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Factors influencing soil macrofaunal communities in post-pastoral successions of western France

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Abstract

The soil macrofaunal communities (Lumbricidae, Formicidae, Coleoptera, Chilopoda, Diplopoda, Isopoda, Arachnida, Gastropoda) were studied in six plots representing different stages in a theoretical post-pastoral succession on chalk grassland. Macrofaunal biomass was high in all the plots (70.2–140.3 g m^{-2}). The macroinvertebrate communities along successional gradients respond to two major environmental factors: the structure of the vegetation, which determines the diversity of microhabitats and life conditions for macroinvertebrates; and the quality of above-ground litter production, which depends on the nature of vegetation and the presence of domestic herbivores. © 1998 Elsevier Science B.V.

Keywords: Soil macrofauna; Diversity; Chalk grasslands; Secondary successions; Post-pastoral dynamics; France

1. Introduction

Soil macroorganisms (i.e. living roots and macroinvertebrates) play a key role in the soil system in that they significantly regulate soil structure and nutrient cycling (Lavelle et al., 1994). In calcareous ecosystems, macroinvertebrates actively help to maintain a highly active mull by improving microbial activity (Scheu, 1990) and litter fragmentation and burial (van der Drift, 1963; Hirschenberger and Bauer, 1994a, b). Some taxonomic groups, such as earthworms, also affect the vegetation pattern by influencing the composition of soil seed banks (Thompson et al., 1994; Willems and Huijsmans, 1994).

For centuries, European chalk grasslands were traditionally used for sheep grazing. Since the abandonment of this practice in the 1950s, natural successional processes have led to woodland extension and/or species-poor coarse grasslands (Smith, 1980). In Upper Normandy, a study was carried out to identify the factors influencing biological diversity in these ecosystems and their response to different kinds of disturbances. As part of this study, we conducted a survey aimed at assessing changes in density, biomass and community structure of soil macrofauna during post-pastoral succession and identifying the main factors responsible for these changes. Soil macroinvertebrate communities were monitored in different stands of a potential succession from a permanent pasture to woody formations on chalky substrate.

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2. Materials and methods

2.1. The sites

We sampled the soil fauna on calcareous slopes of the Seine Valley in Upper Normandy, north-west France. Mean annual precipitation and temperature were, respectively, 804 mm and 9.9°C. Soils were calcareous rendzina with neutral pH, aggregated structure and highly active humus.

Successions in chalk grasslands are complex and can be described as multi-directional processes influenced by many biotic and abiotic factors (Dutoit and Alard, 1996). For this study, six plots were selected to represent different stages of typical secondary successions occurring in this ecosystem after grazing abandonment. Obviously, none of these particular sites had undergone, or is likely to undergo all the described stages. The rationale for this choice was discussed in Dutoit and Alard (1995) in the light of old aerial photographs. It must be stated that some stages (e.g. pine wood) are alternative successions, and others, such as the scrub community are not absolutely necessary steps for the development of the next further stages. Thus, the set of plots cannot be considered as a real succession but as representing an approximate (potential) successional sequence that emphasizes mainly the vertical changes that occur in the vegetation. While this potential succession does not represent a real time series (i.e. chronosequence), it has been designed to reconstruct a tangible successional gradient (i.e. afforestation process).

Plot 1 was an open chalk grassland (pasture) of small perennial species (*Festuca lemanii*, *Carex flaca* and *Lotus corniculatus*) that was permanently grazed by sheep and horses (1.5 Livestock Unit. ha^{-1}).

Plot 2 was a 2 year-old fallow, containing a patchwork of perennial herbaceous plants (*Sesleria albicans* and *Brachypodium pinnatum*) and bare ground.

Plot 3 was a 44 year-old fallow, where the vegetation comprised tussock species (*B. pinnatum* and *S. albicans*) and tall grass, with encroachment from some scrub species (e.g. *Rosa canina*, *Cornus sanguinea* and *Viburnum lantana*).

Plot 4 was a 40 year-old homogeneous scrub vegetation, dominated by *Crataegus monogyna* and *C. sanguinea*.

Plot 5 was a 40 year-old maple wood, dominated by *Acer pseudo-platanus* and *Fraximus exelsior*.

Plot 6 was a 48 year-old pine wood, exclusively composed of *Pinus sylvestris*.

2.2. Sampling and data analysis

Sampling was carried out between March 1994 and January 1995. In every two months, five samples, each 25×25×10 cm, were taken at regular 5 m intervals along a line whose origin was chosen at random and whose direction was perpendicular to the slope. Extraction methodology was a combination of hand sorting (Anderson and Ingram, 1993) and formalin expulsion (Baker and Lee, 1993).

Invertebrates were generally identified to the family level and further grouped into 13 larger units, i.e. lumbricidae earthworms (anecic, epigeic and endogeic), Formicidae (anecic and epigeic), Coleoptera (epigeic and endogeic), Chilopoda, Diplopoda, Isopoda, Arachnida, Gastropoda and others. Biomass (fresh weight m^{-2}) and density (individuals m^{-2}) were recorded for these major groups. Taxonomic richness was estimated as the number of families found in one plot, and biological diversity was calculated from density, using the Shannon index of diversity.

Two basic multivariate analyses were performed using Mac Mul and Graph Mu software for Macintosh (Thioulouse, 1990): principal component analysis (PCA) with environmental variables (Fig. 1) to identify the major environmental factors influencing the communities, and correspondence analysis (CA) based on the mean densities and biomass of the 13 taxonomic units (Fig. 2, including only those groups showing significant differences between plots) to describe the main gradients in soil invertebrate communities.

3. Results

Biomass and density were highest in the pasture and 2-year fallow plots; density was lowest in the 44 year fallow while biomass was lowest in the pine wood (Table 1). Earthworms were the major component of biomass in all the plots, their contribution to biomass being greatest in pasture (96%) and least under pine

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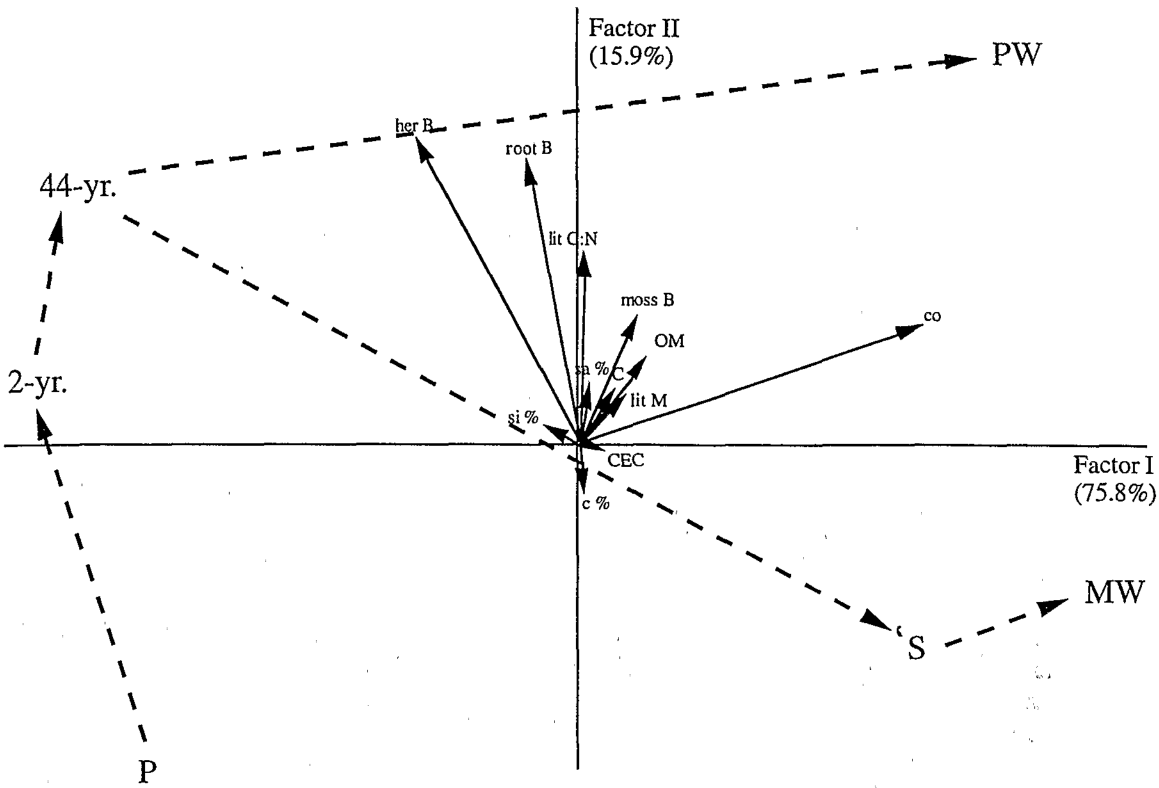

Fig. 1. Ordination of the plots and variables in relation to the first two factors extracted from the PCA. P=pasture; 2 yr.=2 year-old fallow; 44 yr.=44 year-old fallow; S=scrub vegetation; MW=maple wood; PW=pine wood; B=biomass; her=herbaceous; co=tree cover; lit M=litter mass; lit C:N=litter C:N ratio; OM=soil organic matter content; C=soil organic C content; CEC=cation exchange capacity; c=clay; si=silt; sa=sand; dotted lines represent the possible path in the potential series.

(73%). The highest taxonomic richness (N) was found in the 2 year fallow and the maple wood and the lowest in the pine wood. Diversity (H′) and evenness (E) were maximal in the wooded plots (Table 1).

Multivariate analysis revealed the presence of two main factors accounting for 91.7% (PCA, Fig. 1) and 80.7% (CA, Fig. 2) of the total variance observed. The first factor of the PCA explains 75.8% of the environmental variance and separates plots with a high herbaceous biomass from plots with a dense tree cover. The second factor of the PCA accounts for 15.9% of the environmental variance. It separates pine wood and fallows, with a high litter C:N ratio and a high herbaceous and root biomass, from scrub, maple wood and pasture. The first factor of the CA accounts for 46.7% of the variance in the community structure and separates herbaceous plots, where communities were dominated by endogeic populations (78% of total biomass), from woody plots with high populations of epigeic invertebrates (25–28% of total biomass). The second factor of the CA explains 34.0% of the community variance and ordinates the plots in a similar way as does the PCA for environmental variables. It mainly separates the pine wood, where epigeic groups were the most important, from pasture and deciduous plots, where communities were more balanced between endogeics and epigeics.

The plot ordination of these two analyses are similar, allowing us to interpret factors as environmental gradients in the PCA and to assess the effects of these gradients on soil macrofaunal communities in the CA. The first factor is assumed to represent the effect of vegetation structure, which determines the diversity of microhabitats and life conditions for macroinverte-

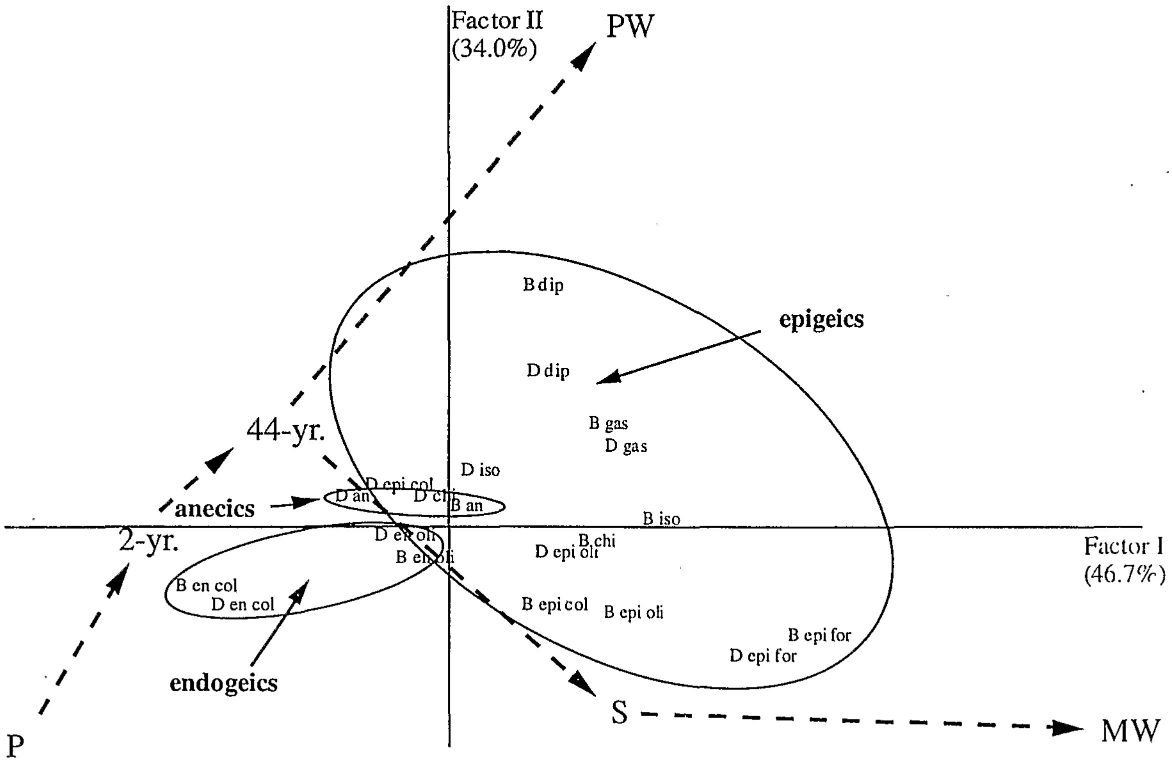

Fig. 2. Ordination of the plots and taxonomic units in relation to the first two factors extracted from the CA. D=density; B=biomass; an=anecic; en=endogeic; epi=epigeic; oli=Oligochaeta; col=Coleoptera; for=Formicidae; chi=Chilopoda; dip=Diplopoda; iso=Isopoda; gas=Gasteropoda; plot abbreviations as in Fig. 1.

brates. The second factor is defined as the effect of the quality of the above-ground litter production, which depends on the nature of the vegetation and the presence of domestic herbivores.

4. Discussion

Macrofaunal biomass was very high (70.2–140.3 g m^{-2}) as compared with other data from beech wood on limestone (12.7–25.5 g m^{-2}, Schaefer and Schauermann, 1990; David et al., 1993). The high biomass can be related to the presence of suitable soil conditions (i.e. neutral pH, high Ca content and high organic matter content) that permit the presence of significant earthworm populations.

Spatial variability of the plant cover is known to increase the diversity of other functional groups (Babel et al., 1992), and the changes in macrofaunal communities during succession can be related mainly to modifications in the structure of the habitat. Thus, the high density of Formicidae in the first two stages of post-pastoral succession may be explained by the preferential establishment of nests of some species in sparsely covered and bare ground (Pontin, 1963). In the 2-year fallow, the development of a diversified vegetation cover, the formation of a litter layer and the subsequent modification of the soil microclimate result in an increase in biomass, density, taxonomic richness and diversity (Scheu, 1992). The low biomass, density and taxonomic richness in the 44-year fallow may result from the dominance of an homogeneous herbaceous cover with low primary production (Scheu, 1992). In the scrub and the woods, the presence of a deep litter layer creates a new habitat and enhances taxonomic diversity and the development of epigeic groups with high density and diversity (Lee, 1985).

Table 1

Macrofaunal density (individuals m^{-2}), biomass (g fresh weight m^{-2}), taxonomic richness (N), biological diversity (H′, Shannon index) and evenness (E) of macrofaunal communities in post-pastoral successions. Standard errors in bracket

Soil macrofauna	Grasslands						Scrub		Woods			
	Pasture		2 year-old fallow		44 year-old fallow				Maple		Pine	
	Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass
Anecic fauna												
Lumbricidae	16	15.4	50	38.6	27	38.5	22	34.4	12	14.6	21	22.3
	(4)	(4.1)	(8)	(7.6)	(4)	(6.8)	(4)	(9.5)	(3)	(5.7)	(4)	(4.5)
Anecic	883	1.2	689	1.0	432	0.3	327	0.7	2	0.0	78	0.3
formicidae	(371)	(0.5)	(412)	(0.8)	(134)	(0.1)	(106)	(0.2)	(1)	(0.0)	(69)	(0.2)
Endogeic fauna												
Lumbricidae	223	74.9	361	90.7	187	65.4	314	45.2	422	46.6	138	28.0
	(26)	(11.2)	(28)	(12.0)	(17)	(8.7)	(27)	(4.4)	(28)	(3.8)	(13)	(3.6)
Coleoptera	62	4.0	37	5.9	17	0.7	15	0.1	15	0.4	3	0.0
	(13)	(0.8)	(6)	(1.2)	(10)	(0.5)	(11)	(0.1)	(3)	(0.1)	(1)	(0.0)
Epigeic fauna												
Lumbricidae	16	2.6	9	0.9	12	1.0	37	1.9	88	6.7	18	1.0
	(9)	(1.8)	(3)	(0.3)	(4)	(0.4)	(18)	(1.0)	(10)	(1.3)	(5)	(0.3)
Epigeic	0	0.0	0	0.0	0	0.0	111	0.1	337	0.3	0	0.0
formicidae	(0)	(0.0)	(0)	(0.0)	(0)	(0.0)	(41)	(0.0)	(164)	(0.1)	(0)	(0.0)
Coleoptera	16	0.3	19	0.3	6	0.0	6	0.1	15	18	0.5	0.1
	(4)	(0.1)	(4)	(0.1)	(3)	(0.0)	(2)	(0.1)	(3)	(0.2)	(3)	(0.0)
Chilopoda	16	0.1	68	0.7	58	0.6	61	0.3	63	0.1	39	0.5
	(5)	(0.0)	(10)	(0.2)	(9)	(0.1)	(9)	(0.1)	(8)	(0.2)	(8)	(0.1)
Diplopoda	0	0.0	2	0.0	1	0.2	3	0.0	3	0.0	9	1.4
	(0)	(0.0)	(1)	(0.0)	(1)	(0.2)	(2)	(0.0)	(1)	(0.0)	(2)	(0.4)
Isopoda	1	0.0	81	0.8	31	0.3	21	0.2	85	1.6	37	0.7
	(1)	(0.0)	(21)	(0.2)	(7)	(0.1)	(5)	(0.0)	(18)	0.4	(7)	(0.4)
Araneida	11	0.1	12	0.1	13	0.1	12	0.1	6	0.0	7	0.1
	(2)	(0.0)	(2)	(0.0)	(3)	(0.0)	(3)	(0.1)	(2)	(0.0)	(2)	(0.1)
Gastropoda	3	1.0	5	0.7	7	6.7	6	1.1	78	9.5	37	14.8
	(1)	(0.5)	(2)	(0.3)	(2)	(3.4)	(2)	(0.6)	(14)	(2.1)	(6)	(3.9)
Other	12	0.9	32	0.6	48	0.4	33	0.7	32	0.6	16	0.9
invertebrates	(3)	(0.3)	(7)	(0.2)	(29)	(0.2)	(10)	(0.2)	(10)	(0.1)	(8)	(0.5)
Total	*1259*	*100.5*	*1365*	*140.3*	*839*	*114.1*	*968*	*84.9*	*1159*	*81.7*	*421*	*70.2*
	(375)	*(14.0)*	*(408)*	*(17.2)*	*(150)*	*(12.5)*	*(154)*	*(118)*	*(178)*	*(7.7)*	*(24)*	*(8.2)*
N	33		40		36		32		37		25	
H′	1.52		2.11		2.21		2.01		2.42		2.78	
E	0.29		0.38		0.41		0.39		0.44		0.55	

The abundance and quality of the organic supply greatly contribute to the modifications observed in macrofaunal populations. The high quality of the litter (i.e. animal dung or leaf litter) in the pasture and the maple wood (C:N ratio =29 and 22, respectively) maintains significant macrofaunal communities (Boyd, 1960; Hutchinson and King, 1980). Conversely, inputs of low quality litter in the 44-year fallow and the pine wood (C:N =36 and 57, respectively) are linked with low biomass, density and taxonomic richness (Nordström and Rundgren, 1973; Cuendet, 1984).

As far as our samples are concerned, no important relationships were found between soil fauna and physical or chemical soil properties, which were consistently suitable for macrofauna in all sites. However, soil parameters are expected to influence macroinvertebrate populations in the older successional stages, especially soil acidification in the maturing pine wood.

5. Conclusions

During secondary succession, macroinvertebrate communities first respond to a structural gradient that reflects the changes in the vegetation structure and resulting modification in microhabitat diversity and life conditions (i.e. diversification of the herbaceous stratum, appearance of a thin litter and/or moss layer). This agrees with Scheu (1992), who concluded that individual earthworm species react only to the availability of preferred microhabitats in the different successional stages. Babel et al. (1992) also demonstrated the great influence of spatial variability of plant cover on the diversity of other functional groups.

The quantity and quality of the litter returned to the soil result directly from the structure and nature of the vegetation. They may therefore be factors of fundamental importance for soil fauna in successional situations (Anderson, 1977). More than a food resource, the litter layer provides suitable habitats for most invertebrate species. Modifications in the form and quality of this litter along successional gradients, therefore, result in a drastic changes in macrofaunal populations.

Further research should focus on the spatial patterns of distribution versus temporal changes of soil macrofaunal communities. Particular emphasis should be given to the contact between several vegetation stages within a successional mosaic. This should provide information on colonisation processes by soil invertebrates in shifting vegetation. The question of whether soil fauna respond only to vegetation succession or play a stimulating, even active, role in successional processes is central to this research. Special attention should also be paid to the dynamics of microhabitat diversity along successional gradients and its relation to the diversity of macroinvertebrate populations.

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