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Food web diagnostics and functional diversity of soil inhabiting nematodes in a natural woodland

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Summary

Functional diversity and detritus soil food web of soil inhabiting nematodes in natural woodland dominated by *Acacia nilotica* L. was studied. Functional diversity was studied in terms of trophic groups assessed by Trophic diversity index (TDI) and Shannon-Weaver index (H'), while food web was diagnosed by channel index (CI). The plant parasitic channel was determined by plant parasitic index (PPI). The stability of the soil ecosystem was measured in terms of maturity index (MI), structure index (SI) and enrichment index (EI). Shannon-Weaver index of the area was recorded as 2.1 ± 0.3 while trophic diversity index 2.6 ± 0.7, maturity index (MI) 3.1 ± 0.2, channel index 62.4 ± 28.1 and structure and enrichment indices 68.1 ± 18.5 and 15.4 ± 13.7 respectively. A high degree of positive correlation was recorded between population of dorylaims and MI while some degree of negative correlation existed between population of plant parasitic nematodes and MI. Population of other nematodes showed a positive correlation with SI and EI. The faunal profile was found to be tilted towards quadrat C giving the idea of relatively undisturbed ecosystem with moderate enrichment and fungal decomposition channel.

Keywords: Channel index; enrichment index; food web diagnostics; functional diversity; India; maturity index

Introduction

Soil nematodes offer great potential for use as indicator of biodiversity and ecological stability, and for assessing the impact of changing land use on soil condition. The assemblage of plant and soil nematode species occurring in a natural or managed ecosystem constitute nematode community. Their role in a soil ecosystem is to recycle nutrients by feeding plant tissue and micro-organisms and liberating minerals for easy absorption by plant roots. Because of varied life spans and different reproductive and survival capacity, the nematode communities have been used as ecological bio-indicators to reflect environmental changes (Freckman, 1982; Samoiloff, 1987; Bongers, 1990). The abundance of each species in the community can be transformed into ecological indices and parameters to measure community changes in diversity and trophic structure (Bongers, 1990), and further to assess soil disturbance levels and decomposition pathways. Nematode communities can be studied on the basis of functional groups which can be regarded as groups of species that have similar effects like predation or herbivory on ecosystem processes. Ecological indices based on the proportional contribution of each nominal nematode taxon, such as Shannon-Weaver Index (H') Trophic diversity index (TDI), Maturity index (MI) and plant parasitic index (PPI) provide focused tools for assessing the stability / disturbance in the ecosystem. The cp (colonizer-persister) values (Bongers, 1990) of species reflect the perceived position on a r-k spectrum based on their reproductive rate and correlated characteristics. The ratio between abundance of two functional groups, i.e., bacteriovores and fungivores, gives an index of the relative contribution of the two main decomposition channels. It is expressed as the Nematode Channel Ratio (NCR). Various functional guilds of nematodes have been described to compute Enrichment index (EI) and Structure index (SI) (Ferris *et al.,* 2001). The enrichment index is based on the expected responsiveness of the opportunistic guilds to the food resourse enrichment. Thus, EI describes whether a soil ecosystem is nutrient enriched (high EI) or depleted (low EI). The SI represents an aggregation of functional guilds with cp values ranging from 3 to 5. SI describes whether a soil ecosystem is structured/matured (high SI) or disturbed/degraded (low SI).

Although a little is known about the abundance of plant and soil nematodes in tropical forests, some studies suggest that the total nematode population at a given site in a tropical forest may range from 8,100 per m^2 to 1,900,000 per

m[2] (Petersen, 1982). Pradhan and Das (1987) recorded monthly mean nematode populations between 151,000 and 661,000/m² for Indian forest dominated by *Shorea robusta* Gaert, F. Other forest soils include 79 species for a Danish forest (Yeates, 1972), 92 species for Slovakian forest (Šály, 1975), and 106 species in South West Germany (Ruess, 1995). Ruess (2003) compared decomposition pathways of different ecosystems. He recorded values of channel index (CI) in crop field, grassland and forest as 18, 24 and 50 respectively. Due to limited knowledge on the nematode community structure of tropical forests in India, the present study was planned. Thus, the objective of the present study was to assess the nematode community dynamics in an undisturbed forest ecosystem

Materials and methods

The site (27° 43' 0" North, 78° 5' 0" East) was an *Acacia* forest located 15 km from Aligarh city on Aligarh-Agra highway, Uttar Pradesh, India. It is a natural woodland of *Acacia* trees covering an area of about 35 ha. Leaf litter covers the upper layer of the soil which is responsible for pH 7.2 of the soil. Available organic carbon of the area was 0.30 %, while available potash and available phosphates 20 g/m² and 1.7 g/m² respectively. This forest is generally free from human interference, as tree cutting is permitted only in the outer area. *Bosephalus tragocamelus* L. (Blue bull) is mainly responsible for grazing in this forest area. Five sampling sites, each covering an area of 5 m² were selected randomly. From each site five cores were collected from a depth of 0 – 10 cm using a steel corer of 5 cm diameter, bulked and mixed to form a single sample. Sampling was done in the months of September 2005, December 2005 and March 2006. Samples were brought to laboratory and further processing was followed according to the method of Tomar *et al.* (2006). Mass slides containing two hundred nematodes per sample were prepared for identification. Identification up to generic level was done mainly using Goodey (1963); Jairajpuri and Khan (1982); Andrássy (1984), Siddiqi (1986), Jairajpuri and Ahmad (1992); Ahmad (1996). Trophic group were allocated according to Yeates *et al.* (1993) and coloniser-persistor (cp) scale was assigned after Bongers (1990). Nematode diversity was described using the univariate measures of the Shannon-Weaver index calculated at genus level (H'). Nematodes were assigned to five main trophic groups (bacteriovores, fungivores, herbivores, omnivores and predators) after Yeates *et al.* (1993). Maturity index was calculated to estimate the relative state of the eco-system studied ($MI = \sum V_i f_i$) (where V_i is assigned cp value
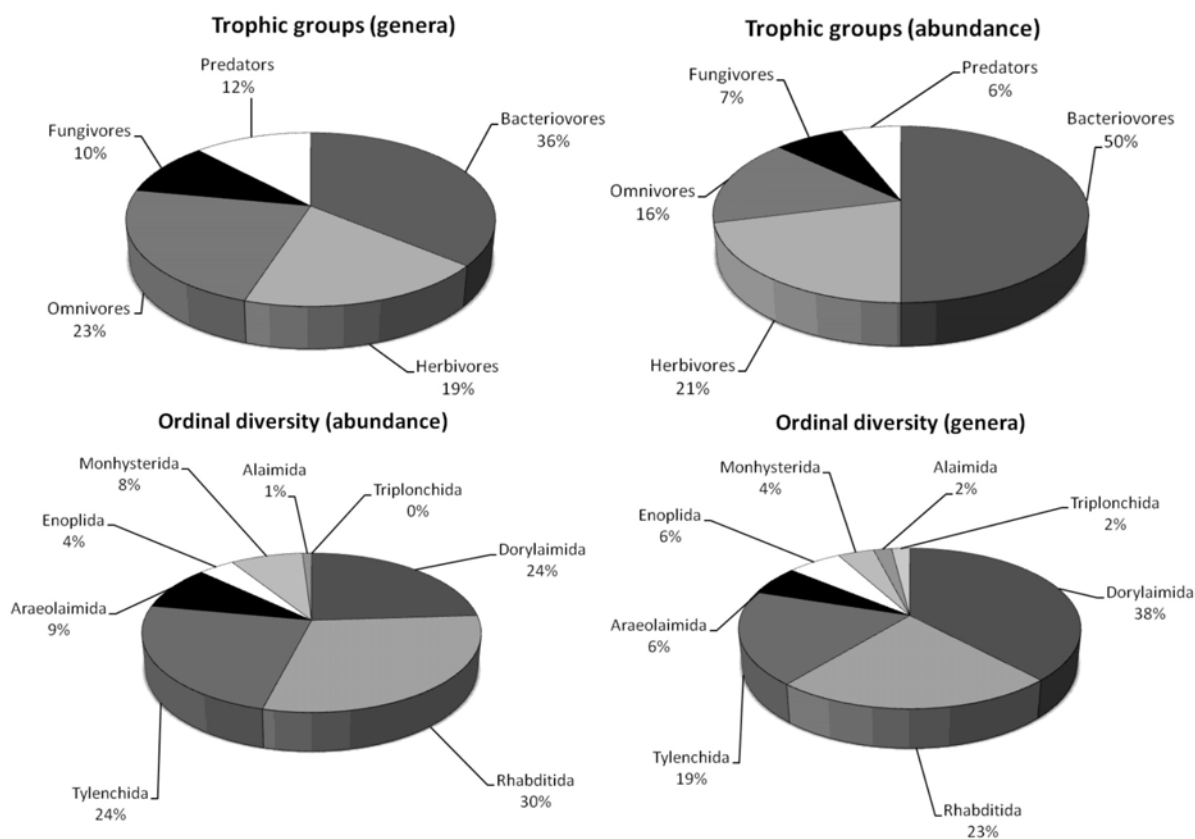

Fig. 1 Community structure of soil inhabiting nematodes in acacia forest

to taxon i, f_i is frequency of that taxon). Trophic diversity was calculated by the trophic diversity index ($TDI = 1 / \sum pi^2$) (Heip et al., 1988) (where P_i is proportion of individual of taxon i^{th} in the total population). The channel index ($CI = 100 \times 0.8 Fu_2 / (3.2Ba_2 + Fu_2)$) (Ferris et al., 2001) (where Fu_2, Ba_2 are assigned functional guilds) was calculated to indicate predominant decomposition pathways (Ruess, 2003). Structure index ($SI = (s/s+b) \times 100$) and enrichment index ($EI = (e/e+b) \times 100$) (where e, b and s are sum products of assigned weights and number of individuals of all genera) were calculated to determine the relative stability of the ecosystem. In all the above-mentioned indices, nematode families were allocated cp scale according to their perceived life history strategy. All the data were subjected to analysis of variance (ANOVA) in SPSS software program. Differences with $P < 0.05$ were considered significant while those with $P < 0.01$ were highly significant. Correlation between indices and trophic groups were done by SPSS.

Results

Diversity and abundance (Fig. 1)
A total of fifty two nematode genera belonging to eight orders and twenty four families were recorded. The number of genera in fifteen samples varied from 7 to 16 per sample while abundance varied from 381 to 1404 individuals per 100 g dry soil. In terms of number of genera, the order Dorylaimida was most frequent followed by Rhabditida, Tylenchida, Enoplida, Araeolaimida, Monhysterida, Alaimida and Triplonchida. In terms of number of individuals, Rhabditida was most abundant, followed by

Table 1. Percent share of nematode genera present in Acacia forest

Genera	Family	c-p Value assigned	Natural Forest %	Genera	Family	c-p Value assigned	Natural Forest %
Bacteriovores				*Tylenchus*	Tylenchidae	2	3.27, S
Acrobeles	Cephalobidae	2	13.6, E	*Xiphinema*	Xiphinematidae	5	0.87, R
Acrobeloides	Cephalobidae	2	0.41, R	**Fungivores**			
Alaimus	Alamidae	5	1.03, S	*Aphelenchus*	Aphelenchidae	2	3.82, S
Chiloplacus	Cephalobidae	2	0.47, R	*Aphelenchoides*	Aphelenchidae	2	1.10, S
Chronogaster	Plectidae	2	7.5, D	*Axonchium*	Belondiridae	5	0.20, R
Cephalobus	Cephalobidae	2	3.68, S	*Dorylaimellus*	Belondiridae	5	0.60, R
Cuticularia	Rhabditidae	2	0.47, R	*Tylencholaimus*	Tylencholaimidae	4	1.70, S
Eucephalobus	Cephalobidae	2	0.39, R	**Omnivores**			
Mesorhabditis	Rhabditidae	1	1.9, S	*Amphidorylaimus*	Dorylaimidae	4	0.34, R
Monhystera	Monhysteridae	1	1.5, S	*Dorylaimus*	Dorylaimidae	4	1.21, S
Prismatolaimus	Monhysteridae	1	6.7, D	*Dorylaimoides*	Mydonomidae	4	3.62, S
Plectus	Plectidae	2	0.75, R	*Eudorylaimus*	Qudsianematidae	5	2.0, S
Panagrolaimus	Panagrolaimidae	1	1.22, S	*Ecumenicus*	Qudsianematidae	4	0.54, R
Rhabditis	Rhabditidae	1	0.82, R	*Kochinema*	Nordiidae	4	0.27, R
Rhabdolaimus	Rhabditidae	1	0.20, R	*Labronema*	Qudsianematidae	4	0.13, R
Tobrilus	Tripylidae	2	0.89, R	*Oriverutus*	Nordiidae	4	1.76, S
Teratorhabditis	Rhabditidae	1	0.12, R	*Poronemella*	Qudsianematidae	4	0.13, R
Wilsonema	Plectidae	2	0.61, R	*Sicorinema*	Qudsianematidae	4	0.20, R
Zeldia	Cephalobidae	1	1.10, S	*Mesodorylaimus*	Dorylaimidae	4	5.47, D
Herbivores				*Thornenema*	Dorylaimidae	4	0.06, R
Boleodorus	Tylenchidae	2	11.99, E	**Predators**			
Basiria	Tylenchidae	2	0.54, R	*Aporcelaimellus*	Aporcelaimidae	5	1.49, S
Hoplolaimus	Hoplolaimidae	3	1.23, S	*Discolaimus*	Qudsianematidae	5	1.90, S
Helicotylenchus	Hoplolaimidae	3	0.46, R	*Discolaimoides*	Qudsianematidae	5	0.48, R
Hemicriconemoides	Criconematidae	3	0.06, R	*Ironus*	Ironidae	4	1.32, S
Merlinius	Belonolaimidae	4	1.70, S	*Laimydorus*	Dorylaimidae	5	0.74, R
Tylenchorynchus	Belonolaimidae	3	0.57, R	*Triypla*	Tripylidae	3	2.05, S
Trichodorus	Trichodoridae	4	0.27, R				

E - Eudominant > 10.0; D - Dominant 5.1 – 10.0; S - Subdominant 1.1 – 5.0; R - Recedents ≤ 1.0

Table 2. Trophic groups of soil inhabiting nematodes in Acacia forest (n = 15, mean ± SD)

Trophic Groups	mean±SD	Range
Bacteriovores	418 ± 151.21	216 – 706
Herbivores	210 ± 94.22	0 – 348
Fungivores	69.38 ± 56.00	0 – 233
Omnivores	121.07 ± 85.11	15 – 291
Predators	57.92 ± 30.9	0 – 125
TDI	2.60 ± 0.75	1.01 – 3.46

Dorylaimida, Tylenchida, Araeolaimida, Monhysterida, Enoplida, Alaimida and Triplonchida. The abundance of dorylaims per sample ranged from 20 – 53.8 %, tylenchids ranged from 0 – 46.7 %, while that of other nematode groups combined together ranged from 23 – 57 %.

Trophic groups (Fig. 1, Tables 1 and 2)
Bacteriovores constituted the most dominant group in terms of number of genera and individuals, followed by herbivores, omnivores, fungivores and predators. The number of bacteriovores in 15 samples ranged from 216 – 706 (418 ± 151.2) per 100 g dry soil, followed by herbivores 0 – 348 (210 ± 94.22), fungivores 0 – 233 (69.38 ± 56.0), and omnivores 15 – 291 (121.07 ± 85.11). The predators were least abundant, 0 – 125 (57.9 ± 30.9). The trophic diversity index (TDI) of the area ranged from 1.0 –

Table 3. Characteristics of Acacia forest (AF*, n = 15, mean ± SD)

Characteristics	mean±SD	Range
Number of nematode Genera	12.33 ± 3.07	7 – 16
Abundance	828.27 ± 257.02	381 – 1404
H'	2.18 ± 0.31	1.39 – 2.57
MI	3.16 ± 0.27	2.67 – 3.67
PPI	3.06 ± 0.37	0 – 3.55
CI	62.49 ± 28.13	0 – 100
EI	15.45 ± 13.73	0 – 49.92
SI	68.15 ± 18.5	27.13 – 100

3.4 (2.6 ± 0.7). Among bacteriovores the genus *Acrobeles* was most dominant while the genera *Boleodorus, Mesodorylaimus, Aphelenchus* and *Aporcelaimellus* were the most dominant among herbivores, omnivores, fungivores and predators, respectively. Least dominant genera among bacteriovores, herbivores, omnivores, fungivores and predators were *Teratorhabditis, Hemicriconemoides, Thornenema, Axonchium* and *Laimydorus,* respectively. All the samples contained bacteriovores and omnivores while herbivores, fungivores and predators were absent from two samples each. In terms of percentage share in a community, the Eudominant genera were *Acrobeles* and *Boleodorus* while the dominant genera were *Chronogaster,*
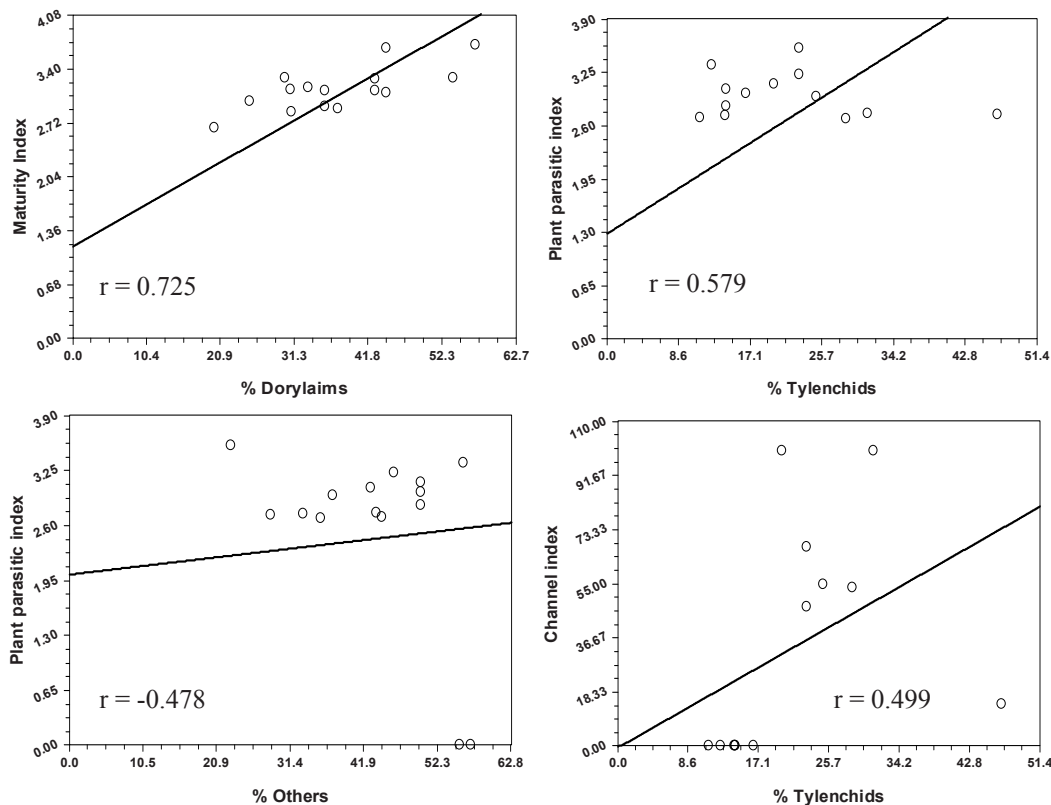

Fig. 2. Correlation graphs between different indices in Acacia forest

Prismatolaimus and *Mesodorylaimus*. The genera *Alaimus, Cephalobus, Mesorhabditis, Monhystera, Panagrolaimus, Zeldia, Hoplolaimus, Merlinius, Oriverutus, Tylenchus, Aphelenchus, Aphelenchoides, Tylencholaimus, Dorylaimus, Eudorylaimus, Aporcelaimellus, Discolaimus, Dorylaimoides, Ironus,* and *Tripyla* were subdominants *while rest were recedents.*

feeding roles (Gupta & Yeates, 1997), than for other mesofauna and they can be used in case studies for biomonitoring and ecological investigations. Analysis of the generic composition of nematode community and determination of dominant genus with the application of current knowledge on their biology is an effective tool in evaluating the role of nematodes in the soil processes (Háněl, 1995, 1998).
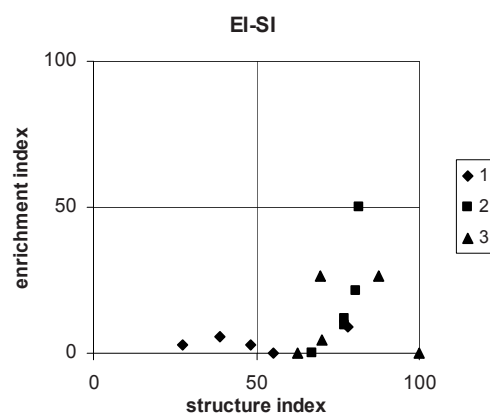
Table 4. Correlation coefficient between different indices

	MI	PPI	NCR	D%	T%	O%	CI	SI	EI
MI	1.000								
PPI	.024	1.000							
NCR	.009	-.264	1.000						
D%	.725**	-.199	-.255	1.000					
T%	-.422	.579*	-.235	-.576*	1.000				
O%	-.227	-.478	.524*	-.321	-.589*	1.000			
CI	-.092	.342	-.524*	-.301	.499	-.279	1.000		
SI	.305	-.435	.387	.027	-.280	.305	-.300	1.000	
EI	-.475	-.386	.245	-.165	-.133	.322	-.439	.386	1.000

** Correlation is significant at the 0.01 levels.
 * Correlation is significant at the 0.05 levels

Functional diversity and food web diagnostics
For assessing the functional diversity and role of nematodes in the forest ecosystem, various indices were calculated using the weighted faunal analysis concept of Bongers (2001). The results are presented in Table 3.
Correlation studies between population of dorylaims, tylenchids and other nematode groups (Table 4, Fig. 2) with various indices obtained in the present study revealed a high degree of positive or negative correlations. A high degree of positive correlation (+0.725) (P < 0.01) was recorded between population of dorylaims and MI, but for rest all other indices it was either negatively correlated or almost no correlation existed. Population of tylenchids were significantly correlated with PPI (+0.579) (P < 0.05), and to a certain level with CI (+0.342) (ns), while some degree of negative correlation was found with MI (-0.422) (ns). No correlation was found with EI. Population of other nematodes showed a positive correlation to a certain level with SI (+0.305) and EI (+0.322) while it was negatively correlated with PPI (-0.478) (ns). The graph plotted between enrichment index and structure index (faunal profile) was found to be tilted towards quadrat C (Fig.3), giving the idea of relatively undisturbed ecosystem with moderate enrichment and fungal decomposition channels (high values of CI).

Discussion

In recent years, much emphasis has been given to belowground diversity and its relationship with above-ground diversity. In soil, nematodes, collembolans and mites are the three groups of mesofauna which are considered as important biological indicators. Of the three groups, nematodes may be the most suitable for environmental diagnosis based on the community structure analysis, because more information exists on their taxonomy and

Fig. 3. Faunal profile for natural forest.
(1,2,3 represent sampling times)

The population fluctuation of herbivores is connected with plant growth in fields while those of bacteriovores with periodic changes of soil water content, and fungivores with fungal root decomposition in the soil. Stress factor as pollution might have a considerable effect on functioning and stability of nematode community because of disappearance of the most sensitive species (cp 4 and cp 5), resulting in decreasing diversity (Korthals *et al.,* 1996). The most sensitive nematode species to pollutants and other disturbances are the predators and omnivores nematodes. The predators regulate other soil biota numerically by feeding at the most dominant prey, which in turn provide an opportunity for recedent species to grow. The omnivores assist predators, bacterivores and fungivores where necessary. As these persistors are the first to disappear, it is likely that system becomes less stable functionally in terms of soil borne plant pathogens and buffering against seasonal and unpredictable nutrient flushes (Bongers & Bongers, 1998).

In the present study fifty two nematode genera were recorded with bacteriovores constituting the most dominant group which is in full agreement with Yeates (2003) report of dominance of bacterial feeders in forest soil. The high value of Shanon-Weaver index (H') in the present study confirm well with the earlier reports for a pine forest, 1.99 (Yeates, 1998) and 2.62 (Yeates, 2003) respectively, but was lower compared to one recorded for a natural forest in Arunachal Pradesh, India (Baniyamuddin *et al.,* 2007). They recorded H' value as high as 3.86, which may be due to the fact that natural forest in that part of India has enormous plant diversity and is probably responsible for much diverse nematode fauna. The high value of MI (3.16) in the present study correspond well with the earlier reports, 2.68 (Háněl, 1996), 2.07 (Pattison *et al.*, 2004) and 3.37 (Baniyamuddin *et al.,* 2007) in the natural forest. TDI also indicated high diversity of trophic groups in this study. Population of dorylaims showed a high degree of positive correlation with MI, as the dorylaims generally represent cp 4 – 5 nematodes (the group having long generation time, low fecundity and great sensitivity to disturbance), and their weighted mean results in high value of MI. Population of tylenchids also significantly correlated with PPI, as majority of tylenchids are plant parasites and are responsible for plant parasitic channel in the ecosystem. The value of plant parasitic index showed the presence of parasitic channels in the food web, which are reported to be present in a mature forest ecosystem (Baniyamuddin *et. al.,* 2007). Ecological indices such as CI, SI and EI provide an insight into the nematode community structure in stressed, enriched, stable structured and decomposition environments, and provide information on the dynamics of the soil food web (Ferris *et al.*, 2001). The percentage of the opportunistic nematode grazers on fungi and bacteria, weighted by their fecundity and life course characteristics gives the nature of decomposition channels through soil food web, which is measured as CI. It gives the degree of fungal participation in the primary decomposition channels of soil food webs. A higher CI at any site indicates a higher proportion of fungal decomposition and reflect the high relative abundance of cp2 fungal feeders (Aphelenchoididae and Aphelenchidae) and the corresponding low abundance of cp1 bacterial feeders (Rhabditidae and Panagrolaimidae). Wasilewska (1997) suggested that high values of CI indicates a slow cycling of elements in the ecosystem because the breakdown of dead tissue by bacteria and fungi releases bio-elements at a rate slower than that caused by phytophages. This may also indicate that there is relatively greater mineralization of nutrients via the decomposition pathways than via consumption of primary production by the nematodes. High CI values recorded in this study imply that decomposition in this natural woodland was fungal dominated food web mainly because of relatively high abundance of cp2 fungal feeders. The SI values in the present study were high in agreement with that of high SI values in the natural woodland (Ferris *et al.*, 2001). This is because of high abundance of omnivores and predators (cp3-5), which suggests a food web with more trophic linkages in the ecosystem (Ferris & Matute, 2003). Higher SI values suggest a complex community structure with more linkages in the food web, greater resilience, and greater buffering of population (Ferris *et al.*, 2001), which potentially provides more biological control to regulate or suppress plant parasitic nematodes (Berkemans *et al*., 2003). EI reflects the availability of resources to the soil food web and the response of primary decomposers to the resources (Ferris *et al.*, 2004). Generally, the low values of EI reflects low abundance of Rhabditidae and dominance of Cephalobidae which is in full agreement with present findings, as EI values are low because of the dominance of Cephalobidae, and low abundance of Rhabditidae.

The graphical representation of EI and SI is termed as faunal profile, where four quadrats (A, B, C and D) can be recognized for different type of soil conditions. The natural forests have food webs predominantly in quadrat C of the faunal profile in full agreement with present results (Fig. 3), indicating structured food webs and relatively low primary productivity. Many areas reflect the effect of management or disturbance. Some appear highly disturbed and nutrient enriched so that opportunistic nematode predominate (quadrat A, Ferris *et al*., 2001), while in some others, the food webs of the managed grasslands have attained some structure while still exhibiting a high level of primary productivity (quadrat B). Other areas may have quadrat C food web similar to that in natural grasslands.

Nematode faunal analysis provides a powerful tool for diagnosis of the complexity and status of soil food webs (Wardle *et al*., 1995; Ritz & Trudgill, 1999) which can also be concluded from present study. The values of indices studied here agree well with earlier reports of these indices from natural forest ecosystems. Accordingly, the present study of the functional diversity and food web diagnostics show natural woodland dominated by *Acacia*, near Aligarh in India as mature undisturbed ecosystem.

Acknowledgments

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