Effects of water level and nutrients on spatial distribution of soil mesofauna in peatlands drained for forestry in Finland.

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Abstract

We investigated the within-site distribution of Enchytraeidae, Collembola, Oribatida, Mesostigmata and Prostigmata relative to varying water level and substrate quality on pine mire sites forming a drainage succession continuum. Collembolans were most intolerant of wetness, favoring drier locations at all stages of the drainage succession. In general, the effect of water level variation on the within-site distribution of the soil fauna was strongest when the site was at an early stage of either progressive or regressive water level change. When the average water level was below 20 cm, it no longer had a significant effect on the distribution of mites, but still affected that of Enchytraeidae and Collembola. Boron was positively correlated with faunal density in several cases, and thus may be the growth limiting nutrient affecting substrate quality for decomposers in these sites. The overall changes in the soil mesofauna in drained peatlands depicted here show that these peatland forests are converging ecologically on upland forests where decomposition in general is much faster than in pristine peatlands. The change caused by restoration shows how labile these ecosystems are also with respect to the mesofaunal community.

Keywords: soil mesofauna, nutrients, organic soil, peatland forests, water level

1. Introduction

In pristine boreal peatlands, high water table level and consequent anoxic conditions take precedence over site nutrient regimes in controlling ecosystem production (Reinikainen et al., 1984), in particular tree stand growth (Jeglum, 1974), and organic matter decomposition (Bridgham et al., 1991; Szumigalski and Bayley, 1996). Peatland drainage for forestry has been carried out widely to improve tree growth in northern and northeastern Europe and some parts of North America and has caused drastic alterations to ecosystem functioning. For instance, soil biological activity increases after drainage (Kozlovskaja, 1974) largely due to the increased aeration of the surface peat (Silins and Rothwell, 1998), but also due to gradual changes in plant composition and the accompanying changes in substrate quality (Latter and Howson, 1978).

Silvan et al. (2000) found a clear increase in soil mesofaunal abundance and a significant correlation with the depth of the site water table level, in a drainage continuum of peatland sites. Soil fauna have been found to increase decomposition, mineralization and respiration in forest soils (Anderson et al., 1985; Setälä and Huhta, 1990, 1991). Macrofauna such as millipedes fragment leaf litter thereby increasing the surface area available for microbial attack and accelerating its break down (Anderson and Bignell, 1980; Cárcamo et al., 2000). Mesofauna (mites, collembolans and enchytraeid potworms) and microfauna (protozoa and nematodes) feed on bacteria and fungal mycelia (Klironomos and Kendrick, 1995) preventing fungistasis and disperse fungal inocula (Visser, 1985). They also affect species distributions in the litter (Parkinson et al., 1979; Newell, 1984) and determine root-microbial interactions that influence seedling establishment (Setälä, 1995). The omnivorous enchytraeid *Cognettia sphagnetorum* Vejd. is an important primary decomposer in boreal and temperate peatlands (e.g. Latter and Howson, 1978). It can be inferred that soil fauna are an important component of ecosystems which should be considered when assessing the environmental consequences of anthropogenic activities such as peatland drainage for forestry. It has been suggested that results from studies on the environmental consequences of drainage for forestry could also be used to estimate the effect of climatic warming on peatland ecosystem functioning (Martikainen et al., 1993; Laine et al., 1996).

In the current work, we used gradient analysis to explore faunal community responses to the drainage succession and regression studies to examine in more detail potential responses of soil fauna to water levels at the site level. We address the following aspects of within-site variation: i) does variation in the water level regulate the within-site distribution of soil mesofauna in all stages of the succession, ii) if so, does the response of animal numbers to the water level remain the same in the course of the succession, and iii) does substrate quality affect the distribution of soil animals. The study was based on a chronosequence approach because drainage succession is a slow process. Comparing sites of similar original (pre-drainage) vegetation composition at various stages of the succession was considered feasible as e.g. Drouk (1995) has shown that the soil faunal community structure is more similar between similar plant associations in different mires than between different plant associations within one mire.

2. Material and methods

2.1. Study sites

The study were those used by Silvan et al. (2000) to compare sites belonging to the same original type at various stages of post-drainage secondary succession. These sites were selected on the basis of extensive earlier studies (e.g. Laiho, 1997; Komulainen et al., 1998) to ensure comparability of sites as much as possible. Five peatland sites were sampled: a pristine undrained tall-sedge pine fen site, comparable sites drained for forestry 12, 26 and ca. 60 years earlier, and a 42-year-old drained site experimentally re-wetted two years earlier. The rewetting included clearcutting and filling in the ditches.

The sites were situated in southern Finland (61°35' - 61°52'N, 24°05' - 24°25'E) where the mean annual temperature is +3°C and the maximum is +16°C in July. The mean annual temperature sum (accumulated mean daily temperatures ≥ +5°C) varies between 1150 and 1250 dd and the annual precipitation is about 650 mm, of which about 240 mm is snowfall.

A mosaic-like pattern of low treed hummocks and treeless lawns is typical of this site type in its natural (undrained) state. The tree stand is sparse and dominated by Scots pine (*Pinus sylvestris* L.), usually with some birch (*Betula pubescens* Ehrh.). Mire dwarf shrubs (e.g. *Betula nana* L., *Ledum palustre* L., *Vaccinium uliginosum* L.) occur on hummocks but tall sedge species (*Carex lasiocarpa* Ehrh., *Carex rostrata* Stokes) dominate the field layer of lawns. In the moss layer, sphagnum (e.g. *Sphagnum fallax* (Klinggr.) Klinggr., *Sphagnum angustifolium* (Russ.) C. Jens.) predominates and the peat is *Carex* dominated. After drainage, sedges are quickly replaced by mire dwarf shrubs which in turn gradually decrease with increasing tree stand growth, giving way to forest species like *Vaccinium vitis-idaea* L. Sphagnum mosses are gradually replaced by *Pleurozium schreberi* (Brid.) and other forest mosses. Vegetation changes after drainage are described in more detail by Laine et al. (1995a), and after restoration by Komulainen et al. (1998). Tree stand volumes were 6, 11, 76 and 278 m^3 ha^{-1} for the undrained site and the 12, 26 and 60 year-old drained sites, respectively (Laiho, 1997).

2.2. Sampling and laboratory analyses

Sampling was done along two parallel transects, ten meters apart, on each site. On the drained sites transects reached from ditch to ditch (30-37 m) but on the undrained site the 30-m-long transects ran in a randomly chosen direction. Samples for measuring mesofaunal abundance were taken at five locations on each transect: transect midpoint, halfway between the midpoint and the transect ends, and halfway between the previous locations and the transect ends. Thus, on drained sites there were relatively more sampling locations near the ditches than in the middle of the strip between ditches to obtain an enhanced drainage effect. Sampling was done once between 7-15 July, 1997. The water table level was measured in each sampling location from a well established at least a day earlier to allow the water level to settle.

Two sets of samples with a surface area of 24 cm^2 were taken from depths of 0-4 cm and 4-8 cm in each location, with the lower level of the living moss layer as the zero-level (the moss layer was included in the sample). Most of the populations were expected to be found in these layers (Markkula, 1981; Hotanen, 1986). Samples were

taken from the lawn-level to eliminate variation caused by microtopography, placed into paperbags and taken either directly to extraction or to be stored at +5°C for a maximum of 7 days before extraction. In the laboratory, one sample set was extracted using the wet funnel method to quantify numbers of enchytraeids (e.g. O'Connor, 1962) and the other with a high-gradient apparatus to quantify numbers of Mesostigmata, Oribatida, Prostigmata and Collembola (Takeda, 1979).

As a coarse measure of substrate quality, total N, P, K, Ca, Mg, Fe and B concentrations were measured from the sample set used in dry funnel extraction after drying at 105°C and grinding through a 2 mm sieve. Nitrogen concentrations were measured on a Leco CHN 600 analyzer and those of the other elements on an ICP analyzer (ARL 3580) after nitric acid-perchloric acid digestion.

2.3. Data analysis.
Canonical Correspondence Analysis (CCA, Ter Braak, 1986) was used to "order" the samples based on their combination of faunal abundances and the gradients in environmental variables measured (location, years after drainage, water table level, N, P, K, Mg, B and Fe). All environmental variables were transformed logarithmically (ln x + 1) as recommended by Palmer (1993). Statistical significance of the first axis was tested using the Monte Carlo simulation available in CANOCO (Ter Braak, 1986) and differences among the site scores for CCA axes 1 and 2 were tested using non-parametric Kruskall-Wallis analysis of variance.

For each site and soil animal group linear regressions were calculated for the relationships between the number of animals and i) the depth of water table level in each measuring location, and ii) substrate element concentrations. The relationships between water table level and soil nutrient concentrations were also checked, to ensure that any correlations between animal numbers and nutrient concentrations were not be in fact caused by a dependence of nutrient concentrations on water level.

To test if the differences in the response to water level among sites (successional stages) were significant, a model with a single slope (but separate constants to account for the difference in animal density levels among sites) was compared with a model fitting a separate slope for each site (e.g. Draper and Smith 1981). If a statistically significant difference between the two models was found for an animal group, it indicated significant differences in the response of that group to water level among sites.

3. Results

3.1. Gradient analysis of the drainage succession
Direct gradient analysis with CCA using sum densities of soil animals in the two layers (0-4 cm + 4-8 cm) yielded very low eigenvalues (0.103) reflecting the poor dispersal of the taxa in the ordination space; all five taxa fell near the middle of the diagram within 0.30 of both axes. Nevertheless, differences in community composition were sufficient to disperse the samples along both ordination axes (Fig. 1) and the Monte Carlo simulation suggested a significant first axis (F = 17.65, p = 0.01). All ten samples from the undrained site occurred in the top right quarter along with nine of the samples from the recently drained site (12 years). Undrained site scores for axis 1 were significantly

different from the re-wetted site and the site drained 26 years before the study (Kruskall-Wallis test, $p < 0.05$). For axis 2 only the re-wetted site and the undrained site had significantly different site scores (Kruskall-Wallis test, $p < 0.05$). Most of the samples from the oldest drained site also occurred in the lower positive quarter of the diagram (Fig. 1). The environmental variables that appeared to determine the gradients in the CCA diagram, according to their correlations with the axes, were water level and nitrogen with axis one and drainage age with axis two (Table 1).

3.2. Within-site relationship of faunal density to water level
In all sites, the abundance of soil animals in the 0-8 cm layer was generally higher where the water table was lower (Fig. 2). The only exception was Mesostigmata in the oldest drained site, which had a negative correlation with the depth of the water table. However, the relationships were not statistically significant in all cases (Table 2). In the undrained site, the density of soil fauna did not correlate significantly with the water level (Table 2). The effect of the variation in water table level on the distribution of soil animals was most pronounced in the youngest (12 years) drained site (Table 2).

Taxa, at the resolution studied, seemed to respond differently to water level variation (Table 2). Collembolans were most sensitive to the height of the water level. The effect of the water level on their distribution was statistically significant in all sites, except for the undrained one. The number of Collembola in the undrained site was very low and they were found in only four of the ten samples. The abundance of Enchytraeidae depended on the water table level in the 12- and 26-year-old drained sites, and the re-wetted site. The abundance of oribatid mites depended on the water table level only in the re-wetted site and that of Mesostigmata only in the youngest drained site, while the abundance of Prostigmata depended on the water table level both in the youngest drained and the re-wetted site.

3.3. Relationship of water level and soil fauna in the course of the drainage succession
When the relationship of water level with soil fauna is considered in the drainage continuum, only Collembola and Enchytraeidae showed a distinct pattern (Table 2). The variation among sites was statistically significant only for Collembola ($p=0.022$). With Collembola, the sites were divided into three groups: the undrained site with its zero slope, the two younger drained sites with intermediate slopes, and the oldest drained site plus the re-wetted site where the response was strongest (Table 2). For Enchytraeidae, the strongest association with water level was found in the more recently drained sites (12 and 26 years) and the re-wetted site where the response was intermediate between the former sites and the oldest drained site. For mites there were no clear groupings that corresponded to the drainage succession

3.4. Effect of water level on the depth distribution of soil fauna
In general, most animals were found in the upper (0-4 cm) layer. Especially where water level was high, there were only scattered occurrences in the deeper (4-8 cm) layer. Variation in water level had a significant effect on the proportion of animals found in the deeper layer only in a few cases: Collembola, Mesostigmata, and Prostigmata in the youngest drained site (Fig. 3, p-values <0.001, 0.014, and 0.009,

respectively), and Enchytraeidae in the re-wetted site (p=0.044). In all these cases, the proportion of the animals found in the deeper layer was higher when the water level was lower.

When the two layers (0-4 cm and 4-8 cm) were examined separately, some differences were found in the response of the animals to water level compared to the entire 8 cm depth. In the youngest drained site, the response of all animal groups was clearer in the deeper layer than in the surface This was the case with Enchytraeidae also in the 26-year-old drained site. In the undrained site, the response of number of Enchytraeidae to water level was significant in the topmost 4 cm, even though it was not in the total 8-cm or the deeper layer. in the re-wetted site, Enchytraeidae and mites reacted more to the water level in the topmost 0-4 cm.

3.5. Within-site relationships of faunal density to substrate element concentrations
There were few significant correlations between soil animals and soil nutrient concentrations. An increase in the peat iron concentration caused a weakly significant negative response in the density of Collembola (p=0.095), Mesostigmata (p=0.059) and Prostigmata (p=0.097) in the re-wetted site, and Enchytraeidae in the 26-year-old drained site (p=0.053). Mesostigmata correlated positively with iron in the undrained site (p=0.086). All mite groups had a negative correlation with calcium concentrations in the youngest (12 years) drained site, p-values being 0.098 for Mesostigmata, 0.029 for Oribatida, and 0.067 for Prostigmata, respectively.

Soil boron concentration had a positive correlation with the numbers of Enchytraeidae (p<0.001), Collembola (0.042) and Oribatida (0.057) in the oldest drained site (Fig. 4), and with Collembola in the re-wetted site (p=0.048). Oribatida correlated positively with nitrogen concentration in the undrained site (p=0.039). Enchytraeidae correlated positively with phosphorus in the 26-year-old drained site (p=0.002), the correlation being stronger than that found between phosphorus and water level in that case (p=0.022). There were no significant correlations between potassium or magnesium concentrations and faunal density.

4. Discussion

The effect of water level on the within-site distribution of soil mesofauna varied among animal groups and over the course of the drainage succession. Collembolans were most intolerant of wetness, favoring drier locations at all stages of the drainage succession represented by the study sites. Enchytraeidae had a strong response to water level in the early stage of the drainage succession. When the water level had dropped deeper its effect on enchytraeid density decreased; after re-wetting the effect "returned". Similarly, mites responded to water level variation in the early stage of drainage succession, and again after re-wetting. When the average water level was below 20 cm, it did not have a significant effect on the distribution of mites any more, but still affected that of Enchytraeidae and Collembola. At the site scale, water level, or the stage of drainage succession, significantly controls the abundance of all animal groups studied (Silvan et al., 2000).

It seems that where the environment is "too" wet, a small variation in water level has no effect on the distribution of soil animals within a peatland site. The overall numbers

are very low and the animals seem to be distributed either randomly or related to factors not measured in this study. The effect of water level variation on the within-site distribution of the soil fauna is strongest when the site is at an early stage of either progressive or regressive water level change. After permanent water level decline, the effect of water level variation diminishes in the top layer but increases below the surface. The opposite happens after regressive water level change.

Although the water content of peat in general remains high even after forestry drainage (Silins and Rothwell, 1998), it appears that the surface peat/litter layer may get too dry for some animal groups (e.g. Mesostigmata in this study) late in the drainage succession. Markkula (1981, 1982, 1986) found that drainage decreased the amount of soil fauna on hummocks, while they increased in hollows. The hummocks may have become too dry for the animals; however, substrate type - moisture interactions (cf. Kaczmarek, 1991), which were excluded on purpose from our study, may also have an effect.

In general, phosphorus, potassium, and some micronutrients such as boron are the factors most often limiting tree growth in boreal peatland forests (e.g. Paarlahti et al., 1971; Brække, 1979). The concentrations of phosphorus and potassium were rather – but not abnormally – low in the tree stands of the sites (Laiho 1997). These elements, however, did not correlate with the distribution of soil fauna. Boron had a positive correlation with faunal density in several cases, and thus may be the growth limiting nutrient affecting substrate quality for decomposers in these sites. High substrate calcium and iron concentrations may seemingly limit the number of soil fauna. Substrate nitrogen concentration had no effect on faunal distribution within our sites, although e.g. *Cognettia sphagnetorum* has been found to prefer substrates with higher nitrogen contents (Latter and Howson, 1978). in our drained sites, the substrate nitrogen concentrations were in general relatively high (> 1%), which may be a reason for its minor effect. At the between-site level, there was a weak correlation between faunal density and nitrogen, which may be partly a reflection of the drainage succession (cf. Laine et al., 1995), as nitrogen concentration usually increases with increasing degree of substrate decomposition (e.g. Williams, 1983).

The effect of forestry drainage on soil animals has been investigated in some earlier studies (Vilkamaa, 1981; Markkula, 1982, 1986), however, our study is the first to include a chronosequence of similar sites at different stages of the drainage succession. Our sites 1-3, from a natural, undrained situation to 26 years after drainage, depict an effective drainage succession. On site 4 (ca. 60 years since drainage) deterioration of the ditch system has caused a slightly regressive development, shown by e.g. the high coverage of *Sphagnum* mosses, even though the water level is still low. Site 5 shows the change caused by reversing the succession by active re-wetting.

The water levels in the undrained and re-wetted sites are in general high (close to the surface) and rather stable. The water levels at the time of sampling represented well a long-term average situation in these sites. The water levels in the drained sites were somewhat higher than long-term averages. Although the actual animal numbers may vary depending on the water level fluctuations, we postulated that the relative differences between drier and wetter microsites would be revealed in our study.

In general, the numbers of soil animals increased in the course of the drainage succession, as reported by Silvan et al. (2000). There is evidence that the community structure, (faunal species composition) also changes with peatland specialists being

replaced by xerophilous and habitat generalists after drainage (Markkula, 1986). This is a phenomenon commonly observed for peatland flora and fauna (Laine et al., 1995b; Vasander et al., 1997). Interestingly, in her study of nematodes in drained peatland meadows, Wasilewska (1991) found that reduced soil moisture may increase the abundance of bacterivores and fungivores more at the expense of phytophages, and thus lead to a slower form of mineralization. The clear increase in soil respiration that has been observed after drainage of peatlands (Glenn et al., 1993; Martikainen et al., 1995; Silvola et al., 1996a), has often been assumed to be due to increased mineralization of the peat substrate. However, a major part of the increased respiration may in fact be due to processes other than mineralization (e.g. Glenn et al., 1993; Silvola et al., 1996b). A better understanding of the food webs of drained peatlands would increase our understanding of their carbon cycle, which has recently been found to be more complicated than has usually been supposed (Minkkinen, 1999).

The overall changes in the soil mesofauna on drained peatlands depicted here show that these peatland forests are ecologically "moving" towards upland forests where decomposition in general is much faster than in pristine peatlands. The change caused by restoration shows how labile this ecosystem is also in respect of the mesofaunal community.

Acknowledgements

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Table 1
Interset correlations of environmental variables with CCA axes.

Variable	Axis 1	Axis 2
Nitrogen	-0.528	0.016
Water level	-0.510	-0.188
Drainage age	-0.216	0.441
Potassium	0.374	-0.257
Magnesium	-0.356	-0.055
Calcium	0.316	0.051
Boron	0.112	-0.165
Iron	0.096	0.140
Phosphorus	0.025	0.115
Location	0.037	0.004

Table 2

Slopes, and their standard errors, of linear regressions between the numbers of soil animals and the water table level.

|	Collembola	Enchytraeidae	Mesostigmata	Oribatida	Prostigmata
Undrained					
slope	-19	120	66	276	158
std error	47	80	59	209	118
p	0.699	0.171	0.298	0.224	0.217
Drained 12 years					
slope	567	1131	309	948	320
std error	76	220	44	600	45
p	<0.001	<0.001	<0.001	0.152	<0.001
Drained 26 years					
slope	454	1106	137	645	504
std error	176	356	111	405	255
p	0.032	0.014	0.253	0.150	0.083
Drained 60 years					
slope	1048	928	-296	1707	410
std error	317	563	156	1118	669
p	0.011	0.138	0.094	0.165	0.557
Rewetted					
slope	1176	612	246	1563	918
std error	379	186	200	481	341
p	0.014	0.011	0.254	0.012	0.027
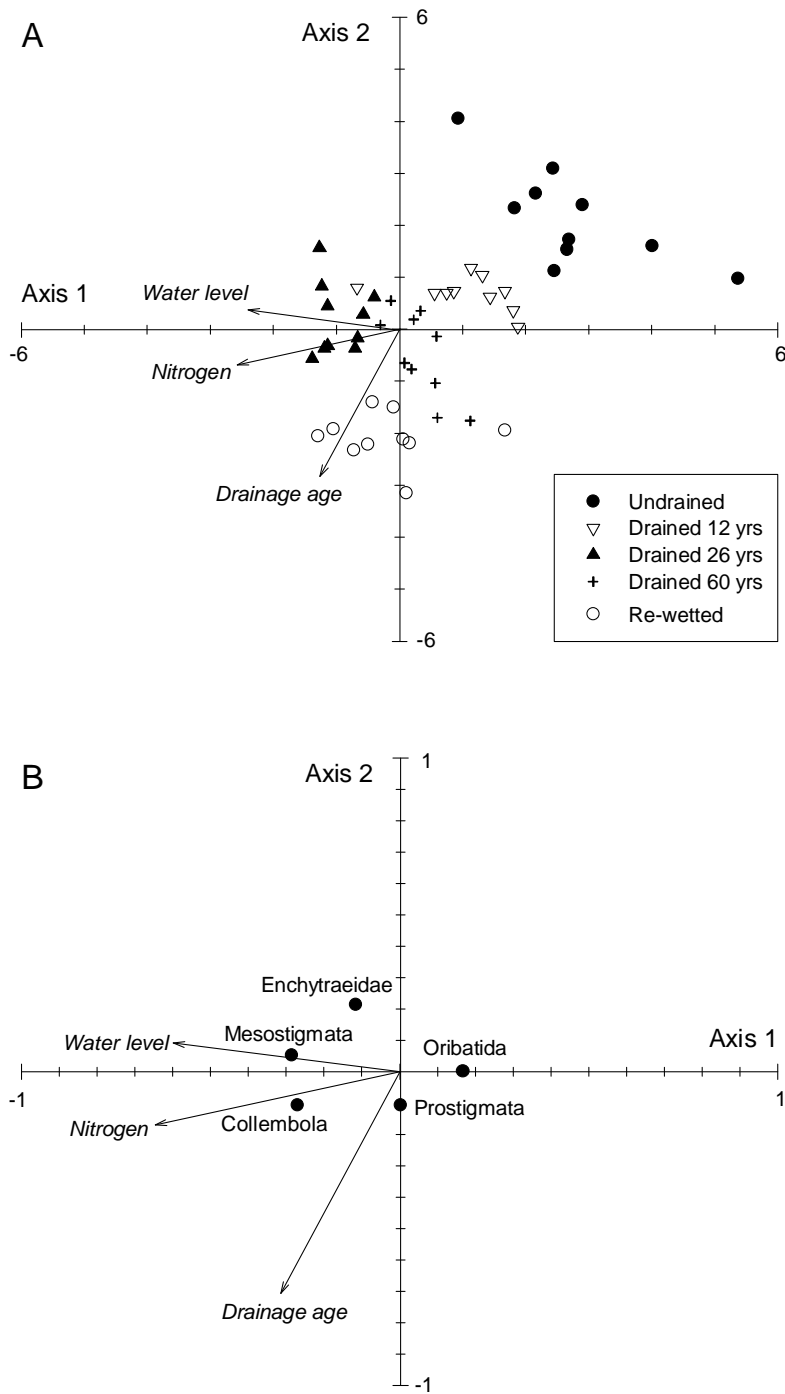
Fig. 1. Canonical correspondence analysis of the study sites based on their mesofaunal composition. A: Sample scores which are linear combinations of environmental variables, with major environmental variables shown (multiplied by four to fit the scale); B: species scores with major environmental variables (original scale). Water level drops with the direction of the vector, and the values of other environmental variables increase.
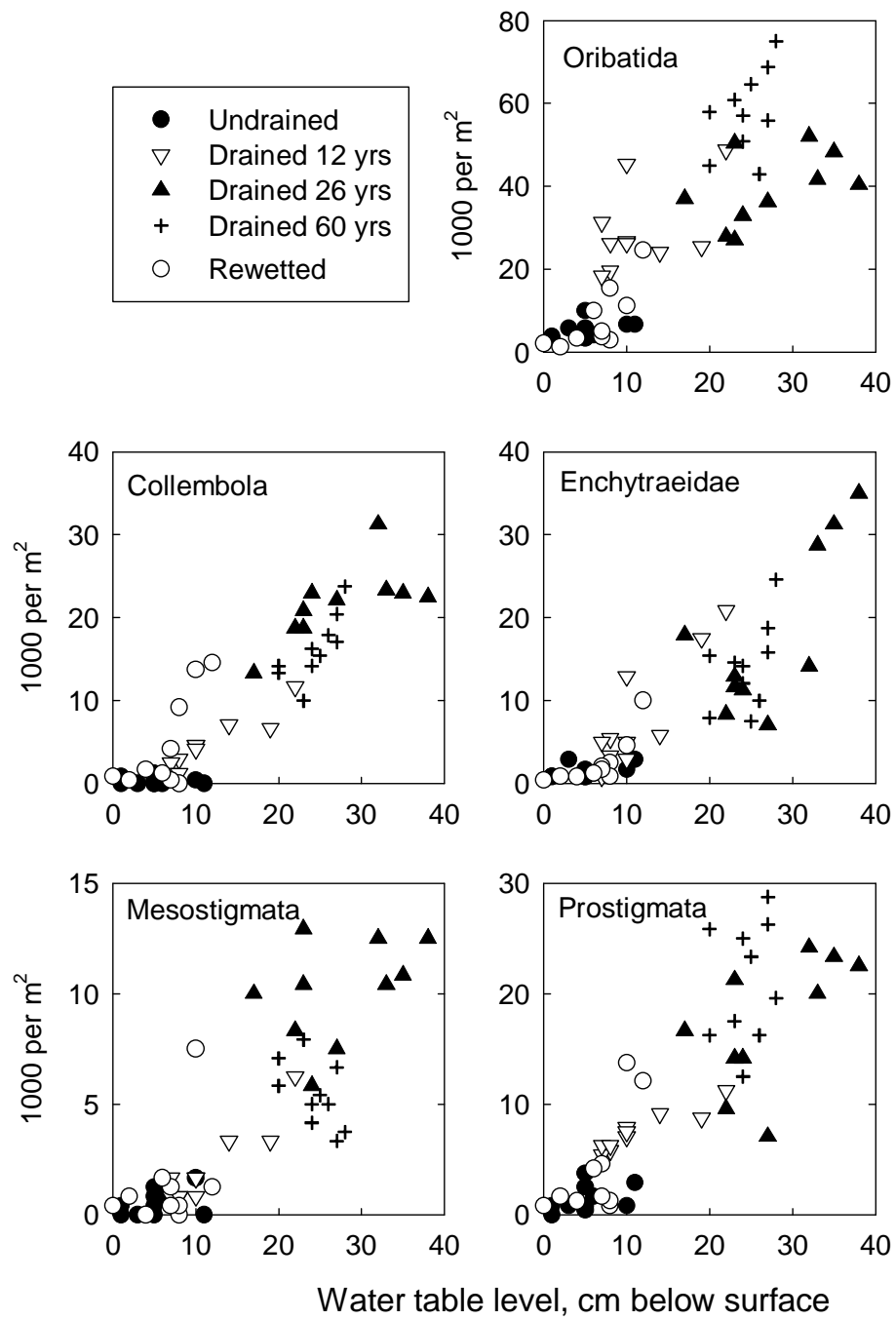
Fig. 2. The occurrence of soil fauna (0-8 cm layer) in relation to water level in the study sites. Note the differences in scales.
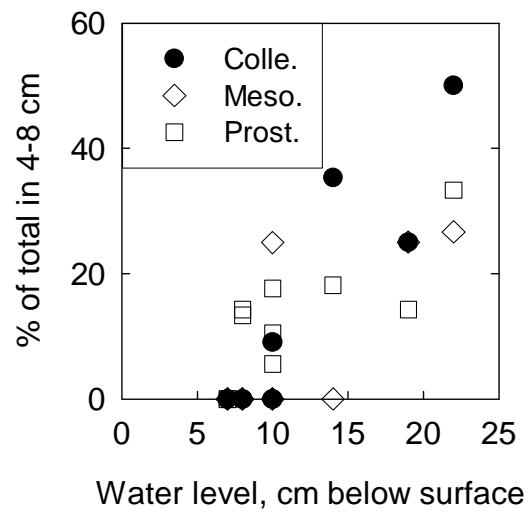
Fig. 3. Proportion of Collembola, Mesostigmata, and Prostigmata found in the deeper layer (4-8 cm) in relation to water level on the 12-year-old drained site.
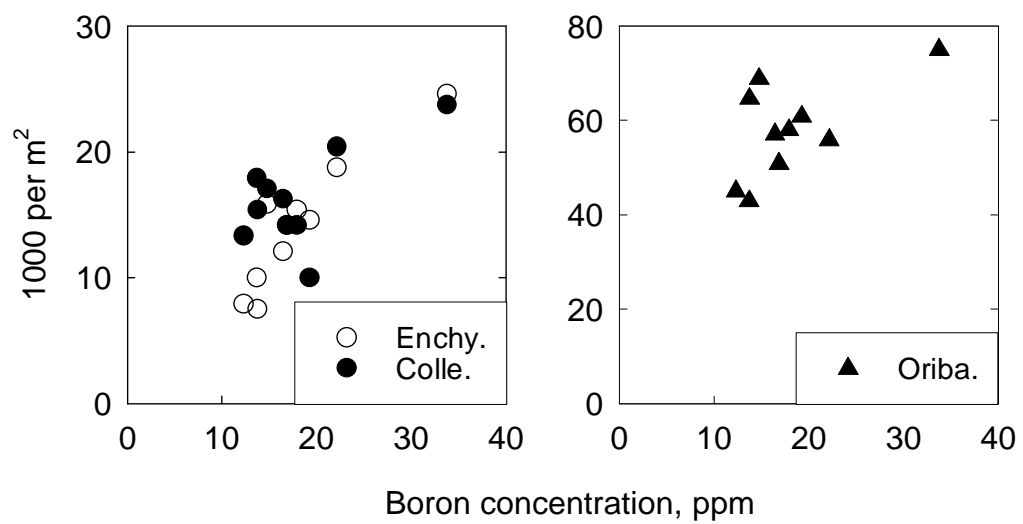

Fig. 4. Relationships between numbers of Enchytraeidae, Collembola, and Oribatida and peat boron concentration in the 60-year-old drained site.