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Population dynamics and vertical distribution of enchytraeids and tardigrades in response to deforestation

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Abstract

In order to increase our present knowledge of the potential impacts of deforestation on the soil ecosystem, we investigated the responses of enchytraeid and tardigrade populations to tree harvesting. The study was conducted in an area of ca. 10 ha located at an altitude of approximately 450 m in the surroundings of the University campus (Vigo, Pontevedra, Spain). Pine forest (*Pinus pinaster* Aiton), with an average density of 400 trees/ha ranging between 10 and 20 years of age, and some young oaks (*Quercus robur* L.) were covering the area. At the end of the summer 1995, approximately 50% of the area was harvested. Soil and animal samples were taken from May 1996 to April 1997 at monthly intervals in both forested and deforested areas. Removal of the trees resulted in a significant effect on enchytraeid population numbers and their response was species-dependent in terms of changes in both population numbers and vertical distribution. Higher mortality rates of enchytraeids were recorded in the absence of trees. August seemed to have been critical for survival of all enchytraeid species as no individuals were found in that month and only a few recovered in the following month. Only *Cognettia sphagnetorum* showed vertical migration in order to avoid adverse conditions. Tardigrades were more abundant in the deforested areas; their ability to enter in a resistant stage could have enabled them to overcome adverse environmental conditions. It is concluded that harvesting of the trees has changed the soil environment and that differences in moisture and temperature conditions are not sufficient to explain the observed differences. The forest soils contained more organic matter than those in the deforested area and therefore differences in the amount and/or quality of the organic matter could be one of the possible explanations for the observed changes in enchytraeid abundance when the forest is removed.

Keywords: Soil fauna; Deforestation; Seasonal dynamics; Vertical distribution; Enchytraeids; Tardigrades

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1. Introduction

Intensification of agricultural practices is leading to an increased rate of deforestation with large areas being converted to arable crops in order to feed the expanding human population (IGBP, 1997). This diminution of the tree cover together with the removal of the felling residues such as twigs and branches, has important effects on the soil ecosystems such as erosion, loss of soil fertility, alterations in the soil water regime, soil compaction and larger temperature fluctuations in the exposed areas.

It has been suggested that soil biodiversity will be greatly affected as a consequence of this landscape fragmentation (GCTE, 1996). In terms of nutrient cycling, any changes in the structure of the soil communities will have important impacts on ecosystem functioning (Swift and Anderson, 1993).

Enchytraeids are known to be abundant in coniferous mor soils and play an important role in nutrient cycling (Briones et al., 1998a,b; Cole et al., 2000; Koutika et al., 2001). Previous investigations have shown that enchytraeid abundance and biomass can increase after cutting mainly due to changes in the abiotic conditions and food supply as a result of the presence of felling residues (Huhta, 1976; Sundman et al., 1978; Lundkvist, 1983), but after a few years, numbers return to their original size. In contrast, long-term studies showed that these organisms are not usually affected by above-ground whole-tree harvesting and the negative effects are only detected at higher trophic levels (Bengtsson et al., 1998; Siira-Pietikainen et al., 2001).

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Within the abiotic factors, temperature and/or moisture content are the main controlling factors of enchytraeid population sizes (Abrahamsen, 1971; Abrahamsen and Thompson, 1979; McColl, 1984; Chalupský, 1994). Adverse conditions can be avoided by downward movements or by adopting resistant stages. Vertical migration seems to be the short-term strategy to overcome temporally adverse conditions (Huhta et al., 1967; Springett et al., 1970; Briones et al., 1997) for some species, whereas others are unable to move down (Briones et al., 1997) and mortality is the most likely outcome.

Little is known about how tardigrades respond to changes in vegetation cover. They are well represented in forest soils where they can reach similar densities to oribatid mites and collembola (Ito, 1999). They act as indirect regulators of nematode abundance (Hyvönen and Persson, 1996).

Tardigrade activity depends on the existence of a water film and fluctuations in temperature and moisture have been suggested as the most influential factors controlling population numbers at the microhabitat level (Kennedy, 1993). However, they can exhibit dormancy stages such as cryptobiosis (Keiling, 1959; Crowe, 1975) which seems to be a successful strategy for withstanding adverse environmental conditions over long periods of time. Other factors such as food availability (Hallas and Yeates, 1972; Nelson and Higgins, 1990), habitat preference (Ito, 1999), altitude (Guidetti et al., 1999; Ito, 1999) and biotic factors (Hyvönen and Persson, 1996; Sohlenius and Bostrom, 1999) have also been indicated as factors which explain differences in their abundance and species composition.

Changes in the composition of the soil community can be indicative of transformation of the ecosystem. For this reason, in this study, we investigate the responses of enchytraeids and tardigrades to deforestation in order to improve our understanding of the survival strategies adopted by these organisms in response to this perturbation. This will allow a better understanding of the potential impacts of deforestation on soil systems.

2. Materials and methods

2.1. Site description

The study was conducted in an area of ca. 10 ha located at an altitude of approximately 450 m in the surroundings of the University campus (Vigo, Pontevedra, Spain) (42° 10'N, 8° 40'W). Pine forest (*Pinus pinaster* Aiton), with an average density of 400 trees/ha ranging between 10 and 20 years of age (around 10–15 m in height), and some young oaks (*Quercus robur* L.) were covering the area. The understorey is dominated by *Pteridium aquilinum* (L.) (Kuhn.), *Rubus* sp. and *Ulex* sp. At the end of the summer 1995, approximately 50% of the area was harvested and *Ulex* sp. and *Erica* sp. are now dominant. Previous sampling prior to felling showed no significant differences in soil organic matter, nitrogen and phosphorous content between the forested and deforested plots (Covelo and Gallardo, 2002).

Table 1
Average values (±S.E.) of soil characteristics in the sampled areas and results from ANOVA (n.s. = $P > 0.05$)

	Forested	Deforested	*P*
Organic matter (%)	26.19 ± 0.55	23.30 ± 0.26	< 0.01
C/N	14.69 ± 0.94	16.43 ± 0.10	< 0.01
Moisture content (%)	35.07 ± 1.08	35.57 ± 1.22	n.s.
pH	4.38 ± 0.06	4.38 ± 0.08	n.s.

According to FAO classification, the soil is a humic cambisol (MOPT, 1992). Soil characteristics (organic matter content, C/N ratio, moisture content and pH) of the forested and deforested areas are shown in Table 1.

The locality is characterised by a humid oceanic climate (average annual temperature 15 °C, average annual rainfall 1500 mm) with mild temperatures in winter and summer. Fig. 1 shows the mean monthly temperature, rainfall and potential evapotranspiration values for the studied period (data supplied by the Territorial Meteorological Centre of La Coruña). It can be seen that the wet period in November, December and January coincides with the lowest temperatures and evapotranspiration rates.

2.2. Sampling

Samples were taken from May 1996 to April 1997 in monthly intervals in both forested and deforested areas. In order to obtain independent measures for statistical analysis purposes, different non-enclosed plots were sampled in the forested and deforested areas each month. Thus, on every sampling occasion, one forested plot (approximately 100 m^2) and one deforested plot were randomly selected on a land-owner basis and the similarity in soil and vegetation characteristics. In each plot, 15 undisturbed soil cores, with associated vegetation, were randomly taken by using 10.5 cm diam. × 25 cm deep PVC cylinders. The cores were sliced horizontally, in the field, into five 2 cm layers to a depth of 10 cm and two subsamples (20 cm^2 each) from each layer were taken, one for animal extractions and one

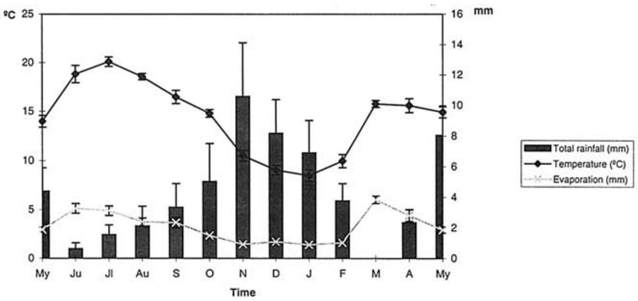


Fig. 1. Mean monthly temperature, rainfall inputs and potential evapotranspiration values at the studied site during the sampling period (data supplied by the Territorial Meteorological Centre of La Coruña).

for physical and chemical analyses. The faunal subsamples ($N = 15$ replicates × five depths × two treatments = 150) were placed separately in plastic bags, whereas the five depth subsamples for soil analyses were mixed resulting in one sample per core ($N = 15$ replicates × two treatments = 30).

A soil temperature probe (Crison T-637) was introduced into the first 10 cm on three different points to obtain three temperature values at each sampled treatment on every sampling occasion.

Samples were transported to the laboratory in a cool box. Invertebrates were extracted within 48 h using a modified wet funnel method (O'Connor, 1955), preserved in 70% alcohol and counted. Enchytraeids were identified to species or to genera and their degree of maturity (presence/absence of clitellum) recorded; only total numbers were recorded for tardigrades. The enchytraeid *Cognettia sphagnetorum* reproduces asexually by fragmentation and was classified as either a whole worm or as a regenerating fragment.

The soil samples were weighed and oven dried (60 °C) to constant weight for moisture content determination. A sieved (<2 mm) subsample of 2–4 g was burned in a muffle furnace (at 250 °C for 1 h and at 500 °C for 3 h) to obtain the organic matter content.

2.3. *Statistical analyses*

All data were log-transformed before statistical analyses. One-way ANOVA followed by the HSD Tukey test was used to compare mean abundance numbers per soil layer and treatment at each sampling date and to test for significant differences between treatments at each date. Values of physical and chemical factors were similarly analysed to detect significant differences between treatments on each sampling occasion.

One-way ANOVA was also used to compare the effects of tree harvesting on total numbers per core at each sampling date followed by two-way ANOVA to quantify interactions between treatment and depth at each date.

The influence of soil temperature, organic matter and moisture content on enchytraeid and tardigrade abundance was analysed by detrended canonical correspondence analysis (Ter Braak, 1986). This technique has been proposed as an alternative to other ordination techniques because it allows a direct relationship between the taxonomical groups and the environmental factors and it is not based on linear relationships. Since rare species can distort analysis, they were downweighted (i.e. their abundance was reduced in proportion to their frequency when the latter was lower than a fifth part of the frequency of the most abundant species). The program utilised was CANOCO (version 2.1), licence number 4112.

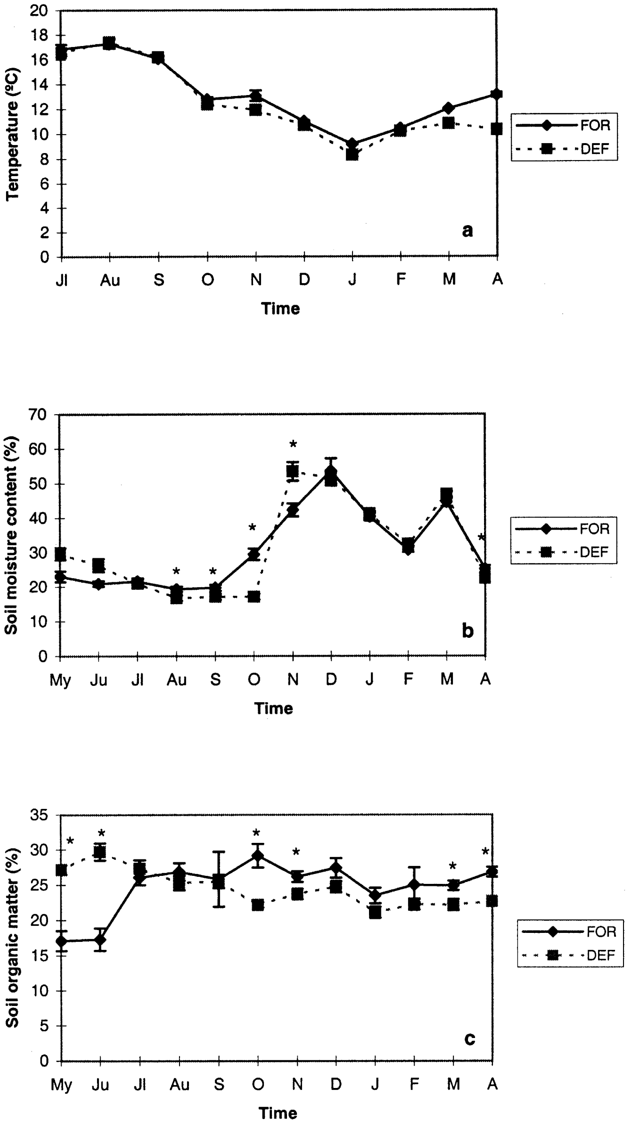


Fig. 2. Soil temperature (a), soil moisture (b) and soil organic matter (c) in the forested and deforested areas during the sampling period.

3. Results

3.1. *Abiotic factors*

The soil temperature in the forested areas was significantly higher ($P < 0.01$) than in the deforested ones, except in July–September when no significant differences were detected (Fig. 2a). In both treatments, maximum temperature values were reached in July–September, whereas the lowest values were recorded in January.

Both treatments showed similar trends in moisture content during the sampling period, with maximum values in the winter months (Fig. 2b). This wet period coincided with a decrease in soil temperatures. Significantly higher moisture contents were recorded in the forested areas than in the deforested ones during August–October ($P < 0.05$) with the exception of November when the deforested areas registered their maximum values ($P < 0.01$).

Initially, the forested areas contained less organic matter than the deforested ones ($P < 0.01$) (Fig. 2c), but in July, the values were very similar and from September onwards, the situation reversed with the forested areas showing higher organic matter content than the deforested ones ($P < 0.05$). This situation remained so until the end of the study period.

3.2. Soil fauna responses

Tardigrades and six species of enchytraeids were collected in the studied areas: *C. sphagnetorum* (Vejdovsky), *C. cognettii* (Issel), *Achaeta* sp. Vejdovsky, *Marionina* sp. Michaelsen and two unidentified species of *Fridericia* Michaelsen characterised on the basis of the number of setae in the bundles. *Fridericia* sp. 1 had four setae per bundle, whereas *Fridericia* sp. 2 had two setae per bundle. Soil fauna responses were reflected as changes in total abundances and vertical distribution.

3.3. Seasonal changes in total numbers

C. sphagnetorum was the dominant species in terms of abundance and it showed its highest population numbers in the presence of the trees. This species reproduces asexually by fragmentation which seems to be influenced by temperature (Standen, 1973). In this study, the maximum number of regenerating worms was recorded in May and July in both treatments (Fig. 3a), coincidental with the higher temperatures. More fragments were collected in the forested areas than in the deforested areas.

C. cognettii showed an irregular pattern in population numbers with abundances being highly variable during the whole experimental period (Table 2). On average, more individuals were recorded in the forested site with its maximum in December (more than 15 000 m^{-2}) when reproduction takes place (Fig. 3b).

Achaeta sp. and *Marionina* sp. also showed higher numbers in the forest soils during the whole experimental period with few exceptions in certain months (Table 2). In contrast to *C. sphagnetorum*, these species reproduce sexually and reproduction usually takes place in autumn and winter (Fig. 3c,d).

Fridericia sp. 1 was only collected in the forest soils with low densities throughout the whole experimental period and its reproduction peak seems to occur in December (Fig. 3e). *Fridericia* sp. 2 was significantly most abundant in the forested soil during the first 5 months of the study. In October, population densities increased at both treatment areas, and towards the end of the experimental period more individuals were collected from the deforested site, although differences were only significant in December and March (Table 2) which corresponds with the reproduction period of this species at this site (Fig. 3f).

Additionally, in the absence of trees, August seemed to have been critical for the survival of all enchytraeid species as no individuals were found in that month, and only two species (*C. sphagnetorum* and *Achaeta* sp.) appear to recover in the following month (Table 2). High mortality rates were also observed for *C. cognettii* and *Fridericia* sp. 2 in July.

Significantly higher numbers of tardigrades were collected in the deforested areas than in the forested ones during the whole experimental period with the exception of September and October when the situation was reversed (Table 2).

3.4. Seasonal changes in vertical distribution

C. sphagnetorum and *C. cognetti* were mainly concentrated in the upper 2 cm. In the forested areas, the upper 2 cm layer contained significantly higher numbers ($P < 0.05$) in nearly all sampling months (Fig. 4a,c). The peak of population occurred in winter in both treatments but this was more pronounced in the forested areas.

In May and June, coincidental with the higher temperatures, *C. sphagnetorum* showed vertical migration towards deeper layers. By August, a reduction in the population numbers was recorded in all five layers, suggesting that mortality was high and it was necessary to wait up to 2 months for the population to recover.

A similar downward migration at the beginning of the experimental period was observed in the deforested areas by both species, although it was more pronounced in the case of *C. sphagnetorum* (Fig. 4b,d).

Achaeta sp. and *Marionina* sp. showed an irregular temporal pattern in density and vertical distribution. In the forest soils, their populations were distributed equally through the soil profile and could be found at any depth at any time (Fig. 4e,g), although the majority of the individuals of *Achaeta* were concentrated in the upper 6 cm. In winter and in absence of trees, the numbers of *Achaeta* sp. increased in the deeper layers (Fig. 4f) and in May, February and March for *Marionina* (Fig. 4h).

In contrast to *Fridericia* sp. 1, which only was recorded in the forest and showed no clear pattern in its vertical distribution, populations of *Fridericia* sp. 2 were well distributed at the studied sites (Fig. 4i,j) and the upper 4 cm contained the majority of the individuals. A downward migration in October (forested) and December (deforested) affecting all deeper layers was also observed and coincided with the reproduction peaks.

Tardigrade populations were mainly concentrated in the upper 2 cm layer (Fig. 4k,l). In the forested areas, the numbers were low except in late autumn and early winter, whereas in the deforested ones, tardigrades showed an irregular pattern of abundance.

3.5. Synecological responses

Canonical correspondence analysis, applied to the mean monthly abundance of the six enchytraeid species and tardigrades and the studied soil factors, produced a first axis

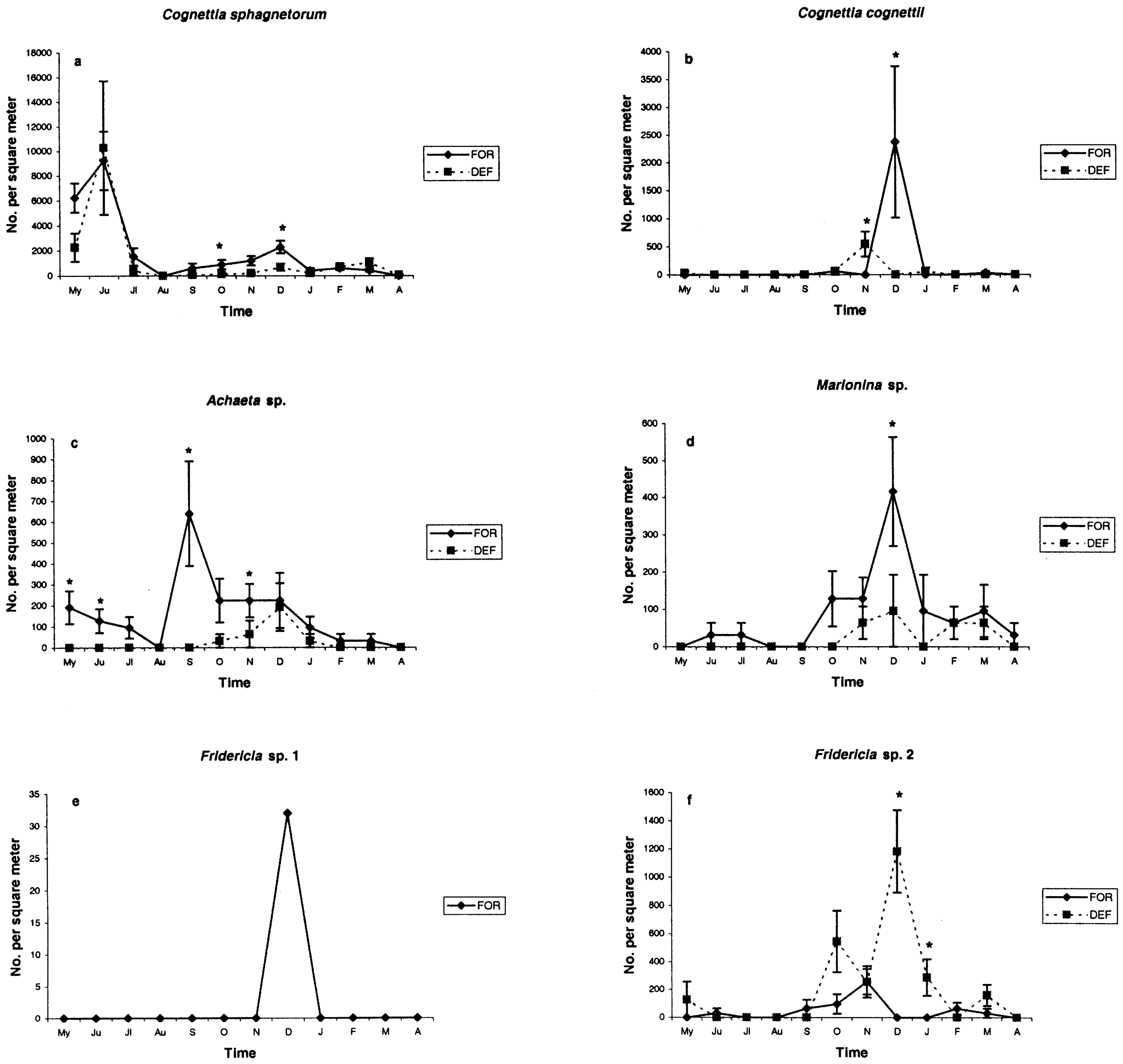


Fig. 3. Total numbers (No. m^{-2}) of regenerating worms of *Cognettia sphagnetorum* (a) and mature worms of *Cognettia cognettii* (b), *Achaeta* sp. (c), *Marionina* sp. (d) *Fridericia* sp. 1 (e) and *Fridericia* sp. 2 (f) during the sampling period in the sampled areas (error bars represent standard errors, * $P < 0.05$).

mainly explained by moisture and organic matter contents (Fig. 5 and Table 3). The inertia percentage for the first axis was 48%.

This axis separates, towards its positive side, one enchytraeid species (*Fridericia* sp. 2) and the tardigrade populations with tendencies to high moisture contents and warm temperatures. In contrast, *Fridericia* sp. 1 was associated with high organic matter content and low values of soil temperature and moisture content.

The remaining enchytraeid species appear close to the origin of the plot and therefore they prefer average values of the studied factors.

4. Discussion

Food availability in the field is an important regulating factor of the populations and numbers are mainly controlled by the amount of nutrients (Huhta, 1976; Sundman et al., 1978; Lundkvist, 1983). If food supply increases after cutting (as felling residues), the soil community would be clearly favoured. In our study, although lower inputs of organic matter were measured in the forested plots between May and June (probably as result of clearing practices at the time of the sampling), a general decrease in soil organic matter content was observed in the deforested plots over

Table 2
Total numbers (No. m^{-2}) of each taxa in each treatment on the different sampling dates, and significant results obtained from ANOVA (Tukey grouping)

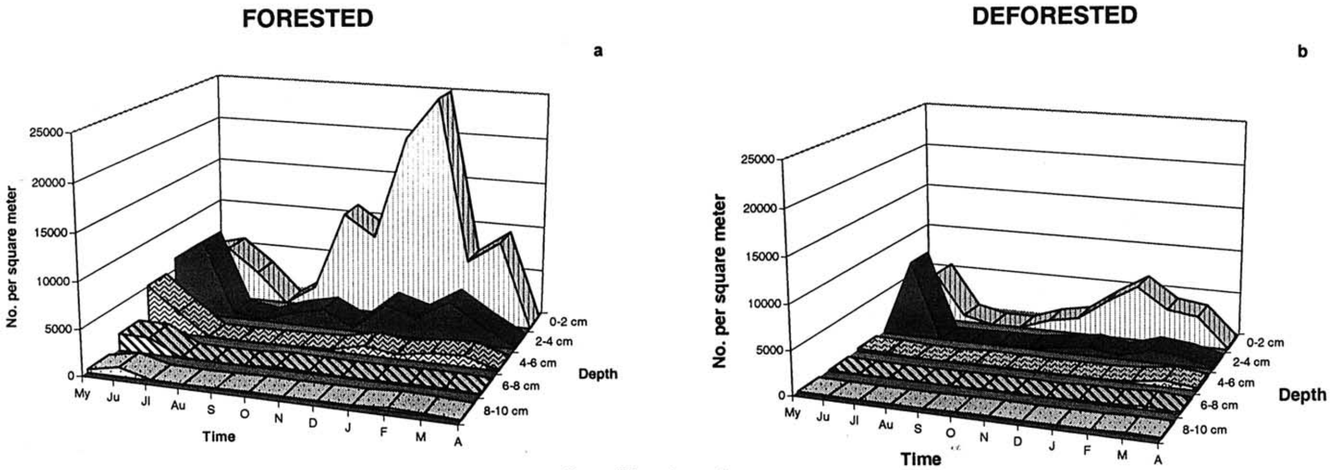
		My	Ju	Jl	A	S	O	N	D	J	F	M	A
C. sphagnetorum	Forested	18 659	19 683	4161	96	3617	13 666	9698	24 836	27 972	12 994	13 186	320
	Deforested	7297	14 722	800	0	256	1568	2624	5377	7009	5857	5857	992
	Treatment	$P < 0.01$	$P < 0.01$	$P < 0.01$	n.s.	n.s.	$P < 0.01$	n.s.	$P < 0.01$	$P < 0.01$	$P < 0.01$	n.s.	$p < 0.01$
	Depth	$P < 0.01$	$P < 0.01$	$P < 0.01$	n.s.	$P < 0.05$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.05$
	Treatment * Depth	n.s.	n.s.	$P < 0.01$	n.s.	n.s.	$P < 0.01$	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
C. cognettii	Forested	0	1472	192	0	64	4673	0	15 330	224	896	2176	0
	Deforested	2432	32	0	0	0	128	2208	608	352	3809	320	64
	Treatment	$P < 0.01$	$P < 0.01$	n.s.	n.s.	n.s.	$P < 0.05$	$P < 0.01$	$P < 0.05$	n.s.	$P < 0.01$	n.s.	n.s.
	Depth	n.s.	n.s.	n.s.	n.s.	n.s.	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	n.s.	n.s.
	Treatment * Depth	n.s.	n.s.	n.s.	n.s.	n.s.	$P < 0.05$	$P < 0.01$	n.s.	n.s.	$P < 0.05$	n.s.	n.s.
Achaeta sp.	Forested	1280	2240	3329	640	4481	6721	3873	3777	2208	832	4673	1440
	Deforested	448	2656	32	0	544	384	1504	1568	384	896	960	960
	Treatment	$P < 0.05$	n.s.	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	n.s.	$P < 0.01$	$P < 0.01$	n.s.	$P < 0.01$	n.s.
	Depth	n.s.	$P < 0.05$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	n.s.	$P < 0.01$	$P < 0.05$	$P < 0.01$	$P < 0.05$
	Treatment * Depth	$P < 0.05$	n.s.	$P < 0.01$	$P < 0.01$	n.s.	$P < 0.01$	$P < 0.05$	n.s.	n.s.	$P < 0.05$	$P < 0.01$	n.s.
Marionina sp.	Forested	288	5889	1888	32	544	2080	2048	3008	1536	448	1760	320
	Deforested	736	512	32	0	0	224	480	128	288	2048	1280	256
	Treatment	n.s.	$P < 0.05$	$P < 0.01$	n.s.	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	n.s.	n.s.	n.s.
	Depth	$P < 0.05$	$P < 0.05$	n.s.	n.s.	$P < 0.05$	n.s.	$P < 0.01$	n.s.	n.s.	$P < 0.05$	$P < 0.05$	n.s.
	Treatment * Depth	n.s.	n.s.	n.s.	n.s.	$P < 0.05$	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Fridericia sp. 2	Forested	1088	2944	480	0	1984	2496	1184	224	832	896	448	608
	Deforested	288	64	0	0	0	2688	1440	5345	1568	768	3681	448
	Treatment	$P < 0.01$	$P < 0.01$	$P < 0.01$	n.s.	$P < 0.01$	n.s.	n.s.	$P < 0.01$	n.s.	n.s.	$P < 0.01$	n.s.
	Depth	$P < 0.01$	$P < 0.05$	$P < 0.05$	n.s.	n.s.	$P < 0.01$	$P < 0.01$	$P < 0.05$	$P < 0.05$	$P < 0.01$	$P < 0.01$	n.s.
	Treatment * Depth	$P < 0.05$	n.s.	$P < 0.05$	n.s.	n.s	$P < 0.01$	n.s.	n.s.	$P < 0.05$	n.s.	$P < 0.01$	n.s.
Tardigrades	Forested	96	288	320	32	928	3841	4353	1120	416	0	96	96
	Deforested	10 370	736	3361	64	32	768	7169	3489	2016	640	2656	0
	Treatment	$P < 0.01$	n.s.	$P < 0.01$	n.s.	$P < 0.01$	$P < 0.05$	n.s.	n.s.	$P < 0.05$	$P < 0.01$	$P < 0.01$	n.s.
	Depth	$P < 0.01$	$P < 0.05$	$P < 0.01$	$P < 0.05$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	n.s.
	Treatment * Depth	$P < 0.01$	n.s.	$P < 0.01$	n.s.	$P < 0.01$	$P < 0.01$	n.s.	n.s.	$P < 0.05$	$P < 0.01$	$P < 0.01$	n.s.

time suggesting that leaching and mineralisation of carbon have been intense after the pine harvesting (Covelo and Gallardo, 2002).

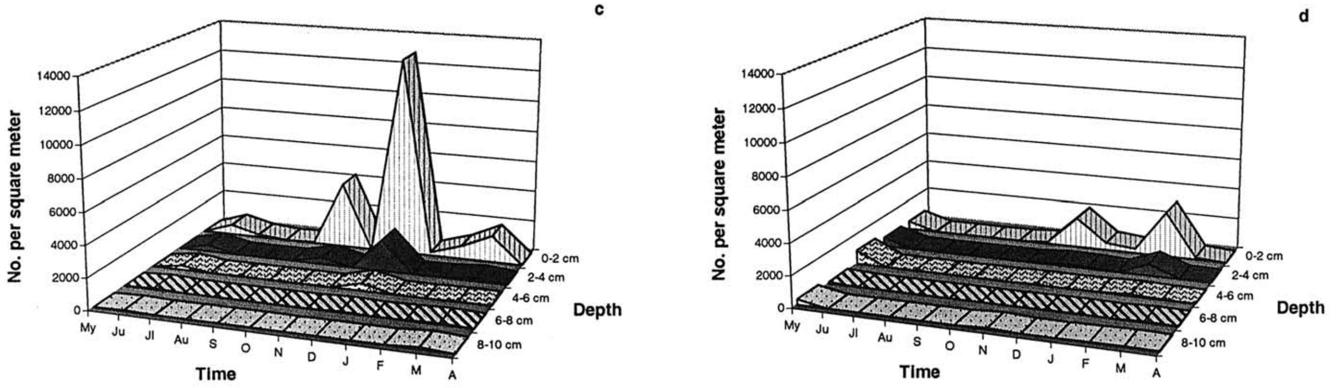
On the other hand, when the clear-cut slash is left on the coniferous forest floor after the felling, the abiotic conditions of the soil also improve leading to increased soil faunal populations (Huhta, 1976; Sohlenius, 1982; Lundkvist, 1983). However, in this study and for some soil organisms, the shelter provided by the undergrowth vegetation in the deforested areas was not sufficient to compensate the absence of the trees. This has led to changes in diversity, population numbers and vertical distribution of their populations. One of the most striking effects is that the responses cannot be generalised and are species-dependent. These responses are fully discussed below:

4.1. Enchytraeids

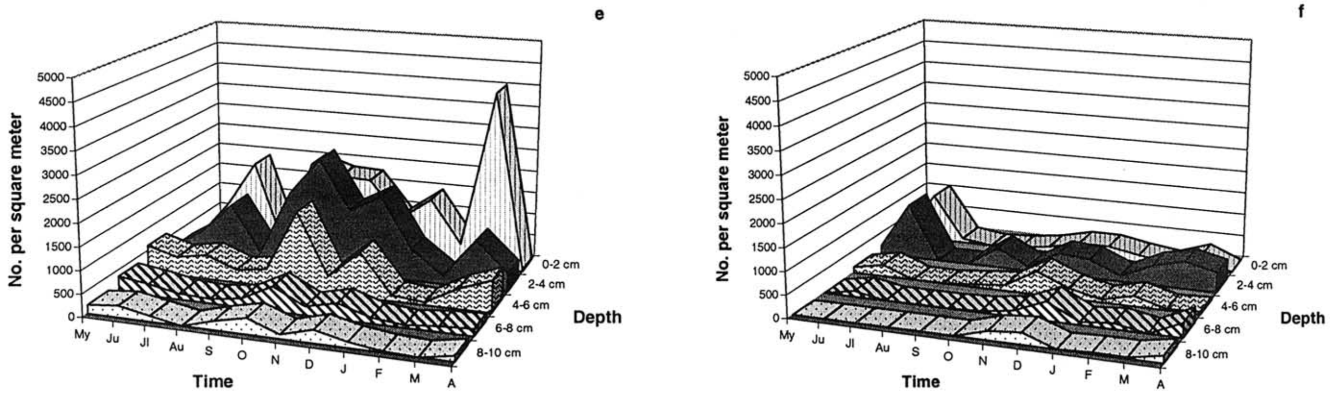
C. sphagnetorum is one of the dominant species in the latest stages of succession (forest) (Chalupský, 1994) and becomes the predominant species in coniferous forest soils where it usually makes up 98–100% of the whole population (Nurminen, 1967; Lundkvist, 1983). This species has been classified as a stress-tolerant species, inhabiting mull, mor and moder humus forms and with asexual reproduction (Graefe and Schmelz, 1999). An increase in the fragmentation rate is considered as a strategy to respond to changes in the environmental conditions (Römbke, 1992; Piliuk, 1997, 2000) and is positively related to temperature (Standen, 1973). Thus, in our study, warmer temperatures in May and June in the forested areas could have led to increased population numbers, which is coincidental with previous findings (Springett, 1967, 1970; Springett et al., 1970; Abrahamsen, 1971; Briones et al., 1997). In contrast, the minimum numbers of *C. sphagnetorum* were recorded in late summer when temperatures were still high but the moisture content was low which could have had a negative effect on survival (Springett, 1967; Springett et al., 1970; Abrahamsen, 1971; Sesma, 1994; Briones et al., 1997). However, Lundkvist (1983) recorded a positive response of



Cognettia sphagnetorum



Cognettia cognettii

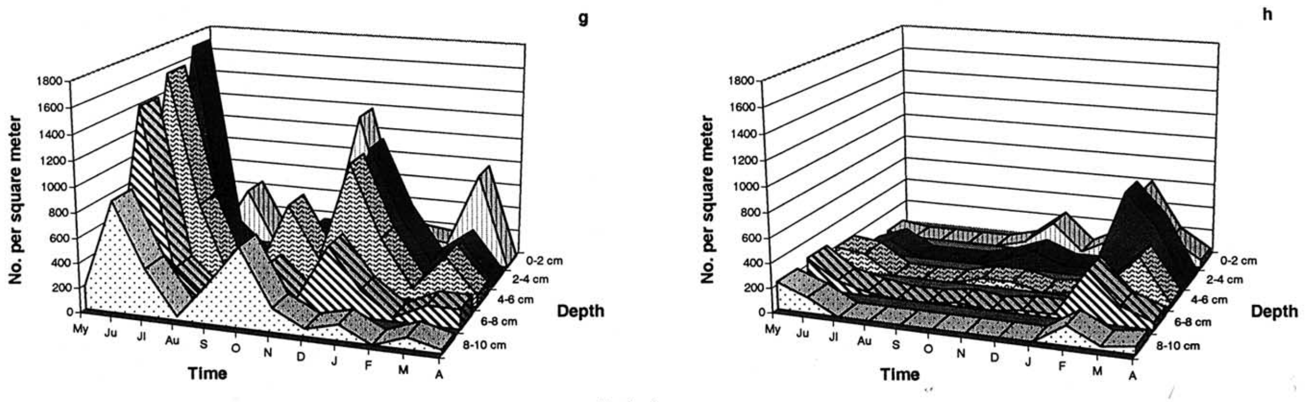


Achaeta sp.

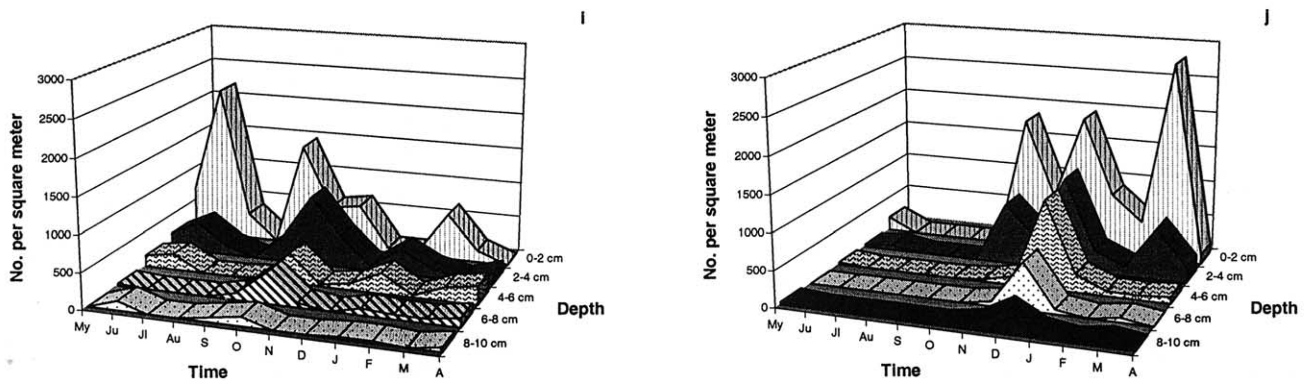
Fig. 4. Vertical distribution (No. m^{-2} in each soil layer) in the forested areas and deforested ones (respectively) of *Cognettia sphagnetorum* (a,b), *Cognettia cognettii* (c,d), *Achaeta* sp. (e,f).

this species to deforestation 2.5 years after felling and numbers increased in the plots covered with residue fellings. This is probably the result of changes in abiotic conditions and food availability which have caused a higher population density. As was stated before, in the present study, the presence of the trees resulted in higher inputs of organic matter to the soil which could explain the observed differences in population numbers.

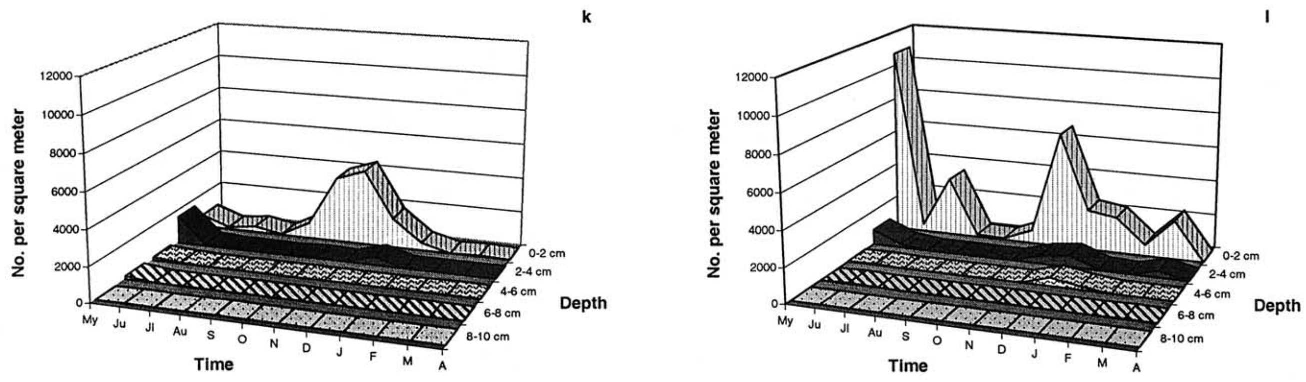
As in previous work (Springett et al., 1970; Briones et al., 1997), *C. sphagnetorum* was able to migrate to deeper layers in response to increasing temperatures and decreasing soil moisture during the summer months. This downward



***Marionina* sp.**



***Fridericia* sp. 2**



Tardigrada

Fig. 4 (continued). Vertical distribution (No. m^{-2} in each soil layer) in the forested areas and deforested ones (respectively) of *Marionina* sp. (g,h), *Fridericia* sp. 2 (i,j) and tardigrades (k,l) at each sampling occasion.

migration was even clearer in the forested areas where all the deeper layers were affected.

C. cognettii is described as a stress-tolerant species (Graefe and Schmelz, 1999) and also showed slight downward migration in response to low moisture content, but it was not as marked as in the previous species.

The rest of enchytraeid species did not show similar downward movements in response to environmental changes and the irregular pattern observed for *Marionina* and the low numbers recorded for *Fridericia* sp. 1 do not allow any clear conclusions to be drawn. Previous data show that the majority of *Fridericia* species are not affected by moisture contents (Graefe and Schmelz, 1999).

Numbers of *Achaeta* did not seem to be affected by seasonality, and population numbers were fairly constant during the experimental period in the forest. However, previous results (Springett, 1967; Springett et al., 1970; Briones et al., 1997) showed a shorter reproductive period (2 months) than at our studied sites (4 months). The contrasting results could be due to different species being present in this study, to differences in climate and soil type

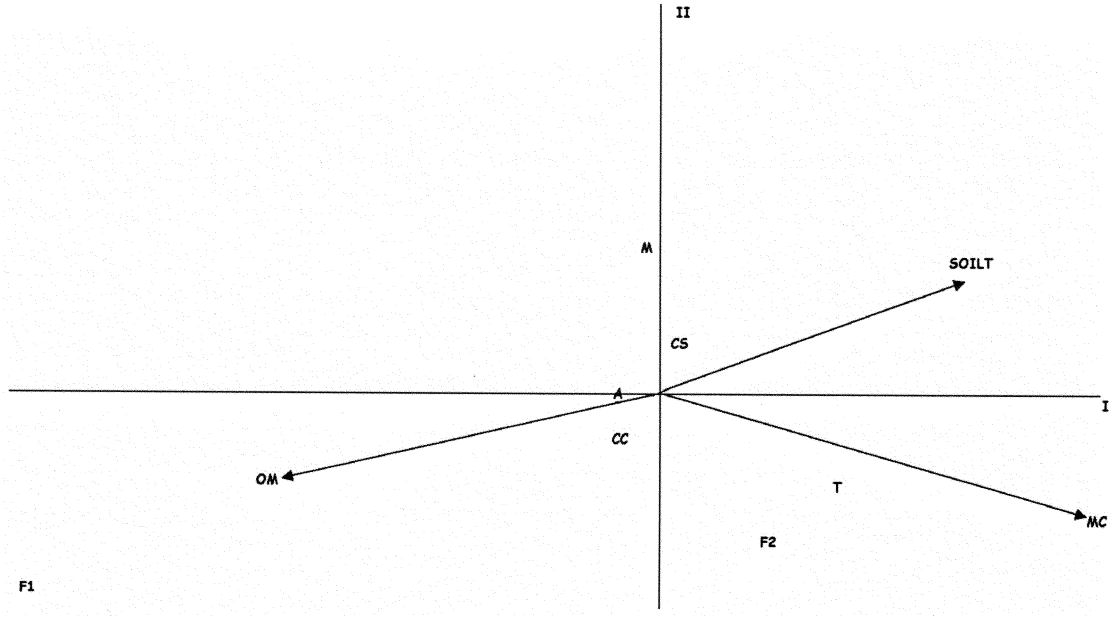


Fig. 5. Detrended canonical correspondence analysis for seven taxonomical groups considered (CS = *C. sphagnetorum*, CC = *C. cognettii*, A = *Achaeta* sp., M = *Marionina* sp., F1 = *Fridericia* sp. 1, F2 = *Fridericia* sp. 2, T = tardigrades) in relation to soil temperature (SOILT), moisture content (MC) and organic matter content (OM).

in the sampled areas or to its life-strategy which is defined as a K-selected persistent species with slow development and a reproduction rate adapted to soil water conditions (Graefe and Schmelz, 1999). *Achaeta* seemed not to show a clear pattern in its vertical distribution and Abrahamsen (1972) describes it as an eudaphic genus because of its deeper distribution in the soil layers when compared with other enchytraeid taxa. Also, Didden and Fluiter (1998) indicated that numbers in deeper layers greatly depend on other factors such as stage of decomposition and differences in food supply and therefore the quality of the organic matter could be the most influential factor explaining the vertical stratification of the enchytraeids in forests.

4.2. Tardigrades

Studies recording population dynamics of tardigrade populations in soils are scarce. Tardigrade activity highly depends on the existence of a water film and the changes in population numbers seem to be mainly related to fluctuations in temperature and moisture (Nelson and Higgins, 1990; Kennedy, 1993; Briones et al., 1997; Sohlenius and Bostrom, 1999). However, other factors such as food availability (Hallas and Yeates, 1972; Sohlenius, 1982; Nelson and Higgins, 1990), habitat preference and altitudes (Guidetti et al., 1999; Ito, 1999) and biotic factors (Hyvönen and Persson, 1996; Sohlenius and Bostrom, 1999) have also been indicated.

Table 3
Interset correlation coefficients between the first two CANOCO axes and the soil factors

	Axis I	Axis II
Soil temperature	0.295	0.228
Moisture content	0.459	–0.231
Organic matter	–0.477	–0.169

In a Swedish pine forest (Sohlenius, 1982), higher abundances of tardigrades were recorded in the control plots in nearly all sampling occasions. However, their populations seemed to be less adversely affected in the plots with slash than in the clear-cut areas which also suggest the importance of the cutting wastes on tardigrade abundance. In our study, they were more abundant in the deforested areas and seem to be related to high soil moisture content. Interestingly, there have been recorded some species which are highly euryplastic in their tolerance limits to climatic conditions, and which are able to survive in very dry habitats as long as there is sufficient water for at least short-term activities (Kinchin, 1994).

Our results also showed that they were mainly concentrated in the upper 2 cm and did not undergo significant migrations. This conclusion is supported by some previous findings, which suggest that tardigrades do not enter into the soil and are rarely found below a depth of 5 cm (Nelson and Higgins, 1990), but which contrasts with earlier work by Sohlenius (1977) who suggested some downward migration during the cold months. It is known that these animals are able to enter into a crytobiotic stage to overcome adverse environmental conditions (Crowe, 1975; Nelson and Higgins, 1990) with a recovery time of 15–20 min (Crowe and Higgins, 1967) which makes it unnecessary to migrate to more favourable microhabitats.

5. Conclusion

Although the primary reasons for enchytraeid and tardigrade responses to deforestation are difficult to decide, it seems clear that in our studied areas different soil animal groups responded differently to the new conditions. When compared with the forested areas, removal of the trees seems to have negative effects on the majority of enchytraeid species which were drastically reduced in numbers (especially in the summer months), whereas for tardigrades, the effect was the opposite and they clearly benefited from the new conditions. Different groups or species may be controlled by different factors (Huhta, 1976). Orders, families and even genera are too heterogeneous for formulating conclusions based on their responses to environmental changes (Huhta et al., 1967), and therefore any information about how individual species respond to perturbation will contribute to get a better understanding of the biological responses to deforestation. With the exception of *C. sphagnetorum*, the remaining enchytraeid species did not show vertical migration to overcome adverse environmental conditions and, as a consequence of this, they were unable to tolerate the new microclimate. It has been suggested that soil moisture and temperature are not sufficient to explain enchytraeid responses to environmental stress, and that they exhibit specific adaptations such as inactive stages (as cocoons) or acceleration or retardation of the reproductive cycle (Didden, 1993). The soils in the forested areas contained more organic matter than those in the deforested ones and therefore differences in the amount and/or quality of the organic matter could be one of the possible explanations for the observed changes in abundance when the forest is removed.

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