
<i>Willemia anophthalma</i> (Boerner, 1901)	WilAno	P	E	GF	E	1	1	O
<i>Xenylla brevisimilis</i> (Stach, 1943)	XenBre	P	H	I	C	47	8	
<i>X. tullbergi</i> (Börner, 1903)	XenTul	P	H	I	C	775	34	

2.4. Statistical analysis

Analysis corresponded to three levels of investigation: at the first level, the abundance and frequency of species were analysed in the whole sample according to their different status to specify the main characteristics of the farm forest community; at the second level, different aspects of the community diversity were investigated. Richness was estimated using the Monod estimator, which is based on species cumulative curves built from bootstrapping techniques [43]. Diversity indices were estimated at the plot level: main taxa, the Berger-Parker index, evenness and beta diversity [79].

These indices are used widely in similar studies on Collembola to provide insights into community structure in the samples.

The last level of investigation was multivariate analysis for studying community structure [74]. Numerous studies have used multivariate analysis to provide the main factors that explain Collembola community structure [9, 11–13, 25, 42, 53, 60, 61]. A correspondence factor analysis was computed on the table of 46 species abundances and eighty samples. This analysis is widely used in ecological studies [73]. It uses a double averaging to produce axes of the best reciprocal ordinations of species and samples. Species are located

at the barycenter of the samples where they have been observed and samples are located at the barycenter of the species they contained. The main axis can be considered as a simplified model of the structure contained in the data [45]. They were used to perform a hierarchical classification of samples in order to distinguish different groups defined by the major structural factors [45]. A square root transformation of the data was made before the analysis to reduce differences between rare and very abundant species.

This analysis helps to identify major characteristics of the collembolan communities which need further investigation with canonical correspondence analysis based on the variables collected to describe the ecological conditions of each sample.

3. RESULTS

3.1. Abundance and frequency of species

The abundance of the 46 species counted ranged from one individual (*W. anophthalma*) to 4 803 individuals (*F. quadrioculata*), for a total of 17 150 individuals. The graph of the species abundance vs. their rank (figure 2) revealed that two species accounted for more than 50 % of all individuals: *F. quadrioculata* and *I. notabilis* (each of which totalled more than 1 000 individuals). It can be seen that 50 % of the species richness represented 97 % of the abundance, showing that the community was on the whole dominated quantitatively by a few species. The most abundant species were generalists (18 species). These species generally have a high reproduction rate, confirmed by the numer-

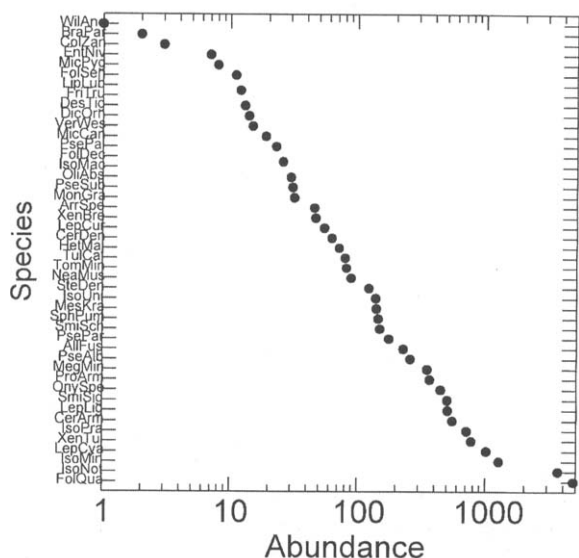


Figure 2. Rank of abundance (log) of the 46 species, all samples pooled. See table 1 for abbreviations of species names.

ous young individuals observed, which allow them to colonise rapidly temporary habitats (dry or saturated habitats associated with micro-climatic conditions).

Some species were especially abundant in extreme habitats: *X. tullbergi* in dry mosses, *I. prasinus* in saturated habitats. *X. tullbergi*, an indifferent species, also colonised temporary habitats.

The frequency ranged from one sample (*B. parvula*, *W. anophthalma*) to 69 samples (*I. notabilis*). The graph of species frequency vs. their rank (figure 3) revealed that two species were present in 80 % of all samples: *I. notabilis* and *L. cyaneus*. Eleven species were present in at least 50 % of samples: *A. fusca*, *C. armata*, *I. notabilis*, *I. minor*, *F. quadrioculata*, *L. cyaneus*, *L. lignorum*, *M. minimus*, *P. alba*, *P. parvulus* and *S. signatus*. All the species with high frequency are forest species, while nine are generalist forest species and four are specialist forest species. Eight secondary species were found in at least 25 % of samples. The other species were scarce or occasional.

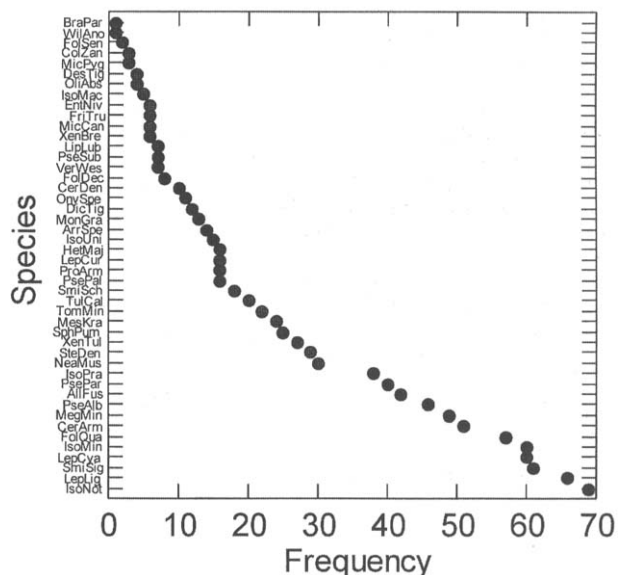


Figure 3. Rank of frequency of the 46 species, all samples pooled. See table 1 for abbreviations of species names.

3.2. Taxonomical status

Poduromorpha was the richest group of species, while Neelipleone was the least rich (figure 4). Abundance percentages for each type were very different. Isotomidae (24 % of all the species richness) accounted for 62 % of all individuals due to their high reproductive rate. Poduromorpha (40 % of all the species richness) was only 17 % of all individuals. In fact, except for *C. armata*, *C. denticulata* and *X. tullbergi*, the other Poduromorpha, such as *N. muscorum*, had

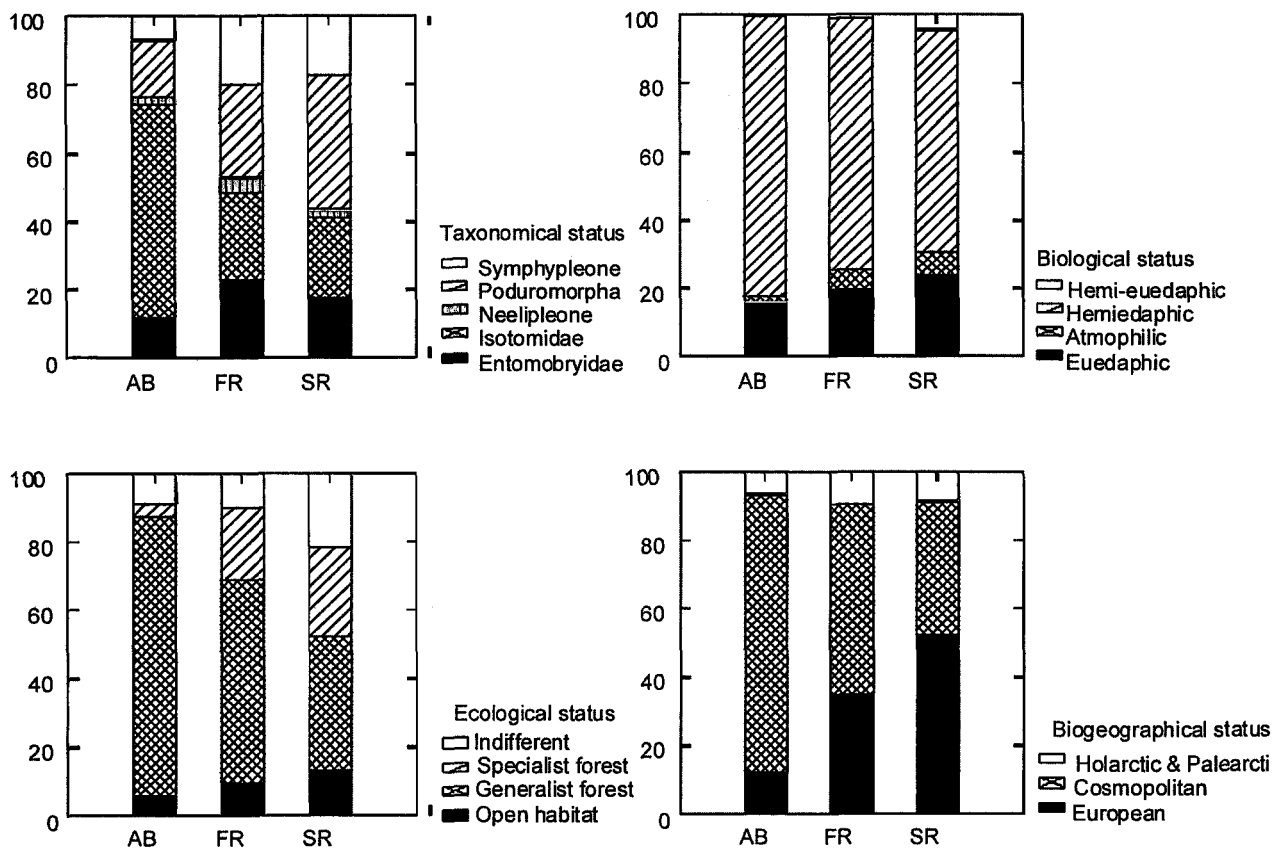


Figure 4. Total Abundance (AB), frequency (FR) and species richness (SR) according to the species status (see text for explanations of species status).

small populations, although their frequencies were high. Poduromorpha (27 %) were more frequent than both Isotomidae and the other taxa.

The data for species abundance were quite normal for the forest, however Poduromorpha abundance was very low in this particular forest. The small size of Poduromorpha populations seemed to be linked to three phenomena: the low rate of reproduction of several Poduromorpha (for instance Neanuridae), the sampling period that does not correspond to the reproductive period (many species have an autumnal reproduction), and several Poduromorpha species are associated with moist habitats, which were rare in the forests studied.

3.3. Biological status

As in typical forests, the hemiedaphic species had the highest species richness, abundance, and frequency (figure 4). The atmophilic and euedaphic species were the least diversified, the least abundant and the least frequent groups. Likewise, the euedaphic species were scarce. These results were consistent with the sampling

method, as heavy litter and humus but very little surface litter had been sampled (where the highest proportion of atmophilic species can be found) and heavy soil (where the highest proportion of euedaphic species can be found).

3.4. Biogeographical status

Species were mainly European (52 % of richness), but cosmopolitan species were the most abundant and frequent species (figure 4). There were no endemic species. In comparison, in the Pyrenees, 25 % of endemic species were found in the forest of Neouvielle [16], 30 % in the riparian area of Arize [25] and 40 % in cold habitats [42].

3.5. Ecological status

Forest species had the highest species richness, abundance and frequency. There are principally generalist forest species, such as *F. quadrioculata*, *I. minor* and *I. notabilis*. *F. quadrioculata* dominated in litter

and humus, while *I. minor*, *I. notabilis*, *L. cyaneus* and *L. lignorum* were more common in litter than in humus. These species and other generalist forest species, such as *H. major*, *M. krausbaueri*, *M. minimus* and *S. signatus*, are known to increase in disturbed environmental conditions, such as deforested strips [12, 32].

Some forest species were specialist, e.g. *C. armata*, *L. lubbocki*, *M. grassei*, *N. muscorum*, *P. alba*, *P. parvulus* and *P. palmiensis*. They were less diversified, less abundant (except *C. armata*), and less frequent than generalist forest species. Environmental conditions probably do not favour their development.

P. palmiensis is typical of plain forest, while some species are more like mountain forest species, for example *F. sensibilis*, *P. parvulus* and *P. suboculata*. This last species is a specialist species of mountain forests, being only found in Nere (seven samples, 31 individuals), the area nearest to the Pyrenees.

There were six open habitat species (*B. parvula*, *C. denticulata*, *I. maculatus*, *I. prasinus*, *S. pumilis* and *T. callipygos*). This group had the smallest species richness, abundance and frequency, except for *I. prasinus*, which is a hygrophilous species that was abundant and frequent in the Nere area, where the forest is moister than in Brag. These species are generalist open species. They are also abundant and frequent in deforested strips, along with generalist forest species [11, 12, 32]. There were no specialist open habitat species, although some samples were located in clear-cut areas without tree shelter.

There were ten indifferent species: *D. tigrina*, *E. nivalis*, *F. truncata*, *I. unifasciatus*, *M. candida*, *M. pygmaea*, *P. armata*, *S. schoetti*, *X. brevissimilis* and *X. tullbergi*. They were often present in temporary habitats, such as moss. *X. tullbergi* is not only a characteristic moss species [10, 16, 20], it is also a robust species that colonises several extreme habitats [16] and increases under influence of trampling in forest [49].

In summary, the whole Collembola community was mostly made up of forest generalist species, with few forest specialist or open habitat species, and numerous indifferent or ubiquitous species. This Collembola community seemed characteristic of managed fragmented forest in this area.

The community could be divided into three groups according to the level of frequency-abundance of the species and their ecological affinities. First, six main species were identified with high abundance and frequency, principally generalist forest species: *F. quadrioculata*, *I. minor*, *I. notabilis*, *L. cyaneus*, *L. lignorum* and *S. signatus*. The second group contained 22 species that were less frequent but were associated with forest habitat conditions. These two groups were combined to define a core fauna for farm forest Collembola in the area studied (table I). The third group (eighteen species) contained infrequent species and species that were associated with particular habitat conditions.

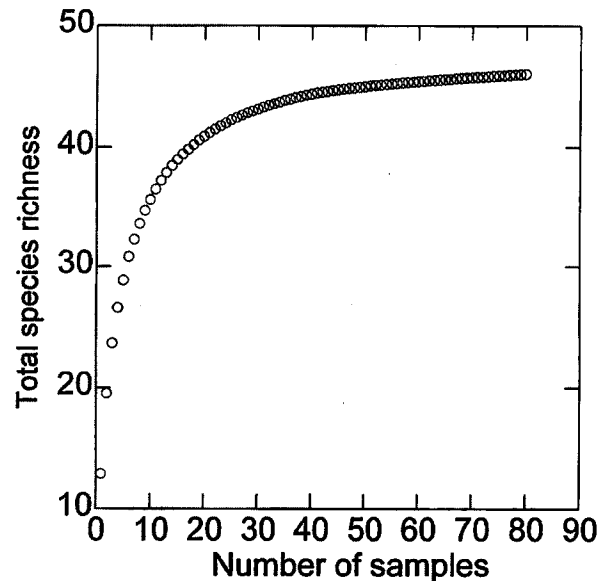


Figure 5. Cumulative richness curve calculated with repeated re-sampling of the whole sample (bootstrapping).

3.6. Diversity

The species richness comprised a total of 46 species ($n = 80$). This richness corresponded to 98.4 % of the total species richness provided by the Monod estimator (figure 5). This confirmed that this sampling covered almost the entire diversity of forests in this area.

F. quadrioculata was the main species in 44 % of samples, and *I. notabilis* was the main species in 24 % of samples. Species richness per sample ranged from three to 23 species. Mean species richness per sample (250 cm³) was quite low, with 13 (± 1) species. The evenness index ranged from 0.3 to 0.91, with a mean value of 0.68 (± 0.3), and the Berger-Parker index ranged from 16 to 81 %, with a mean value of 43 % (± 3.45). Beta diversity was large (2.45). Thus the samples presented a high heterogeneity in their composition, reflecting the high diversity in forest conditions in the sample. However, the frequency of two main species, *F. quadrioculata* and *I. notabilis*, corresponding to the major part of the abundance in all samples, indicated that there were some common and strong ecological features among the community.

3.7. Community structure

The main point to note in the correspondence analysis results was the low dispersion of the samples (figure 6). The majority of samples were found near the origin and corresponded to the less differentiated communities, which included the most common spe-

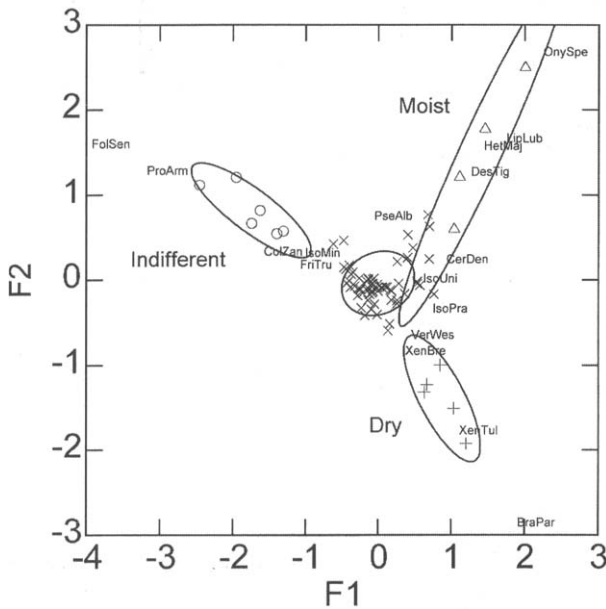


Figure 6. First factorial plane (F1XF2) of the correspondence analysis. Samples are represented by symbols according to the group obtained by hierarchical classification. Species clustered around the origin are not labelled. See *table 1* for abbreviations of species names.

cies. The whole sample had been constructed to represent the diversity in farm forest conditions; thus, a structure showing greater differences between the types of plots or between samples was expected. In fact, the Collembola communities found in farm forest had few differences between them and the differences in ecological conditions did not lead to marked modifications.

Three factors were needed to account for 35 % of the total variability, five factors for 50 % with a first factor accounting for 12 % of the total variability. The first three factors were interpreted according to the available knowledge on ecological preferences of the species they separated.

The first factor separated the samples with high abundance of euedaphic or indifferent species (*P. armata*) on the negative side and, on the positive side, the samples with high abundance of species which are associated with extreme environment: very moist (*Onychiurus* sp.) or very dry (*X. tullbergi*).

The second factor integrated a component linked to the water content of the soil: species associated with driest conditions were on the negative side, and on the positive side species associated with moist conditions.

The third factor seemed to be associated with logging practices. On the positive side (around the origin in the first factorial plan), samples were found in copice with standard stands, and on the negative side (away from the origin in the first factorial plan) clear-cutting stands, which seemed to be less homogeneous.

The hierarchical classification of samples with a complete link and Euclidian distance applied to the first three factors of the correspondence analysis separated four groups according to the distance step between nodes in the hierarchical tree of classification. The first group corresponded to the samples around the origin. The 28 core species identified in abundance and frequency analysis were clustered around the origin and indicated that those samples were typical of the farm forest habitat conditions. The three other groups were associated with samples dominated by indifferent species, moist samples and dry samples. This confirmed that the collembolan community was quite uniform between samples, except for a few situations where particular species had high abundances due to their affinity with certain ecological conditions.

4. DISCUSSION

The collembolan fauna of farm forest exhibited particular characteristics that highlight differences from communities in other larger forests. The total richness was low compared to other areas. For example, the Preissac plain forest near Toulouse exhibited 63 species (unpubl. data), although the sampling was not limited to the top soil habitat. In Pyrenean forests, species richness is higher: 124 species in the Pyrenees ranges [16], 96 species in cryophilous habitats of Neouvielle ranges [42] and 73 species in Arize riparian habitats in Pyrenees [25]. This is due to a higher level of endemism and a wide diversity of habitats.

Isotomidae were the most abundant and frequent, but Poduromorpha presented the highest species richness. In the natural forest, Poduromorpha is often the most diversified, abundant, and frequent group [16]. This might suggest that Poduromorpha do not find conditions moist enough in the forests studied to generate large populations. This dryness could be created by logging activities that frequently remove the shelter provided by trees, or fragmentation, which increases the air flux speed through small wood-lots.

The Collembola community was dominated by generalist forest species, which were the most abundant and frequent, exhibiting the highest species richness. The main species observed were *F. quadrioculata*, *I. minor*, *I. notabilis*, *L. cyaneus*. These four species also dominate in deforestation associated with the strips of ski stations in mountain forests [11, 12, 32]. In comparison, specialist forest species, such as *C. armata*, *P. alba* and *P. parvulus*, had a lower species richness, abundance, and frequency. Only six open habitat species were present, but they were mainly generalist species demonstrating their adaptive potentialities, except for *I. prasinus*, linked to the moist Nere area; thus, clear-cutting seemed not to have introduced as many open habitat species as might have been expected. In fact, logged areas are not real open habitats at the collembolan scale: logging residues protect the soil,

and there are always small microhabitats that are unaffected by logging.

The collembolan community, where generalist forest species are numerous and abundant, characterises clear forests; the specialist forest species are preferentially associated with thick and large forests [56, 61–63]). Hemiedaphic species remained dominant in the community, and there was no increase in euedaphic species richness as had been observed in deforestation [11], although with a more intensive sampling of heavy soil. Cosmopolitan species were well represented in this community because they are species that do not require restricted environmental conditions.

In summary, the collembolan fauna of farm forest seemed poorly specialised, being dominated by generalist forest species. These species are also numerous when habitats open out due to logging and clear-cutting. Similar results were found in studies about deforestation and reforestation. In this case, there was a rupture of the biocenotical balance inside collembolan communities: low species richness, few specialist species and numerous and abundant generalist species [11, 12, 32]. As in studied farm forests, the perturbation of edaphic biotopes in forests increased the generalist species to the detriment of specialist species. However, in all cases, they were always forest species and very few lawn species in spite of the existence of artificial open habitats. There was also a comparable collembolan community associated to anthropic perturbations such as cultivation [31], fire impact [47, 50], clear-cutting effects [66, 72], introduction of exotic tree species [18, 19, 69] and settling effects [61].

Some species are characteristic of anthropic influences such as *X. tullbergi* and *S. signatus* that are particularly abundant in these farm-forests. They are also associated with trampling effects [61].

Management practices appeared to be less important than ecological conditions, and they could only be seen on the third factor in the correspondence analysis; however, it appeared that clear-cut was associated with dry or moist plots, while coppice with standards was associated with less strict conditions. It therefore seems that standards are sufficient to maintain buffered conditions and that clear-cuts could induce two particular communities associated with dry or wet conditions. It is well known that clear-cut can cause drier conditions through an increase in evaporation or wetter conditions through a decrease in water intake by trees in places with a superficial water table.

In conclusion, the Collembola community of farm forest seems to be linked continually to forest conditions, in spite of a long history of marked disturbances through fragmentation, edge effects and logging. In fact, we did not expect to find so few open habitat species, even in clear-cut areas; however, very specialised species were reduced in abundance and frequency, showing the negative impact of disturbances on the most sensitive species. Generalist forest species were

dominating in the community because of their high adaptive potentialities.

Work is now needed to predict whether the long-term tendency is impoverishment in the community or whether the shifts in logging and silvicultural practices are able to maintain or increase Collembola diversity.

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