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ORIGINAL PAPER

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Relationships between Collembola, soil chemistry and humus types in forest stands (France)

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Abstract Soil samples were taken under four tree species in various forest sites located in southern France. For each sampled A horizon of the soil profile, pH, organic matter content, C:N ratio and amounts of exchangeable cations (K, Ca, Mg) were measured, and collembolan fauna was extracted using Berlese-Tullgren funnels. A total of 78 species representing 11 families and 47 genera were identified. The relationships between Collembola and soil parameters were determined by co-inertia analysis which corresponds to the simultaneous Correspondence Analysis of the collembolan data table and the Multiple Correspondence Analysis of the environmental data table. The analysis revealed that the distribution of 10 species was related to pH, organic matter content via C and N and to base cations (K, Ca, Mg). Samples, linking these collembolan species and chemical parameters, were clustered according to humus forms. Collembola seem to be linked closer to the physical structure of humus than to its chemical parameters. Their specific contribution to pedogenetic processes as yet remains to be clarified.

Keywords Collembola · Soil chemistry · Humus forms · Forest conditions

Introduction

Microarthropods are, with numerous species and individuals occupying a wide range of ecological niches, good representatives of soil biodiversity. A large proportion of this fauna plays a part in the decomposition of organic matter and nutrient cycling (Faber 1992), two key processes in forest ecosystem functioning (Bardgett et al. 1998). The mesofauna present in a habitat depend upon many factors including pH (e.g. Loranger et al. 2001), pedoclimate (e.g. Seasted and Crossley 1981), aeration (e.g. Vreeken-Buijs et al. 1998), organic matter composition (e.g. Merilä and Ohtonen 1997), nutrient availability (e.g. Bird et al. 2000), humus type (e.g. Theenhaus and Schaefer 1995) and effect of the vegetation cover (e.g. Paquin and Coderre 1997). Soil and litter arthropods, such as Collembola, are thus considered to be useful bioindicators of changes in soil quality determined by these factors and influenced by ecological conditions or silvicultural practices (Huhta et al. 1967; Hole 1981; Detsis et al. 2000).

The soil can be acknowledged as another biotic frontier, along with the forest canopy, of the terrestrial biota, constituting a huge reservoir for biodiversity (André et al. 1994) and, according to Hågvar (1998), conservation of soil biodiversity is “perhaps the most important and challenging task for soil biologists”. Therefore, conservation of soil biodiversity implies maximum information on the behaviour of species, especially narrow-distributed species (endemics) which are of great interest (Deharveng 1996), and their ecological role in a habitat we want to protect. Much ecological and taxonomic information is still waiting to be discovered (André et al. 1994; Paquin and Coderre 1997; Chagnon et al. 2000a) and for some collembolan species detailed knowledge is almost non-existent (Hopkin 1997). Several studies have shown that collembolan communities are related to humus type (Hågvar 1983; Ponge et al. 1986; Schaefer and Schauermann 1990; Chagnon et al. 2001), which is often related to soil acidity (Ponge 1983; Hågvar 1990). Less research has been done on relationships between Collembola and soil chemical characteristics other than pH (Hågvar and Abrahamsen 1984; Chagnon et al. 2000b; Loranger et al. 2001). The main objective of the present study was to improve our understanding of relations between Collembola and soil chemical parameters (pH, basic cations, C, N and C/N ratio) using a co-inertia analysis. Another aim of this study was to find out to what extent vegetation cover influences certain chemical parameters and thus plays a

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role in relationships between Collembola and soil chemistry.

Materials and methods

Study sites

The study was conducted in two regions of southern France: the Central Pyrenees and the Monts de Lacaune. Samples were taken from varied biotopes in order to cover a wide range of possible habitats. Forest stands were represented by 11 native European beech (*Fagus sylvatica* L.) forests and by conifer plantations: *Picea abies* (L.) Karst. (11 plots), *Pseudotsuga menziesii* (Mirb.) Franco (6) and *Abies alba* Mill. (2). These stands are growing on Cambisols or Luvisols (FAO 1998) formed mainly on acid rocks (granite, gneiss, schist) but also in some cases on limestone. The climate shares Atlantic and mountain features with a mean annual rainfall ranging from 1,000 to 2,000 mm, according to geographical and altitudinal (670–1,450 m) conditions. The sites were characterised by two forms of humus: a moder form and a mull-moder transition form.

Sampling procedure

At each sampling plot, we collected the organo-mineral A horizon under the superficial litter layer (O horizon) which was also sampled but is not considered here. We only considered samples from the A horizon, because its fauna is more directly linked to soil characteristics (Ponge 1993; Chagnon et al. 2000b; Loranger et al. 2001) and the A horizon is also less dependent on soil surface variations. Five samples were collected in each plot situated in the Pyrenees and 10 samples were collected in each plot situated in the Monts de Lacaune. Each sample consisted of 250 cm^3 of this A horizon taken in the first 10 cm of the soil just under the O horizon. A cylinder-gauge was not suitable for sampling in the studied soils because of the presence of roots, stones and micromammal tunnels in many samples.

The arthropods were extracted from soil samples with Berlese-Tullgren funnels at a temperature of 18-23°C for 7 days. Collembola were identified to species level and their abundance recorded. Soil samples were sieved through a 2-mm screen to get the fine particle portion on which chemical analyses were performed. pH (H_2O) was determined in a suspension with a soil:solution ratio of 2.5. Organic carbon (C) was determined by the Anne method, total nitrogen (N_{tot}) was measured by the Kjedahl method and exchangeable cations were extracted using the Schollenberger and Dreibelbis method (Aubert 1978).

Statistical analyses

Faunal determinations and chemical analyses were performed on a total of 210 samples covering the 30 stands.

The study of collembolan species and soil chemistry relationships was carried out using the co-inertia (or co-structure) method (Dolédec and Chessel 1994) which is based on the simultaneous analysis of two data tables, one containing the collembolan species abundances at all sampling plots and one containing the chemical variables, divided into classes, at the same sampling plots. Each data set was treated separately by Correspondence Analysis (COA) for the fauna data set and via Multiple Correspondence Analysis (MCA) for the chemical data set. Co-inertia analysis gives a simultaneous ordination of the samples and the variables (species or chemical classes) for the Collembola and the soil data tables and maximises both the correlation and the projected variance on the axes (Mercier et al. 1992). This method is a correspondence analysis variant of the inter-battery analysis of Tucker (1958) and has been presented as an alternative to the canonical correspondence analysis of Ter Braak (1986). We tested the non-significance of rare (low number) species in these statistical analyses. Those which were present in less than 5 of the 210 samples (40 species) were then excluded from the analyses due to too great an uncertainty about their relation with an environmental factor (Ponge 1993). The analyses were performed using the computer programs ADE4 and StatLab.

Results

Collembolan fauna and its relation with sampling sites

A total of 13,025 specimens representing 78 species of Collembola were identified (Table 1). Of these 78 species, 19 were endemic to the Pyrenees, 1 was endemic to Monts de Lacaune and 1 other endemic species was common to both sites. Eighteen species together formed over 90% of the total number of individuals with three species, *Cryptopygus debilis*, *Folsomia manolachei* and *Isotomiella minor*, representing more than 50% of the total abundance. Forty species were selected for statistical analysis owing to their presence in more than 5 samples allowing a possible relationship between these species and chemical soil properties to be tested.

A COA was performed to ordinate sampling locations according to collembolan species (Fig. 1). Out of the 40 species analysed, 14 were significantly correlated with the factorial plane and 6 were significantly correlated with both axes. The major determinants of the first axis (% total inertia =12.8) were the following species, *Cryptopygus debilis*, *F. quadrioculata*, *I.* cf. *paraminor*, *Mesaphorura macrochaeta*, and *Oncopodura crassicornis*, on the negative side, and *Ceratophysella luteospina*, *F. decopsis*, *F. manolachei*, *I. minor*, and *Pseudisotoma monochaeta*,

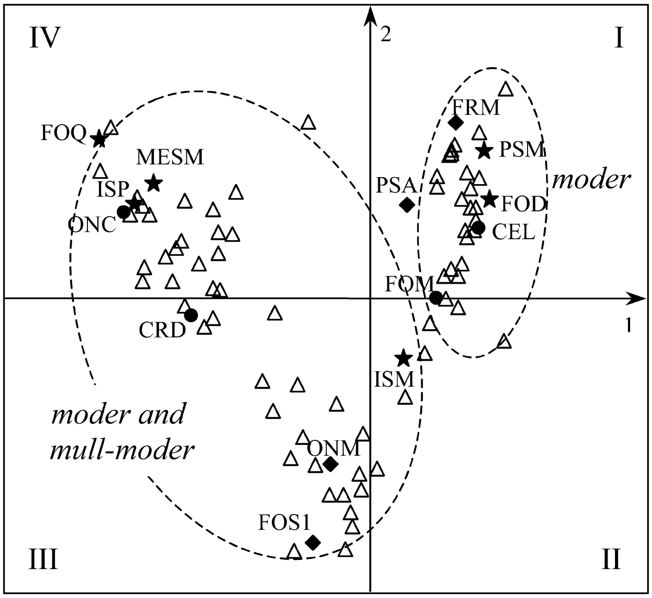

Fig. 1 Correspondence analysis of soil samples and collembolan species (see Table 1 for the Collembola codes used). ● Collembola linked to the first axis, ◆ Collembola linked to the second axis, ★ Collembola linked to both axes 1 and 2

Table 1 List of Collembola with their abundance and their codes used in the analyses (**endemic species**)

Code	Species	Central Pyrenees		Monts de Lacaune			
		Spruce	Beech	Spruce	Douglas fir	Silver fir	Beech
ANS	**Anurida** sp.	0	2	0	0	0	0
ARS	*Arrhopalites* cf. *serious* (Gisin), 1947	1	1	0	0	0	11
ARP	*Arrhopalites pygmaeus* (Wankel), 1869	0	18	0	0	0	0
ARS	*Arrhopalites* sp.	36	37	0	0	0	0
BRP	*Brachystomella parvula* (Schaeffer), 1896	1	1	0	0	0	0
CEA	*Ceratophysella armata* (Nicolet), 1841	11	51	0	0	0	0
CED	*Ceratophysella denticulata* (Bagnall), 1941	1	13	0	1	0	5
CEL	*Ceratophysella luteospina* (Stach), 1920	0	0	69	191	41	111
CET	**Ceratophysella tuberculata** (Cassagnau), 1959	0	8	0	0	0	0
CRD	**Cryptopygus debilis** (Cassagnau), 1959	181	845	0	0	0	0
DED	**Deutonura deficiens** (Deharveng), 1979	9	6	0	6	3	0
DIO	*Dicyrtomina ornata* (Nicolet), 1841	2	1	0	0	0	0
FOD	*Folsomia decopsis* Steiner, 1958	0	0	97	0	0	197
FOM	*Folsomia manolachei* Bagnall, 1939	370	308	93	788	314	641
FOQ	*Folsomia quadrioculata* (Tullberg), 1871	27	88	0	0	0	0
FOS1	***Folsomia* sp. 1**	2	570	0	0	0	0
FOS2	*Folsomia* sp. 2	0	0	6	10	5	19
FRC	***Friesea* cf. *cauchoisi***	0	5	0	0	0	0
FRP	***Friesea* cf. *pyrenaica***	0	6	0	0	0	0
FRM	*Friesea mirabilis* (Tullberg), 1871	18	1	56	91	1	0
FRT	***Friesea troglophila* Cassagnau, 1958**	1	8	0	0	0	0
HEM	*Heteromurus major* Moniez, 1889	1	1	0	0	0	0
HEN	*Heteromurus nifidus* (Templeton), 1835	0	1	0	0	0	0
HYMS	***Hymenaphorura* sp. 1**	0	10	0	0	0	0
HYS	*Hypogastrura* sp.	2	1	0	0	0	0
IST	*Isotoma tigrina* Axelson, 1902	1	0	0	0	0	0
ISV	*Isotoma viridis* Bourlet, 1839	7	2	0	0	0	0
ISP	***Isotomiella* cf. *paraminor***	185	234	0	0	0	0
ISM	*Isotomiella minor* (Schaeffer), 1896	352	882	46	762	491	607
ISQ	*Isotomodes* cf. *quadrisetosus*	1	3	0	0	0	0
KAT	***Kalaphorura tuberculata* (Moniez), 1891**	0	0	10	99	0	20
LEC	*Lepidocyrtus cyaneus* Tullberg, 1871	37	52	0	0	0	0
LELA	*Lepidocyrtus lanuginosus* (Gmelin), 1788	8	2	0	0	0	0
LELI	*Lepidocyrtus Ugnorum* Fabricius, 1793	0	0	38	135	57	3
LIL	*Lipothrix lubbocki* (Tullberg), 1871	1	0	1	1	0	2
MEM	*Megalofhorax minimus* Willem, 1900	23	66	6	16	4	10
MEH	*Mesaphorura hylophila* Rusek, 1971	5	0	0	0	0	0
MEM	*Mesaphorura macrochaeta* Rusek, 1976	213	181	0	0	0	0
MIC	*Micranurida candida* Cassagnau, 1952	0	2	0	0	0	1
MIS	*Micranurida* sp.	0	3	0	0	0	0
MOC	**Monobella calva** Bedos&Deharveng, 1998	11	0	0	0	0	0
MOG	*Monobella grassei* (Denis), 1923	2	2	0	0	0	4
MUA	**Mucrella acuminata** (Cassagnau), 1952	3	18	0	0	0	0
NEM	*Neanwa muscorum* (Templeton), 1835	1	0	0	0	0	0
NEM	*Neelus murinus* Folsom, 1896	3	10	0	0	0	0
ONC	*Oncopodura crassicornis* Schoebotham, 1911	29	103	0	0	0	0
ONA	**Onychiurus ariegicus** Deharveng, 1979	0	19	0	0	0	0
ONG	*Onychiurus* cf. *granulosus*	0	0	11	0	0	0
ONI	*Onychiurus* cf. *insubrarius*	5	23	0	0	0	0
ONM	**Onychiurus gr minutus** Denis, 1932	57	116	0	0	0	0
ONP	*Onychiurus pseudogranulosus* Gisin, 1951	2	12	0	0	0	0
PAC	*Paratullbergia callipygos* (Boerner), 1903	54	110	0	0	0	4
PAN	*Parisotoma notabilis* (Schaeffer), 1896	148	59	53	169	57	32
PRA	*Protaphorura armata* (Tullberg), 1869	28	70	66	132	4	125
PSM	*Pseudachorudina meridionalis* (Bonet), 1929	0	2	0	0	0	0
PSP	*Pseudachorutes palmiensis* (Boemer), 1903	4	1	0	0	0	0
PSPA	*Pseudachorutes parvulus* Boemer, 1901	35	0	0	0	0	0
PSM	*Pseudisotoma monochaeta* sp. a	30	14	27	324	100	14
PSA	*Pseudosmella alba* (Packard), 1871	162	20	79	211	14	149
PSD	*Pseudosinella duodecimoculata* Bonet, 1931	21	9	0	0	0	0
SCS	**Schaefferia subcaeca** Deharveng&Thibaud 1980	0	4	0	0	0	0
SCU	*Schoettella ununguiculata* (Tullberg), 1869	0	0	0	1	0	0
SES1	*Seira* sp. 1	0	0	0	0	0	1
SMIS	*Sminthurides* sp.	1	1	0	0	0	0
SME	*Sminthurinus elegans* (Fitch), 1863	0	3	0	0	0	0
SMN	*Smmfhurinus niger* (Lubbock), 1868	0	2	0	0	0	0
SMSI	*Sminthurinus signatus* (Krausbauer), 1898	3	33	0	59	0	63

Table 1 (continued)

Code	Species	Central Pyrenees		Monts de Lacaune			
		Spruce	Beech	Spruce	Douglas fir	Silver fir	Beech
SMS	**Sminthurinus sp.**	1	0	0	0	0	0
SPP	*Sphaeridia pumilis* (Krausbauer), 1898	1	0	0	0	0	0
SUSa	**Superodontella sp. a**	0	4	0	0	0	0
SUSb	**Superodontella sp. b**	0	3	0	0	0	0
TEU	**Tetracanthella cf. uniseta**	0	1	0	0	0	0
TER	**Tetracanthella recta** Deharveng, 1987	0	9	0	0	0	0
TOM	*Tomocerus minor* (Lubbock), 1862	0	19	0	9	7	32
TRP	*Triacanthella perfecta* Denis, 1926	0	0	0	1	0	4
WIAN	*Willemia anophthalma* Boemer, 1901	1	16	0	0	0	0
WIAS	*Willemia aspinata* Stach, 1949	9	8	0	0	0	0
XEM	*Xenylla maritima* Tullberg, 1869	1	0	0	0	0	0

on the positive side. The second axis (% total inertia =8.6) was correlated with *Folsomia* sp.1, *I. minor*, and *Onychiurus* gr *minutus* on the negative side, *F. decopsis*, *F. quadrioculata*, *Friesea mirabilis*, *I.* cf. *paraminor*, *Mesaphorura macrochaeta*, *Pseudosinella alba*, and *Pseudisotoma monochaeta* on the positive side.

These species were present in 72 soil samples distributed in the plane of the COA according to three distinct groups. One group, composed of 27 samples, was situated in quadrants I and II and characterised moder humus forms. Another group of 29 samples was mainly distributed in the IV quadrant, representing moder and numerous mull-moder humus forms. Samples of these two groups were correlated to both axes of the COA. A third group of 19 samples, mainly correlated to the second axis on the negative side, was distributed in quadrants II and III and also corresponded to mull-moder or moder forms.

Soil chemical parameters and their relation with sampling sites

Data for each chemical parameter are presented in Table 2 according to the mean value found in each sampling plot. Humus form determination was based not only on the physical-chemical characteristics of the A horizon but also on the morphological features of the O horizons. Soil chemical parameters were grouped at random into three classes of equal size (Table 3) and a MCA was used to ordinate the samples according to these different classes. For each chemical parameter, one of the three classes was at least correlated to axis 1 (% total inertia =24) or axis 2 (% total inertia =13.8) of the MCA (Fig. 2).

Sample co-ordinates were distributed into the factorial plane according to three units. (1) Forty four samples (moder), distributed in quadrants III and IV, were related to the lower pH (<3.8), to the higher values of C and N_{tot} (>12% C and >0.7% N_{tot}) and to the higher values of the three major cations (>0.4 meq.100 g^{-1} K^{+}, >2 meq.100 g^{-1} Ca^{2+}, >0.8 meq.100 g^{-1} Mg^{2+}). (2) Forty one samples (moder), distributed in quadrants II and III, depended on the following chemical parameters: 3.8< pH <4.0, 8.4< C% <12.2 and 0.4< N_{tot}% <0.7. (3) The last group was made up of 68 samples (mull-moder, moder), mainly distributed in quadrants I and II, which were characterised by the higher pH values (4.0< pH <5.3), a low organic matter content with C <8.4% and N_{tot} <0.4%, the lower values of K and Mg (<0.18 meq.100 g^{-1} and <0.5 meq.100 g^{-1} respectively) and C:N >19 in some cases.

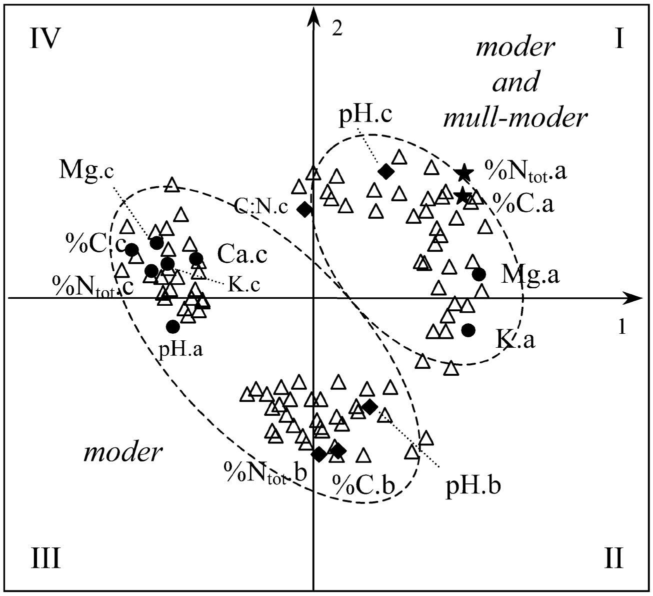

Fig. 2 Multiple correspondence analysis of soil samples and soil parameters according to their classes. ● Parameters linked to the first axis, ◆ parameters linked to the second axis, ★ parameters linked to both axes 1 and 2

Relationships between Collembola and soil chemical parameters

The inertia analysis, projected on the co-inertia plane, showed that only the first axes of the COA and the MCA were well correlated (0.79) to the co-inertia axes. The preliminary analyses of COA and MCA showed 28

Table 2 Mean (*SEM in parentheses*) of soil parameters in each plot analysed

	Humus forms	C%	N%	C/N	pH	K^+	Ca^{++}	Mg^{++}
						(meq.100g^{-1})		
Central Pyrenees								
Spruce plantation	1 mull-moder	3.9 (0.38)	0.27 (0.02)	14.5 (0.28)	4.7 (0.08)	0.25 (0.10)	3.25 (0.80)	0.56 (0.11)
	2 moder	9.0 (0.63)	0.40 (0.08)	25 (3.17)	4.2 (0.19)	0.14 (0.01)	0.39 (0.08)	0.31 (0.04)
	3 mull-moder	4.2 (0.25)	0.23 (0.02)	19 (2.4)	4.2 (0.09)	0.18 (0.03)	1.04 (0.30)	0.25 (0.03)
	4 moder	10.5 (1.33)	0.73 (0.13)	15 (1.80)	4.0 (0.18)	0.21 (0.02)	1.87 (0.85)	0.67 (0.21)
	5 mull-moder	6.8 (0.46)	0.32 (0.02)	21 (1.15)	4.2 (0.04)	0.22 (0.05)	1.16 (0.11)	0.81 (0.26)
	6 mull-moder	7.0 (0.67)	0.35 (0.03)	20 (1.94)	4.5 (0.03)	0.25 (0.03)	1.54 (0.18)	0.33 (0.08)
	7 mull-moder	9.6 (0.74)	0.49 (0.07)	20 (1.60)	3.8 (0.02)	0.33 (0.03)	3.54 (0.71)	1.51 (0.22)
	8 moder	9.0 (0.96)	0.39 (0.05)	24 (2.88)	4.2 (0.07)	0.1 (0.02)	0.91 (0.25)	0.37 (0.09)
	9 moder	15.9 (0.67)	0.69 (0.05)	23 (0.73)	4.1 (0.11)	0.83 (0.33)	2.89 (0.67)	1.18 (0.23)
Beech forest	1 mull-moder	6.4 (0.52)	0.35 (0.03)	18.5 (0.90)	4.6 (0.17)	0.17 (0.02)	6.60 (3.15)	1.05 (0.40)
	2 mull-moder	8.6 (0.16)	0.38 (0.01)	23 (1.24)	4.0 (0.04)	0.22 (0.03)	0.71 (0.20)	0.40 (0.02)
	3 mull-moder	3.2 (0.17)	0.23 (0.02)	14.5 (0.81)	4.6 (0.05)	0.21 (0.05)	2.23 (0.44)	0.44 (0.11)
	4 mull-moder	13.0 (1.68)	0.84 (0.13)	16 (0.63)	4.9 (0.09)	0.40 (0.07)	13.58 (1.81)	1.42 (0.17)
	5 mull-moder	10.9 (2.50)	0.51 (0.12)	21.5 (0.70)	4.1 (0.14)	0.31 (0.06)	1.57 (0.30)	0.87 (0.30)
	6 mull-moder	7.9 (0.47)	0.41 (0.03)	19 (0.92)	4.5 (0.03)	0.46 (0.03)	1.92 (0.40)	0.50 (0.05)
	7 moder	16.7 (3.6)	0.70 (0.16)	24.5 (0.92)	3.6 (0.08)	0.53 (0.09)	4.24 (1.34)	1.42 (0.34)
	8 mull-moder	5.0 (1.05)	0.33 (0.06)	14.5 (0.45)	4.4 (0.07)	0.30 (0.07)	1.56 (0.15)	0.47 (0.10)
	9 mull-moder	16.4 (1.57)	0.82 (0.06)	20 (0.77)	4.3 (0.05)	0.58 (0.05)	7.47 (1.09)	1.69 (0.34)
Monts de Lacaune								
Douglas fir stand	1 mull-moder	9.6 (0.75)	0.68 (0.02)	14 (0.68)	3.9 (0.05)	0.33 (0.04)	2.27 (0.49)	0.58 (0.08)
	2 moder	14.2 (0.92)	0.70 (0.04)	20.5 (0.54)	3.6 (0.02)	0.28 (0.03)	1.42 (0.18)	0.63 (0.07)
	3 mull-moder	8.3 (0.64)	0.47 (0.06)	19 (1.30)	3.9 (0.02)	0.18 (0.01)	1.53 (0.25)	0.51 (0.04)
	4 mull-moder	10.1 (0.72)	0.63 (0.04)	16 (0.42)	3.8 (0.03)	0.16 (0.02)	1.69 (0.24)	0.57 (0.05)
	5 moder	12.6 (1.05)	0.89 (0.04)	14 (0.58)	3.8 (0.05)	0.33 (0.03)	1.50 (0.16)	0.79 (0.07)
	6 moder	15.8 (2.09)	0.89 (0.08)	17.5 (0.67)	3.6 (0.04)	0.41 (0.05)	1.37 (0.33)	1.76 (0.11)
Spruce plantation	1 mull-moder	23.7 (1.04)	1.08 (0.04)	22 (0.60)	3.5 (0.03)	0.57 (0.06)	3.29 (1.02)	1.44 (0.17)
	2 mull-moder	9.8 (0.74)	0.59 (0.04)	16.5 (0.43)	3.9 (0.02)	0.16 (0.02)	0.70 (0.07)	0.40 (0.03)
Beech forest	1 mull-moder	10.8 (0.55)	0.60 (0.03)	18 (0.56)	4.1 (0.05)	0.42 (0.02)	2.80 (0.42)	0.83 (0.09)
	2 mull-moder	13.9 (1.14)	0.86 (0.06)	16 (0.42)	3.6 (0.02)	0.55 (0.03)	2.29 (0.30)	0.86 (0.09)
Silver fir stand	1 mull-moder	15.2 (1.10)	0.92 (0.04)	16.5 (0.50)	3.6 (0.04)	0.38 (0.02)	1.28 (0.25)	0.60 (0.05)
	2 moder	9.3 (0.81)	0.57 (0.03)	16 (1.04)	3.9 (0.03)	0.11 (0.01)	0.61 (0.13)	0.31 (0.05)

Table 3 Classes of equal sizes of the soil chemical parameters

Soil parameters	Class a	Class b	Class c
C (%)	2.4–8.4	8.4–12.2	12.2–30.7
Ntot (%)	0.17–0.46	0.46–0.70	0.70–1.34
C:N	8–16	16–19.5	19.5–35
pH	3.3–3.8	3.8–4.0	4.0–5.3
K (mEq.100 g^{-1})	0.03–0.19	0.19–0.39	0.39–2.2
Ca (mEq.100 g^{-1})	0.19–1.11	1.11–1.98	1.98–18.98
Mg (mEq.100 g^{-1})	0.12–0.44	0.44–0.81	0.81–2.88

common significant samples and the Collembola and chemical characteristics of these samples could then be linked (Fig. 3). Eleven samples (moder), distributed in quadrants III and IV of the co-inertia analysis, were characterised by the chemical parameters correlated to the first axis of the MCA on the negative side: pH <3.8, $12.6< C\% <28.8$, $0.7< N_{tot}\% <1.3$, $0.4< K^+$ (meq.100 g^{-1}) <1, $2.0< Ca^{2+} <10.6$ and $0.8< Mg^{2+} <2.4$. The Collembola linked to these samples were *Ceratophysella luteospina*, *F. decopsis*, *F. manolachei*, *I. minor*, *Pseudisotoma monochaeta*. Eighteen samples (mull-moder), situated in quadrants I and II, were characterised by C% <8.4, $N_{tot}\%$ <0.4, K <0.18 meq.100 g^{-1} and Mg <0.5 meq.100 g^{-1}. The Collembola found under these conditions were *Cryptopygus debilis*, *F. quadrioculata*, *I.* cf. *paraminor*, *Mesaphorura macrochaeta*, and *Oncopodura crassicornis*.

Discussion

The occurrence of Collembola has often been related to humus forms (Hågvar 1983; Ponge et al. 1986; Schaefer and Schauermann 1990; Chagnon et al. 2000a) which were well differentiated into mull, moder or mor according principally to the pH. In the present study, as expected from the nature of the parent rock (mainly granite or gneiss), the pH of all samples was very low (pH <5.3). The general acidity of the soils analysed led to a low differentiation of humus type, most being moder forms and others being transition "mull-moder" humus rather than real mull humus forms. In spite of the small differences, the COA (Fig. 1) showed a group of Collembola (*Ceratophysella luteospina*, *Folsomia decopsis*, *Folsomia manolachei*, *Friesea mirabilis*, *Pseudisotoma monochaeta*, *Pseudosinella alba*) related to moder soils. The other collembolan species (*Cryptopygus debilis*, *Folsomia quadrioculata*, *Isotomiella* cf. *paraminor*,

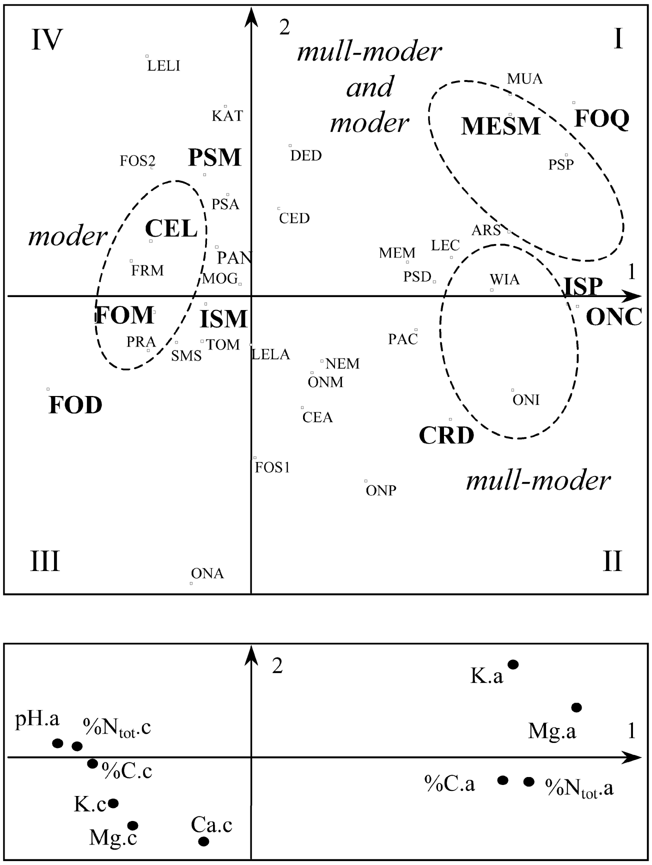

Fig. 3 Co-inertia analysis of collembolan species with regard to classes of chemical parameters (see Table 1 for the Collembola codes used). Parameters (●) and Collembola (in *bold*) linked to the first axis

Mesaphorura macrochaeta, *Oncopodura crassicornis*), playing a part in the COA, characterised mull-moder or moder soils indifferently. This relationship with humus types was still valid in the co-inertia analysis (Fig. 3). Species associated with moder humus can be characterised as species that could live in very poor conditions. Indeed, high C and N_{tot} contents suggested a low decomposition of the organic matter and pH <4 was a threshold below which nutrient deficiency was generally observed. The position of species linked to mull-moder humus forms was attributed to a faster turn-over of the organic matter (weak C and N_{tot} content).

Soil pH has been found to be strongly associated with soil arthropod distribution (Schaefer and Schauermann 1990; Van Straalen and Verhoef 1997; Chagnon et al. 2001; Loranger et al. 2001) which led to a number of collembolan species being classified as acid-tolerant or acid-intolerant. Ponge (2000) defined pH 5 as a threshold value separating two groups of soil-dwelling species according to their response to acidic conditions. In spite of the acidity of the soils analysed in the present study, some species like *Heteromurus nitidus* (1), *Mesaphorura hylophila* (5), *Monobella grassei* (8), *Onychiurus pseudogranulosus* (14) and *Pseudosinella alba* (635) were present even though they had previously been classified as acid-intolerant species (Ponge 2000). Nevertheless, the low numbers of *Heteromurus nitidus*, *Mesaphorura hylophila*, *Monobella grassei* and *Onychiurus pseudogranulosus*, imply that care must be taken in any interpretation because of a great uncertainty about their association with a specific factor. Moreover, the low abundance of these species could be explained by the presence of acidophilic species which were favoured by their ability to compete in low-pH soil (Hågvar 1990). However, *Pseudosinella alba* (present in the two study areas) was one of the most frequent species (about 5% of the total abundance) and was found in many soil samples with pH ranging from 3.5 to 5 and was linked in the COA to the moder humus forms. With these new data, *P. alba* seems rather to be a pH-indifferent species than acid-intolerant.

Soil acidity also masked the influence of the vegetation on humus characteristics. The difference in concentration of base cations released to the soil (Augusto and Ranger 2001) between deciduous trees (e.g. beech) and coniferous trees (e.g. spruce or Douglas fir) was not conclusive in our study. Moreover, Collembola were not distributed according to the vegetation cover (beech, spruce, Douglas fir) confirming Ponge's results (1993) which showed that Collembola were not directly influenced by vegetation but rather by soil chemistry. This hypothesis was especially confirmed for Collembola living in the deepest humus horizons (Chagnon et al. 2000b).

Co-inertia analysis showed relationships between soil parameters and ten collembolan species well represented in the A horizon. These species, belonging to four different families, Isotomidae, Hypogastruridae, Onychiuridae and Oncopoduridae, underline the striking variability in the chemical preferences of Collembola (Van Straalen and Verhoef 1997; Chagnon et al. 2000b). It is also interesting to note that species from the same family and even the same genus showed different relationships to soil chemistry. Hågvar and Abrahamsen (1984) observed various behaviour patterns in *Mesaphorura* species according to soil fertility levels. In the present study, the family concerned was Isotomidae in which the genera *Folsomia* and *Isotomiella* contained species linked to opposing chemical parameters.

Our results showed relationships between Collembola and exchangeable cations (K, Ca, Mg) as already underlined by Hågvar and Abrahamsen (1984) and Chagnon et al. (2000b, 2001). Nevertheless, the direct action of these soil parameters on specific species is difficult to show because ecological information about this relationship is still lacking. In addition, the association of collembolan species with soil chemical conditions could also be explained by the indirect action of the microflora or the competition between different collembolan species for limited resources (Hågvar and Abrahamsen 1984). The relationship between Collembola and exchangeable cations was particularly important for the study sites in which the parent material was poor in bases, soil exchangeable cation resources depending principally on the microarthropod activity in the decomposition of the organic matter.

Endemic species were of fundamental importance in the characterisation of communities (Benito and Sanchez 2000) and they are well known to be more vulnerable to disturbance (Deharveng 1996). Their presence, suggesting a particular biotope, constitutes a priority for the conservation of the biological richness of an area. In our study, two endemic species (*Cryptopygus debilis*, *Isotomiella* cf. *paraminor*) were linked to soil parameters characterising humus tending to the mull humus form. Too little information is available on endemic species to conclude as to any species-specific relationships to certain chemical factors. Geographical location is also a very important factor for these species which are limited to restricted areas suggesting well-defined ecological preferences.

The results of this study confirm that even in fairly similar conditions Collembola remain good indicators of changes in humus forms. According to the humus types, Collembola were then linked to pH, nutrient content or organic matter, soil chemical parameters that characterise humus type.

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