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Nematode communities of natural and managed beech forests – a pilot survey

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Summary

The soil nematode communities of natural beech forests and managed beech forests were surveyed in order to examine which community parameters, if any, would be suited to differentiate between the two management regimes. Nematodes were collected from mineral soil at three sites, each including managed and adjacent natural beech forests.

Following enumeration and identification of nematodes to family level, relative abundance of trophic groups, adult/juvenile ratio, Shannon-index, Plant Parasitic Index (PPI) and Maturity Index (MI) were determined.

A clear separation of samples according to site was found in a Canonical Community Ordination (CANOCO) that related nematode data and various soil parameters in each sample. Beech forests of Mid-Zealand (Suserup) had significantly lower sand content, higher pH, higher PPI and higher nematode diversity according to the Shannon-index than the forests of North Zealand (Farum and Rankeskov). A distinct difference in the distribution of families was observed between sites, which could be governed by differences in texture and pH. The MI of the two old natural forest sites (Farum and Suserup) was significantly higher than the comparable managed sites, while this was not the case for Rankeskov, which is in a less mature state. There was a significantly higher adult/juvenile ratio and higher relative abundance of bacterial feeders in the natural forests compared to the managed forests. The apparent relation between pH and Maturity Index in beech forests is discussed. We suggest dead wood

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input to be the driving variable leading to the observed differences in the nematode community between managed and natural forests of Zealand, Denmark. The marked site differences found in this study emphasizes the need to carefully choose reference areas where soil conditions etc. are very similar to the managed forest in question when reference schemes for nature-based forestry are being developed.

Key words: Free-living nematodes, natural beech forest, forest management, community structure

Introduction

In North-western Europe, natural forests are very scarce and act as refuges for many rare species of plants, animals and fungi associated with degenerated old trees and woody debris. In nature-based forestry where trees are harvested by partial cutting, the aim is to achieve managed forests that structurally resemble the natural forests with regard to natural regeneration of trees, the presence of a multistoried canopy and a higher input of dead wood to the forest floor. The combination of these factors acts to provide many different habitats, and ensure the high biodiversity that characterizes a natural forest, not only in the tropics but also in temperate regions (Christensen & Emborg 1996). Furthermore, it is assumed that nature-based forestry would lead to less leaching of nutrients from the soil compared to the traditional clear-cutting practice (Bauhus & Bartsch 1995). In order to obtain a reasonable balance between environmental and economical aspects of nature-based forestry, forest managers require indicators of the different functions of the ecosystem. One of the very important functions of soil is decomposition. The relative abundance of free-living microbial-feeding nematodes reflects the productivity of the primary decomposers in soil enriched with organic resources (Rønn et al. 1996; Griffith et al. 1993). Furthermore, there is accumulating evidence from studies of soil of relatively immature ecosystems that man-made disturbance such as contamination with heavy metals (Korthals et al. 1996; Nagy 1999), changing the pH-value (de Goede 1993), adding of nutrients to soil (Yeates & King 1997) and changing irrigation scheme (Porazinska et al. 1998) can lead to a shift in the nematode community at the family level e.g. an increase in proportion of nematodes with a colonizer life-strategy in contrast to nematodes with a persister life-strategy as reflected by the Maturity Index (Bongers 1990). It has not yet been determined whether the nematode community can be a suitable indicator of long-term management disturbance level in the more mature ecosystem of a beech forest. The objective of this study is to investigate if management of beech forests has an effect on the nematode community and which nematode community parameters, if any, would be informative in distinguishing between natural forests and traditionally managed forests and thereby add a tool to a reference scheme for nature-based forestry.

Materials and Methods

Sites

Two sites in North Zealand (Farum and Rankeskov) on sandy mull and one site in Mid-Zealand (Suserup) on clay-rich mull were included in the study. Each site includes a natural and a managed forest seperated by less than a 1000 m. There were no evident differencies in soil type or microclimate between pairs of managed and natural forests. The natural forest at Farum has been left untouched since 1905. In Suserup natural forest, partial cutting in 1914–18 and a few plantings in 1961 have been the only major management events since 1800, and the forest is otherwise untouched. Suserup and Farum natural forest sites are both structurally characterized by a multistoried canopy and a large amount of dead wood on the forest floors. Rankeskov natural forest was categorized as such because the forest is a descendent of the native forest, like the two other natural forests included in this study. However, there has been heavy partial cutting of trees in Rankeskov natural forest until 1987 when the forest was finally left untouched. As a result the structure of Rankeskov natural forest still to a large extent has the appearance of a typical managed even-aged beech stand and with less dead wood on the forest floor than Farum and Suserup. All the managed forests of the study were typical even-aged stands consisting of ca. 110 year old beech trees (Friss Møller 1997).

Collection and processing of samples

Within each site a 10 × 10 m plot was laid out at least 50 m from the edge of the forest. Soil samples were collected at 4 randomly chosen grid intersections of each plot in November 1999. In situ soil respiration was measured with an infrared CO_2-analyzer (EGM-2®, PP-systems, London, UK) after removal of the litter layer and fermentation layer. Soil cores (5 cm. depth, 10 cm wide) of the uppermost layer of the mineral soil were collected and brought to the laboratory in sealed plastic bags and stored at 5 °C. The following day each sample was separately sieved and mixed. Organic C-content was measured as loss on ignition. Water % and pH in water were measured. An index of texture was obtained by suspending 5 g of the mineral fraction of the samples obtained after 2 hours at 600 °C in a 20 ml 5 % sodiumhexametaphosphate on a shaker overnight followed by sedimentation in glass tubes, to which had previously been added 70 ml water. After 24 h the thickness of the layer of sedimented particles (mostly sand) was recorded. Nematodes were extracted with a modified Baermann funnel method, enumerated and fixed in 80 °C formaldehyde (4 %). Approximately 30 nematodes from each sample were identified to family level according to Bongers (1994) and assigned to trophic group according to Yeates et al. (1993).

Data analyses

The nematode data and the environmental data were analyzed with multivariate statistics using a redundancy analysis (CANOCO 4®, Center for Biometry Wageningen, Microcomputer Power, Ithaca NY). Relative abundances of 33 nematode families observed (Table 1) combined with the Shannon index, Maturity Index, Plant Parasitic Index (Bongers 1990) and adult/juvenile ratio for the 24 samples was treated as the ‘species’ file. All values in the ‘species’ file were log-transformed. The five environmental variables were included in a separate file. Focus of scaling was on interspecies distances and species scores were not transformed. The species data table was centred and standardized by species. The graphical presentation shows ‘species’, environmental variables and samples in a triplot (Fig. 1). With univariate statistics, significance of effects of sites and forest management on the nematodes was obtained by a two-way ANOVA using Sigma Stat 2.03 (Jandell Scientific®, Chicago, Illinois, USA) un untransformed data, except for the relative abundances of bacterial feeders that were arcsine transformed before tested. Multiple pair-wise comparisons were subsequently performed with Tukey’s test. In some cases correlations between dependent variables were tested using Pearson’s Correlation Coefficient.

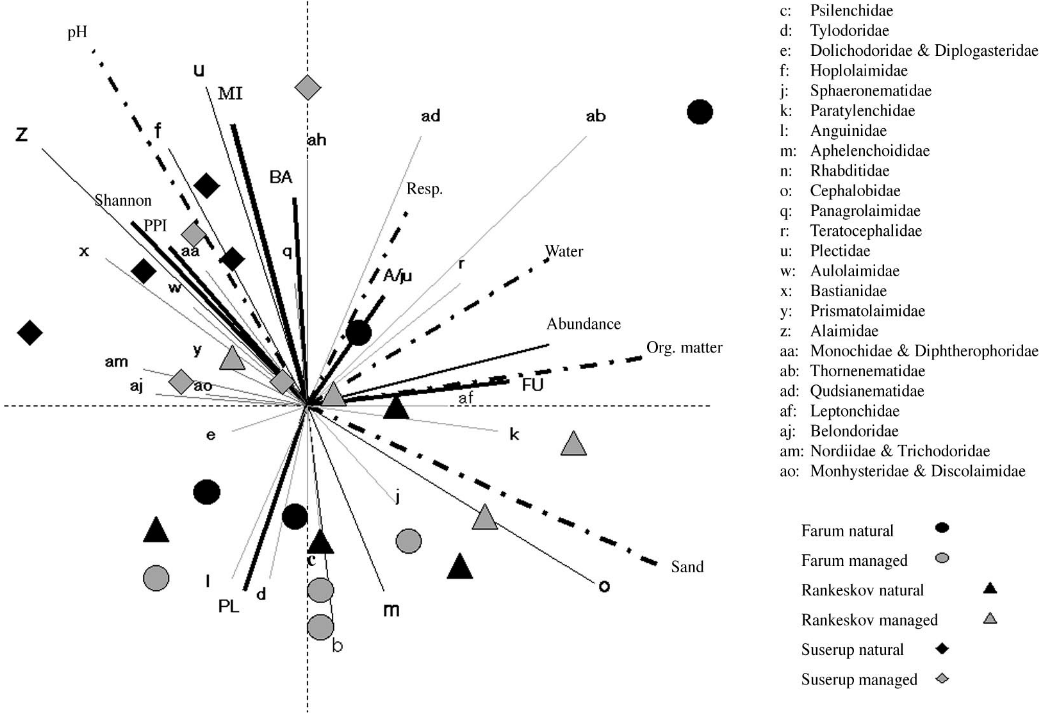

Fig. 1. Ordination (RDA) analysis of nematode data and environmental data. Vectors for environmental variables (pH, respiration, water, sand and organic matter) are represented by heavy dotted lines. Derived nematode parameters (MI, PPI, bacterivores (BA), fungivores (FU), plant feeders (PL), Shannon index and adult/juvenile ratio (A/ju)) are represented by heavy solid lines. Nematode families are represented by thin grey lines except for the 6 most abundant taxa, which are represented by thin black lines. Signatures refer to individual samples

Table 1 Relative abundance (%), cp-values (1-5) and feeding groups (PL: plant feeders, BA: bacterial feeders, FU: fungal feeders) of the nematodes families found in soil from 3 beech forest sites of Zealand (Farum, Rankeskov, Suserup) with managed (man) and natural (nat) stands

	Farum		**Rankeskov**		**Suserup**			
	nat	man	nat	man	nat	man	*cp-value*	*feeding*
Tylenchidae	31	33	45	42	16	25	2	PL
Psilenchidae			1				2	PL
Tylodoridae	3	11	2	4	4	4	2	PL
Dolichodoridae	1					1	3	PL
Hoplolaimidae	1			3	14	15	3	PL
Pratylenchidae						3	3	PL
Criconemertidae		2					3	PL
Hemicycliophoridae		1					3	PL
Paratylenchidae				1			2	PL
Anguinidae	1	4		1		1	2	PL-FU
Aphelenchoididae	10	12	8	8			2	FU
Rhabditidae		6	6	1	7	6	1	BA
Cephalobidae	16	24	19	17	5	6	2	BA
Osstellidae						2	2	BA
Panagrolaimidae						2	1	BA
Teratocephalobidae	13	4	6	5	4		3	BA
Diplogasteridae		1			1		1	BA
Monhysteridae	8		5	1	6	2	2	BA
Plectidae	3		3	1	10	12	2	BA
Achromadoridae					1	1	3	UE
Aulolaimidae					1		3	BA
Bastianiidae					2	1	3	BA
Prismatolaimidae	2		1	1	5	3	3	BA
Alaimidae				2	17	6	4	BA
Mononchidae					2		4	PR
Thornematidae	4					1	5	FU
Nordiidae					1		4	PL/OM
Qudsianemertidae	1				1	1	4	FU
Discolaimidae						1	5	PR
Leptonchidae	2			11		1	4	FU
Diphtherophoridae			3	2	4	1	3	FU
Trichodoridae						1	4	PL
Belondoridae						1	5	PL
Not determined	2					3		

Results and Discussion

The CANOCO triplot and site effects

With one exception, the sample points from Mid-Zealand (Suserup) group separately from the sample points from North Zealand (Farum and Rankeskov) in the CANOCO-triplot (Fig.1). This indicates a clear regional dissimilarity within the material. The Mid-Zealand sample cluster is thus placed in the second quadrant of the diagram, while the North Zealand sample points spread across the remaining 3 quadrants, with 13 points placed in the lower two quadrants (Fig. 1). The environmental factors that seem to explain most of this separation are soil texture and pH. Suserup sites have a significantly higher pH, (P= 0.001, pH-vector points to the Suserup sites) and a lower sand content than Farum and Rankeskov sites (P= 0.001, sand vector points away from the Suserup sites) (Fig. 1). Water content of the soil samples and in situ respiration do not show a geographical pattern similar to pH and texture (Fig. 1). Organic matter and the relative abundance of fungal feeders are closely related (vectors are parallel in Fig. 1), which seems reasonable since active hyphae in soil are often seen in close association with organic particles, and the active hyphae that contain protoplasm are probably the most desirable food items for fungal feeding nematodes. However, this correlation was only significant if the Rankeskov site was excluded from the analysis, (Pearson's Correlation Coefficient = 0.812; P= 0.0001). The fungal feeders- and organic matter-vectors do not point to a cluster of samples, i.e. no samples are characterized by particularly many or few fungal feeders. Furthermore, independent of management, all sites are rich in organic material and local variability within sites exceeds differences between sites. Bacterial feeders are proportionately more abundant in the Suserup sites (Fig. 1 and Fig. 3). Of the 6 most abundant nematode families Alaimidae, Hoplolaimidae and Plectidae points to the Suserup sample cluster while Aphelenchoididae, Cephalobidae and Tylenchidae points to the North Zealand cluster. It is especially striking that the bacterial feeding Alaimidae are almost absent in North Zealand and that Cephalobidae are much more abundant here (Table 1). We suggest this reflects a competitive advantage of Alaimidae in clay-rich soils with many small pores that can be reached and explored by nematodes with very slender heads such as Alaimidae, while broad-headed Cephalobidae may be better adapted to sandy soils. There is a significantly higher diversity (P= 0,005, Shannon-vector points to Suserup in Fig. 1) in the Suserup sites compared to North Zealand and also a significantly higher PPI (P= 0,037, PPI-vector points to Suserup in Fig. 1).

Nematode community parameters and forest management

Sample points in the CANOCO-triplot from the natural forest group separate from the managed forest sample points for the Farum site, and a slightly similar tendency seems to be the case for Suserup and Rankeskov (Fig. 1). When sample points are projected onto the vector for Maturity Index, samples from natural forests within Farum and Suserup sites generally score higher than the samples from managed sites (Fig. 1). The two old natural forests of Suserup and Farum have a significantly higher Maturity Index than the comparable managed sites, while this is not the case for Rankeskov (two-way ANOVA, P= 0,003). The different amount of dead wood deposition in the two management regimes could be the main factor involved. We hypothesize that

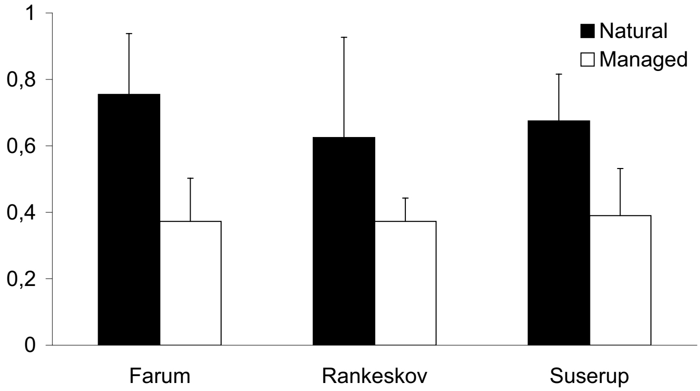

Fig. 2. Adult/juvenile ratios of nematodes in natural and managed forests from three sites in Zealand. The adult/juvenile ratio was significantly higher in natural forests (P = 0,046; two-way ANOVA) Error bars refer to 1 S.E.

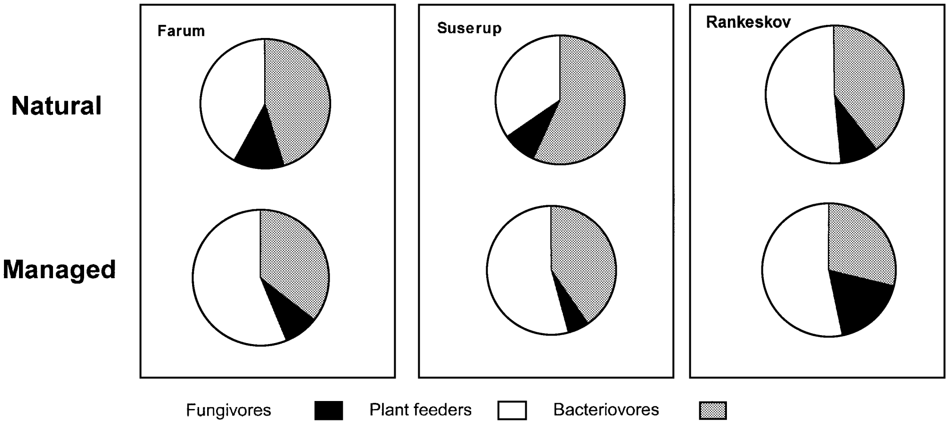

Fig. 3. Relative distribution of trophic groups of nematodes in natural and managed forest from three sites in Zealand. Relative abundance of bacterivores is significantly higher in natural forests (P = 0,008; two-way ANOVA)

dead wood–input could alter physico-chemical conditions in soil and/or alter the species pool and migration potential of nematodes in favour of K-strategists. Considering the very short life-cycles of nematodes, usually between a few days and a year (Nicholas 1984), physical disturbance in a managed beech forest of 110 years of age and not visited by foresters except for occasional thinnings, is not likely to affect the nematode community directly. The triplot suggest that pH is the single environmental factor that is best correlated with the Maturity Index (Fig. 1). A scatter plot of pH values found in the 24 samples against MI values indicates that MI is dependent on pH in beech forest over a relatively narrow pH-range, possibly in an unimodal fashion (Fig. 4). During decomposition of dead wood, various organic acids are produced which could in theory act to lower soil pH to less than 5. This could have happened in Suserup natural forest where the pH is lower than in the nearby managed site. In the Farum site pH of both sites is low irrespective of management. Alphei (1998) examined the nematode community of a mull (pH = 6) and a moder (pH = 3) beech forest and found no significant difference in MI, but a difference in distribution of cp-groups. This does not contradict our results since the unimodal relation peaks at pH = 4,8. Many of the nematode families, which are considered to be fungal feeders, also have high cp-scores and the peak in MI at pH = 4,8 could reflect optimum conditions for fungal activity. However this is not the case in our material, where the higher MI in natural forests reflects a shift in cp-groups within the bacterial feeders i.e. fewer Rhabditidae (cp: 1) and Cephalobidae (cp: 2) in Farum natural forest, and more Alaimidae (cp: 4) in Suserup natural forest compared to the managed sites (Table 1). At both sites Teratocephalidae (cp: 3) were more abundant in natural forests (Table 1). A near neutral pH-value is optimal for bacterial activity and could partly explain a shift towards opportunistic bacterial feeders and hence a drop in MI when pH is above 5 (Fig. 4). Bloemers et al. (1997) found very high values in MI, around 3.58, in a tropical forest soil over a range of management disturbances, however the extraction method used was very different from the one used in the present study, complicating comparisons. Yeates (1997) also found higher MI values in New Zealand soils compared to values typically reported in European studies. Thus care should be taken in comparing MI-values from different biogeographical regions. The present investigation suggests, however, that the nematode cp-groupings are meaningful in forest as well as arable soil ecology within the European temperate range.

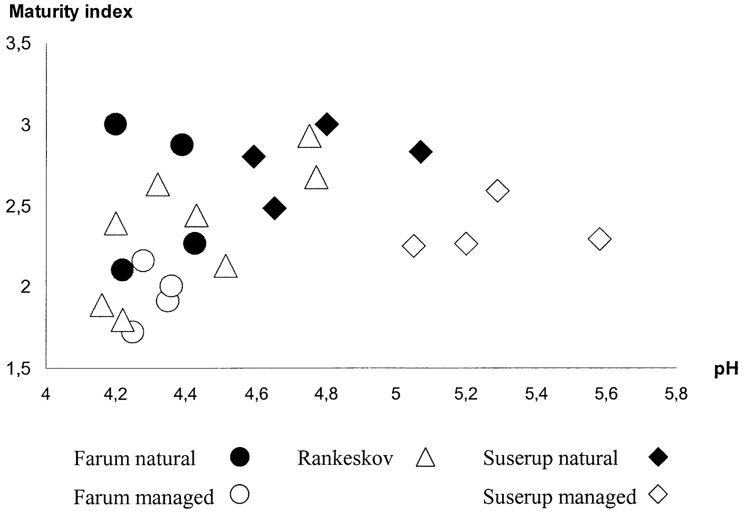

Fig 4. Relation between Maturity Index and pH for all samples. The distribution fits significantly (P=0,043; polynomial regression) to a second order function. Maturity Index is significantly higher in the two old natural forests (Farum & Suserup) compared to the nearby managed sites

The adult/juvenile–ratio was significantly higher in the natural forests compared to the managed forests (P = 0,046) (Fig. 2). This supports the finding of a higher Maturity Index in old natural forest sites, since nematode families with high cp-scores, are characterized by small gonads and a relatively low fecundity (Bongers 1990), indicating that these nematodes allocate a smaller proportion of their resources to reproduction. This could again lead to a population age structure with fewer juvenile individuals. The relative abundance of bacterial feeders was overall significantly lower (P= 0,008) in managed forest soils compared to natural forest soils (Fig. 3). The fungal feeders and root hair feeders are not always clearly separated on the family level, e.g the family Anguinidae contains species of both categories (Yeates et al. 1993). The division of these two groups seen in Figure 3 should therefore only be considered indicative and for this reason we have not tested the statistical significance of their distribution. A high input of dead organic material could be expected to reduce the relative proportions of herbivory (plant root feeders) to microbivory (bacterial feeders and fungal feeders) in the nematode community due to a relative increase in the activity of the primary decomposers. Other workers have found the higher relative abundance of bacterial feeders in early succesional phases of natural beech forest (Armandariz & Arpin 1996) and sand dunes (de Goede et al. 1993) compared to later successional phases. The plant community of the managed forests in this study can be considered to be in an artificial over-mature state, since understory canopy and seedlings were almost absent, while young and old trees and seedlings were mixed in the natural forest plots

Conclusion

Even though a relatively small data set was available, a very consistent pattern was detected. There was a clear separation of different geographical regions within 130 km distance in the small Island of Zealand, Denmark. Alaimidae, Plectidae and Hoplolaimidae were all more abundant in clay rich mull (pH ca. 5,2) which had a higher diversity compared to the sandy mull (pH = 4,5) where Aphelenchoididae and Cephalobidae were more abundant. Moreover, it was found that two old natural forests with a high amount of dead wood on the forest floor had a higher Maturity Index than the comparable managed forests, and that MI appears to interact with pH in a unimodal fashion. The adult/juvenile–ratio and relative abundance of bacterial feeders were higher in all natural forests, but as expected the effect was less pronounced in a less mature natural forest with less dead wood on the forest floor. Due to large geographical variation, further development of a monitoring scheme for the soil microfauna in nature-based forestry is thus recommended to rely on reference data from the area of interest. Future research could demonstrate the mechanisms behind a possible stimulation of long-lived nematodes by dead wood in forests, i.e. whether it acts as food resource or refuge during periods of harsh conditions inevitably encountered when life covers several seasons.

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