DIVERSITY AND ECOLOGICAL INTERACTIONS OF SOIL AND FOREST LITTER NEMATODES FROM A SCOTTISH WOODLAND

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Summary. Heron Wood (Peebleshire, Scotland) is part of the Dawyck Botanic Garden (Ordnance Survey grid reference NT(36)175355), which is situated on the Silurian rock system characteristic of the Scottish Borders. It lies on a NW slope of a hill covered with shallow stony soils, which are acidic and almost lime-free. The dominant vegetation is represented by beech (*Fagus*) and birch (*Betula*), with oaks (*Quercus*) being subdominant. Our analysis revealed 50 genera of nematodes belonging to six orders (Tylenchida, Rhabditida, Teratocephalida, Araeolaimida, Enoplida, and Dorylaimida). Five main ecologico-trophical groups revealed were: bacterial feeders, fungal feeders, plant feeders, animal predators and omnivores. In the forest litter, bacterial feeders were represented by fourteen genera (29.8%), animal predators by eleven genera (23.4%), omnivores by nine genera (19.1%), fungal feeders by four genera (8.5%), and plant feeding nematodes by nine genera (19.1%). In the soil, bacterial feeders (seven genera = 35%) and omnivores (seven genera = 35%) were the dominant groups. The representation of the other trophic groups in the soil varied from 5% (one genus of fungal feeders) to 10% (two genera of predators) and 15% (plant feeders - three genera). In comparison with the litter, there was a considerable decrease of taxonomic diversity in the soil (in soil only twenty genera of nematodes were revealed, while in leaf litter 47 were revealed). There were also remarkable differences in the recorded ecological interactions. These results may provide a valuable reference for further ecological and biodiversity studies.

Keywords: Ecologico-trophical groups, nematode abundance, nematode community.

Nematodes are one of the most abundant groups of the soil and litter fauna, and they play an important role in regulating microbial communities (Krivtsov *et al.*, 2006; Krivtsov *et al.*, 2007b; Torr *et al.*, 2007). However, very few animal ecologists study them, probably because of the difficulties of identifying them to species by morphological methods (Torr *et al.*, 2007). The abundance and species richness of nematodes can be affected by changes in the environment and they may, therefore, be of value in determining changes in soil and litter properties. Understanding the role of microfauna in these processes is an important factor in our understanding of their relationship with plant communities (Wardle, 2006).

A number of studies have considered the abundance of nematodes in a variety of soil and litter habitats (e.g. in grasslands, cultivated areas, managed forests of beech, spruce, Douglas fir and Scots pine) and their role in determining soil structure and functioning, as well as involvement in abiotic and biotic environmental interactions (Hodda and Wanless, 1994a,b; Robertson and Freckman, 1995; Alphei, 1998; Panesar *et al.*, 2000, 2001; Sohlenius and Bostrom, 2001). Some studies have provided valuable information on nematode biodiversity (Hodda and Wanless, 1994b; Panesar *et al.*, 2001; Foucher *et al.*, 2004). However, research simultaneously considering taxonomic diversity and ecological interactions of nematodes with both biological and abiotic factors, whilst contrasting forest litter and soil horizons, remains scarce. The purpose of this paper was to describe such a study conducted at the Dawyck Cryptogamic Sanctuary, which is an important site for ecological research.

MATERIALS AND METHODS

Site Description. Heron Wood (Peebleshire, Scotland) is situated within the area belonging to the Dawyck Botanic Garden. It is 7.5 hectares in size and has a 10,000 m^2 plot delineated for the purposes of ecological research (Krivtsov *et al.*, 2007a). In each quarter of this plot, there are two smaller plots (each 100 m^2 in size). The layout of the sampling site is in accordance with standard practice used by the Forestry Commission, and covers a range of woodland habitats (dominated by beech, birch and oak) and a clear area covered with grass (dominated by *Holcus lanatus* L.). Further information on Heron Wood and relevant research at this site is available from our previous publications (Krivtsov *et al.*, 2003a,b, 2004a,b, 2005, 2006, 2007b).

Sampling and analysis. Composite samples of forest floor (consisting predominantly of forest litter) and soil cores (taken from the soil surface down to approximately 10-15 cm depth after removing litter) were collected monthly during Sept-Dec 2001 (32 samples each month: eight plots, four replicates from each plot) using a plastic sampling frame (approximately 150 cm^2) and a manual soil corer. The exact positions of sampling points were determined *a priori* using a random number generator. In the laboratory, litter samples were hand sorted and the litter composition was determined on a percentage (weight for weight) basis. Moisture content was determined via weight loss after drying for 48 hr at 80 °C. Soil was sieved, and the subsequent determinations were carried out on the <2 mm fraction.

Nematodes were routinely identified into three trophic groups using a light microscope. Baermann funnels (we used 5 g of fresh fragmented litter, whilst for soil 10 g of the fraction < 2 mm) were used for the extraction of nematodes. The major groups included microbial feeders (MFN), plant feeders (PFN), and predators. After determination of the dry weights of the soil and litter samples, nematode abundance was estimated per 100 g of dry weight (all abundances are, therefore, reported to 100 g dry weight).

Routine identification of nematodes for the purpose of separation into the three trophic groups mentioned above was carried out using pharyngeal morphology plus the behaviour of live material, movement being the important characteristic (Paramonov, 1962). To compile a taxonomic list, a limited number of nematodes were randomly selected for a more precise identification down to the genus and, where practicable, species level using dichotomous and polytomous keys.

In addition to the data on nematodes, the data set analysed also contained a number of variables available from the monitoring programme conducted on the site (Krivtsov *et al.*, 2003a,b, 2004a, 2005, 2006). Data were handled using SPSS and Microsoft Excel. For the purpose of the ANOVA analysis the nematode abundance data were transformed using Log(var + 1).

RESULTS AND DISCUSSION

Changes in the abundance of nematodes (specimens per 100 g) throughout the period of this research are given in Figures 1 and 2, whilst the list of recorded taxa is given in Table I. The results of the statistical analysis are presented in Tables II to IV. Nematodes appeared to be considerably more abundant in litter than in soil; however, that might partly have resulted from the differences in the extraction procedures. The most numerous group in all the habitats studied were MFN. In the soil, the abundance of both MFN and PFN was significantly dependent on the month and the plot, as well as on the plot × month interaction (Table II). In the litter, however, the effect of plot was not significant, whilst the effects of other factors were.

Taxonomic diversity. Our analysis revealed 50 genera of nematodes belonging to six orders (Tylenchida, Rhabditida, Teratocephalida, Araeolaimida, Enoplida, and Dorylaimida). Five main ecologico-trophical groups revealed were: bacterial feeders, fungal feeders, plant feeders, animal predators and omnivores. In the forest litter, bacterial feeders were represented by fourteen genera (29.8%), animal predators by eleven genera (23.4%), omnivores by nine genera (19.1%), fungal feeders by four genera (8.5%), and plant feeding nema-

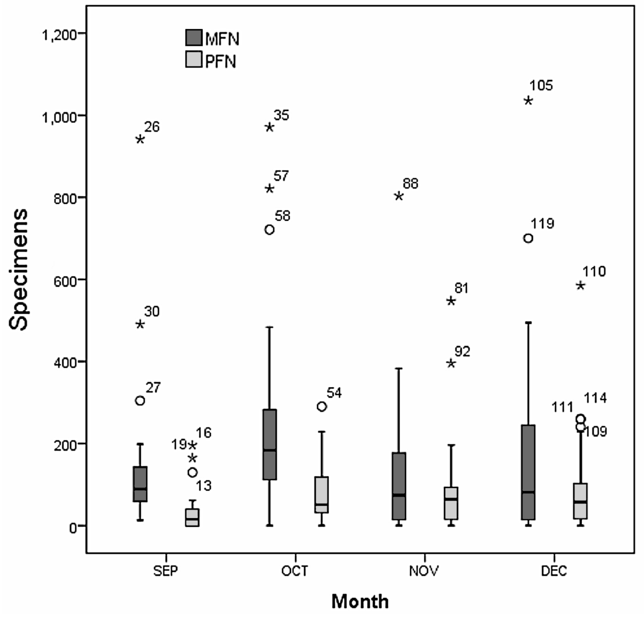

Fig. 1. Abundance of Microbial and Plant Feeding Nematodes (coded, respectively, as MFN and PFN) in the soil (specimens per 100 g). Outlier samples are labelled with the sample's number.

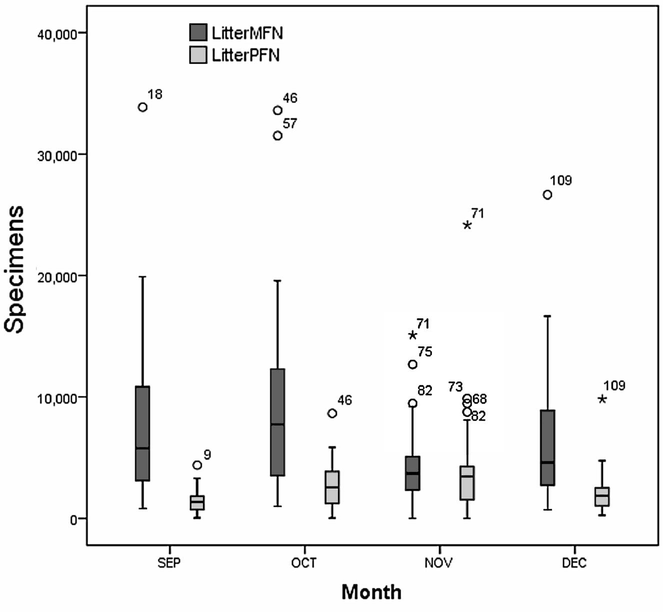

Fig. 2. Abundance of Microbial and Plant Feeding Nematodes (coded, respectively, as MFN and PFN) in the litter (specimens per 100 g). Outlier samples are labelled with the sample's number.

Table I. List of nematodes identified in the soil and litter of the Heron Wood Reserve.

Genera and species of nematodes	Ecologo-trophical groups of nematodes (feeding type)	Presence in litter	Presence in soil
Acrobeloides	bacterial feeding	Yes	Yes
Agmodorus	fungal feeding	Yes	No
Alaimus	bacterial feeding	Yes	Yes
Amphidelus	bacterial feeding	Yes	No
Anaplectus	bacterial feeding	Yes	No
Aphelenchus	fungal feeding	Yes	No
Basiria	plant feeding	Yes	No
Bastiania gracilis	bacterial feeding	Yes	No
Brachonchulus	predacious	Yes	No
Cephalobus	bacterial feeding	Yes	Yes
Cobbonchus	animal predation	Yes	No
Criconemella	plant feeding	Yes	No
Demaniella	bacterial feeding	Yes	No
Diplogasteroides	bacterial feeding	Yes	No
Dorylaimus	omnivorous	Yes	Yes
Enchodelus	omnivorous	Yes	Yes
Eucephalobus	bacterial feeding	Yes	Yes
Eudorylaimus	omnivorous	Yes	No
Granonchulus	animal predation	Yes	No
Helicotylenchus	plant feeding	Yes	Yes
Hemicycliophora	plant feeding	Yes	No
Iotonchus	animal predation	Yes	No
Kochinema	omnivorous	Yes	No
Labronema	omnivorous	Yes	Yes
Limonchulus	animal predation	Yes	No
Mesodorylaimus	omnivorous	Yes	Yes
Mononchus	animal predation	Yes	No
Nordia	omnivorous	No	Yes
Onchulus	animal predation	Yes	No
Paraphelenchus sp.	fungal feeding	Yes	No
Paraphelenchus pseudoparietinus	fungal feeding	Yes	Yes
Paratripyla	animal predation	Yes	Yes
Plectonchus	bacterial feeding	Yes	No
Plectus	bacterial feeding	Yes	Yes
Pratylenchus	plant feeding	Yes	Yes
Prionchulus	animal predation	Yes	Yes
Prismatolaimus	bacterial feeding	No	Yes
Prodorylaimus	omnivorous	Yes	No
Protorhabditis	bacterial feeding	No	Yes
Psilenchus	plant feeding	Yes	No
Qudsianema	omnivorous	Yes	Yes
Rhabditoides	bacterial feeding	Yes	No
Teratocephalus	bacterial feeding	Yes	No
Tetylenchus	plant feeding	Yes	No
Thornenema	omnivorous	Yes	No
Tripyla	animal predation	Yes	No
Trischistoma	animal predation	Yes	No
Tylencholaimus	fungal feeding	Yes	No
Tylenchus	plant feeding	Yes	Yes
Wilsonema	bacterial feeding	Yes	No
Xiphinema	plant feeding	Yes	No

Table II. Results of the univariate ANOVA.

Effect	Soil		Litter	
	MFN	PFN	MFN	PFN
Site	**	**	NS	NS
Month	**	**	**	*
Site* Month	**	*	**	**

* effect significant at the 95% probability level
** effect significant at the 99% probability level
NS = non-significant
MFN = Microbial Feeding nematodes
PFN = Plant Feeding Nematodes

todes by nine genera (19.1%). In the soil, bacterial feeders (seven genera = 35%) and omnivores (seven genera = 35%) were the dominant groups. The representation of the other trophic groups in soil varied from 5% (one genus of fungal feeders) to 10% (two genera of predators) and 15% (plant feeders = 3 genera). In comparison with the litter, there was a considerable decrease of taxonomic diversity in the soil (in soil only twenty genera of nematodes were revealed, while in leaf litter 47 were revealed).

Although scientific research involving biodiversity of Scottish soil nematodes has mainly concentrated on grasslands and cultivated land (Taylor *et al.*, 1994; Marshall *et al.*, 1998), a number of previous studies addressed species richness of nematodes in Scottish forest and woodland habitats (Boag 1974, 1977; Foucher *et al.*, 2004; Keith *et al.*, 2006; Torr *et al.*, 2007). These studies provide an opportunity for comparison with the results of our research.

Mesodorylaimus was one of the most abundant taxa found in our samples. The other common taxa included *Acrobeloides*, *Alaimus*, *Dorylaimus*, *Eucephalobus*, *Eudorylaimus*, *Helicotylenchus*, *Plectus*. Representatives of these groups have been identified in samples from Scotland before (Foucher *et al.*, 2004), along with the representatives of the less common genera *Xiphinema*, *Prodorylaimus*, *Rhabditoides*, *Teratocephalus*; our results are therefore in line with the previous research. It should be noted, however, that some genera found in our samples (*Basiria*, *Labronema*, *Paraphelenchus*, *Prionchulus*, *Tetylenchus* and, in particular, a very common genus on our site *Qudsianema*) were not reported in the study cited (Foucher *et al.*, 2004).

Another survey of the nematode genera associated with trees in Scotland (Boag, 1974) showed that *Tylenchus sensu lato*, *Aphelenchoides*, *Tylencholaimus*, *Trichodorus*, *Helicotylenchus*, *Rotylenchus*, *Criconemoides s.l.*, *Hemicriconemoides*, *Tylenchorhynchus*, *Pratylenchus* and *Paratylenchus s.l.* were commonly found in soil samples collected from around the roots of coniferous and deciduous trees, and that only *Criconemoides s.l.* appeared to have a significant preference for deciduous woods. This list appears to be somewhat different from ours, as we have only registered *Pratylenchus*, *Tylencholaimus*, *Tylenchus* and *Helicotylenchus* out of the species reported to be common in Scottish forest soils. It should be noted, however, that the previous research was characterised by a wider habitat coverage, whilst our samples are from a specific woodland.

Ecological interactions. The data sets containing the abundance of nematodes belonging to the three broadly defined trophic groups (i.e. MFN, PFN and predators) and a number of biological and abiotic variables (available from parallel investigations) have been analysed by non-parametric correlation analysis (Tables III and IV).

In the soil, PFN showed a positive correlation with moisture content, whilst both PFN and predators were positively related to pH. This indicates a preference for birch and grass dominated plots (beech plots are drier and more acidic). Negative effects of pH at this site have been noted before (Krivtsov *et al.*, 2007b), whilst research elsewhere reported an increased abundance of nematodes in a birch woodland compared to other habitats studied (Keith *et al.*, 2006). Predators were the only group showing a highly significant negative relation with the soil structure (i.e. relative amount of particles <2mm), which might relate to their hunting strategies.

As in the litter, all nematode groups showed positive relationships with flagellates, but the correlation with ciliates was significant only for MFN. Also, in contrast to the litter, there were no positive relationships with ergosterol; in fact a highly significant negative correlation between predators and ergosterol was revealed by the analysis. At the same time predators were positively related to bacteria. These relationships might be indicative of omnivory, and might also have been influenced by the fact that, in the autumn, some considerable proportion of fungal biomass may be redistributed from the soil into the litter layer. Also in contrast with the litter, there were no significant correlations between nematodes and mites, whilst collembola were positively related to both MFN and PFN.

In the litter, nematodes appear to show a preference

Table III. Correlation analysis on soil data.

		MFN	PFN	Pred
Kendall's Tau-b	moisture	0.093	0.246(**)	-0.027
	pH	0.110	0.130(*)	0.155(*)
	Soil organic content	0.069	0.081	-0.040
	<2mm soil fraction	-0.088	0.035	-0.266(**)
	root	0.022	-0.054	0.038
	Index of total microbial biomass	-0.118	0.082	-0.185(**)
	glomalin	0.144(*)	0.054	-0.105
	bacteria	0.068	0.042	0.206(**)
	Cryptostigmatid soil	0.060	0.018	0.070
	Mesostigmatid soil	0.092	0.123	0.075
	Collembola soil	0.202(**)	0.150(*)	0.072
	MFN	1.000	0.369(**)	0.208(**)
	PFN	0.369(**)	1.000	0.162(*)
	Pred	0.208(**)	0.162(*)	1.000
	Soil flagellates	0.145(*)	0.186(**)	0.290(**)
	Soil ciliates	0.121(*)	0.105	0.091
	Ergosterol	-0.110	-0.003	-0.241(**)

* Correlation is significant at the 0.05 level (2-tailed).
** Correlation is significant at the 0.01 level (2-tailed).
MFN = Microbial Feeding nematodes
PFN = Plant Feeding Nematodes
Pred = Predators

Table IV. Correlation analysis on litter data.

		MFN	PFN	Pred
Kendall's Tau-b	wood	-0.074	0.051	0.097
	seeds	-0.198(**)	-0.127(*)	-0.019
	grass	0.260(**)	0.148(*)	-0.063
	roots	0.085	0.105	-0.021
	beech	-0.102	-0.098	-0.155(*)
	birch	0.056	0.182(**)	0.035
	oak	-0.011	0.090	-0.104
	moss	0.035	0.017	-0.008
	Dry litter total	-0.186(**)	-0.079	0.024
	Litter density	-0.186(**)	-0.079	0.024
	moisture	0.408(**)	0.354(**)	0.073
	Ergosterol	0.235(**)	0.055	0.000
	Bacteria	0.014	0.012	0.048
	Cryptostigmatid mites	0.127(*)	0.108	0.050
	Mesostigmatid mites	0.150(*)	0.094	0.037
	Collembola	0.060	0.013	-0.086
	Flagellates	0.228(**)	0.153(*)	0.161(*)
	Ciliates	0.159(**)	0.245(**)	0.179(**)
	MFN	1.000	0.432(**)	0.119
	PFN	0.432(**)	1.000	0.195(**)
	Pred	0.119	0.195(**)	1.000

* Correlation is significant at the 0.05 level (2-tailed).
** Correlation is significant at the 0.01 level (2-tailed).
MFN = Microbial Feeding nematodes
PFN = Plant Feeding Nematodes
Pred = Predators

towards higher moisture content and abundant grass cover (significant correlations for MFN and PFN), whilst a number of correlations suggest a negative relationship with the remains of beech-dominated vegetation: significant negative correlations of MFN and PFN with seeds (fraction dominated by heavy beech seeds) and negative correlation between predators and beech leaves, positive correlation between PFN and birch leaves. These relationships are broadly in line with findings of the previous research (Krivtsov *et al.*, 2007b). All nematode groups were positively related to cilliates and flagellates (the most abundant groups of protozoa), perhaps indicating similar habitat preferences. There were also positive correlations of MFN and cryptostigmatid and mesostigmatid mites; the exact nature of these is at present unclear and forms part of the scope for future analysis.

Remarkably, none of the nematode groups in the litter showed significant relationships with bacteria. The lack of correlations may suggest that bacterial abundance may have considerably exceeded nematodes requirements, and was mainly controlled by other factors. However, MFN were significantly correlated with ergosterol, thus indicating that fungal hypha might have been a preferred food source. This makes sense, as the study was conducted during an autumn period of intense fungal fruiting, when fungal levels in the litter are particularly elevated (Krivtsov *et al.*, in preparation).

CONCLUSION

The present study provides simultaneous records of nematode taxonomic diversity and ecological interactions in the litter and soil horizons of Heron Wood Reserve, a Scottish woodland important for ecological research. Both nematode abundance and taxonomic diversity appeared to be considerably greater in the litter horizon than in the soil; however, that might partly have resulted from the differences in the extraction procedures. There were also remarkable differences in the recorded ecological interactions. The nematode biodiversity and ecological interactions reported here were indicative of the specific conditions of the study and may, therefore, prove valuable for future comparisons with research conducted elsewhere. In particular, they are likely to provide a useful reference for studies on managed habitats that analyse effects of management practices, and further studies on natural ecosystems to determine the extent of possible environmental change.

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LITERATURE CITED

Alphei J., 1998. Differences in soil nematode community structure of beech forests: Comparison between a mull and a moder soil. *Applied Soil Ecology, 9*: 9-15.

Boag B., 1974. Nematodes associated with forest and woodland trees in Scotland. *Annals of Applied Biology, 77*: 41-50.

Boag B., 1977. Factors influencing occurrence and abundance of nematodes in forest soils in eastern Scotland. *Annals of Applied Biology, 86*: 446-450.

Fitter A.H., Gilligan C.A., Hollingworth K., Kleczkowski A., Twyman R.M. and Pitchford J.W., 2005. Biodiversity and ecosystem function in soil. *Functional Ecology, 19*: 369-377.

Foucher A.L.J.L., Bongers T., Noble L.R. and Wilson M.J., 2004. Assessment of nematode biodiversity using DGGE of 18S rDNA following extraction of nematodes from soil. *Soil Biology and Biochemistry, 36*: 2027-2032.

Hodda M. and Wanless F.R., 1994a. Nematodes from an English chalk grassland - population ecology. *Pedobiologia, 38*: 530-545.

Hodda M. and Wanless F.R., 1994b. Nematodes from an English chalk grassland - species distributions. *Nematologica, 40*: 116-132.

Keith A.M., van der Wal R., Brooker R.W., Osler G.H.R., Chapman S.J. and Burslem D.F.R.P., 2006. Birch invasion of heather moorland increases nematode diversity and trophic complexity. *Soil Biology & Biochemistry, 38*: 3421-3430.

Krivtsov V., Bezginova T., Salmond R., Liddell K., Garside A., Thompson J., Palfreyman J.W., Staines H.J., Brendler A., Griffiths B. and Watling R., 2006. Ecological interactions between fungi, other biota and forest litter composition in a unique Scottish woodland. *Forestry, 79*: 201-216.

Krivtsov V., Brendler A., Watling R., Liddell K. and Staines H.J., 2007a. Some aspects of forest soil and litter ecology in the Dawyck Cryptogamic Sanctuary with a particular reference to fungi. *Acta Ecologica Sinica*, *27*: 813-834.

Krivtsov V., Garside A., Brendler A., Liddell K., Griffiths B.S. and Staines H.J., 2007b. A study of population numbers and ecological interactions of soil and forest floor microfauna. *Animal Biology, 57*: 467-484.

Krivtsov V., Griffiths B.S., Salmond R., Liddell K., Garside A., Bezginova T., Thompson J.A., Staines H.J., Watling R. and Palfreyman J.W., 2004a. Some aspects of interrelations between fungi and other biota in forest soil. *Mycological Research, 108*: 933-946.

Krivtsov V., Illian J.B., Liddell K., Garside A., Bezginova T., Salmond R., Thompson J., Griffiths B., Staines H.J., Watling R., Brendler A. and Palfreyman J.W., 2003a. Some aspects of complex interactions involving soil mesofauna: analysis of the results from a Scottish woodland. *Ecological Modelling, 170*: 441-452.

Krivtsov V., Liddell K., Bezginova T., Salmond R., Garside A., Thompson J., Palfreyman J.W., Staines H.J., Watling R., Brendler A. and Griffiths B., 2003b. Ecological interactions of heterotrophic flagellates, ciliates and naked amoebae in forest litter of the Dawyck Cryptogamic Sanctuary (Scotland, UK). *European Journal of Protistology, 39*: 183-198.

Krivtsov V., Liddell K., Bezginova T., Salmond R., Staines H.J., Watling R., Garside A., Thompson J.A., Griffiths B.S. and Brendler A., 2005. Forest litter bacteria: relationships with fungi, microfauna, and litter composition over a winter-spring period. *Polish Journal of Ecology, 53*: 383-394.

Krivtsov V., Walker S.J.J., Staines H.J., Watling R., Burt-Smith G. and Garside A., 2004b. Integrative analysis of ecological patterns in an untended temperate woodland utilising standard and customised software. *Environmental Modelling & Software, 19*: 325-335.

Marshall B., Boag B., McNicol J.W. and Neilson R., 1998. A comparison of the spatial distributions of three plant-parasitic nematode species at three different scales. *Nematologica, 44*: 303-320.

Panesar T.S., Marshall V.G. and Barclay H.J., 2000. The impact of clearcutting and partial harvesting systems on population dynamics of soil nematodes in coastal Douglas-fir forests. *Pedobiologia, 44*: 641-665.

Panesar T.S., Marshall V.G. and Barclay H.J., 2001. Abundance and diversity of soil nematodes in chronosequences of coastal Douglas-fir forests on Vancouver Island, British Columbia. *Pedobiologia, 45*: 193-212.

Paramonov A.A., 1962. *Osnovy fitogel'mintologii.* Izdatelstvo Akademii Nauk, Moscow, SSSR.

Robertson G.P. and Freckman D.W., 1995. The spatial-distribution of nematode trophic groups across a cultivated ecosystem. *Ecology*, *76*: 1425-1432.

Sohlenius B. and Bostrom S., 2001. Annual and long-term fluctuations of the nematode fauna in a Swedish Scots pine forest soil. *Pedobiologia, 45*: 408-429.

Taylor C.E., Brown D.J.F., Neilson R. and Jones A.T., 1994. The persistence and spread of *Xiphinema diversicaudatum* in cultivated and uncultivated biotopes. *Annals of Applied Biology, 124*: 469-477.

Torr P., Spiridonov S.E., Heritage S. and Wilson M.J., 2007. Habitat associations of two entomopathogenic nematodes: a quantitative study using real-time quantitative polymerase chain reactions. *Journal of Animal Ecology, 76*: 238-245.

Wardle D.A., 2006. The influence of biotic interactions on soil biodiversity. *Ecology Letters, 9*: 870-886.

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