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Status of soil nematode communities during natural regeneration of a subtropical forest in southwestern China

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Summary – Forest recovery has been extensively evaluated using plant communities but fewer studies have been conducted on soil fauna. This study reports the status of soil nematode communities during natural re-establishment after deforestation in a subtropical forest in southwestern China. Soil nematode communities of two secondary succession stages, shrub-grassland and secondary forest, were compared with those of virgin forest. Shrub-grassland had higher herbivore relative abundance but lower fungivore and bacterivore relative abundance than forests. Between secondary and virgin forest, the latter had higher abundance of bacterivores. Shrub-grassland had lower nematode diversity, generic richness, maturity index and trophic diversity index than virgin forest, whereas there were no differences in these indices between secondary forest and virgin forest. The small differences in nematode community structures between secondary forest and virgin forest suggest that soil nematode communities recovered to a level close to that of the undisturbed forest after up to 50 years of natural succession.

Keywords – ecosystem, restoration, secondary succession, soil nematodes, subtropical forest, trophic group.

Across the world, great efforts have been made to restore forests on degraded lands (Chazdon, 2008). Forest coverage in many countries began to increase owing to both active (tree planting) and passive (natural regeneration) restoration over the past decades (FAO, 2005). It is suggested that forest restoration programmes not only enhance forest biomass and carbon sequestration, but also improve ecosystem functions and recover many components of the original biodiversity (Chazdon, 2008; Kardol & Wardle, 2010). The effectiveness of forest restoration has been extensively evaluated using plant communities as the key indicator. However, the status of below-ground biodiversity is less understood, despite wide recognition of the links between below-ground soil biodiversity and above-ground systems, and their roles in regulating ecosystem functions (Leon *et al.*, 2003; Todd *et al.*, 2006; Heneghan *et al.*, 2008; Cuesta *et al.*, 2012). Bardgett *et al.* (2005) suggested that the above-ground and below-ground restoration processes can occur over different time-scales and may not be synchronous. For example, during a 22-year natural re-establishment of heath land on an abandoned agricultural land, changes in below-ground food webs lagged behind those in above-ground vegetation (Holtkamp *et al.*, 2008). Therefore, in order to understand the value of forest restoration on biodiversity conservation and ecosystem services enhancement, the status of below-ground biodiversity should be integrated into the traditional floristic focus (Kardol *et al.*, 2005; Bautista-Cruz *et al.*, 2012).

Among below-ground biota, nematodes possess unique attributes that make them particularly useful indicators of soil recovery after disturbance (Nombela *et al.*, 1999; Ne-

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her, 2010). Nematodes are abundant in all soils, including stressed and disturbed ones (Neher *et al.*, 2005). Nematode communities are often sensitive to habitat disturbance and they show a characteristic sequence of recolonisation after disturbance (Ettema & Bongers, 1993). Furthermore, they are represented in a wide array of trophic groups (herbivores, bacterivores, fungivores, omnivore-predators), reflecting resource availability and changes of environmental conditions in the soil (Yeates *et al.*, 1993; Yeates & Williams, 2001). Finally, nematodes impact ecological processes both directly and indirectly due to their central position in soil food webs, and can play a critical role in ecosystem functions (Neher, 2010). Some studies have investigated the nematode recovery processes in meadow land (Háněl, 2003, 2010), sand dunes (Zhi *et al.*, 2009) and pasture (Nombela *et al.*, 1999; Wasilewska, 2006) along several major successional stages. In comparison, the nematode communities in forest ecosystems have received less attention and only a few studies have been conducted in some subtropical (Brzeski *et al.*, 1995; Armendáriz & Arpin, 1996; Panesar *et al.*, 2001; Thornton & Matlack, 2002) and tropical forests (Diemont & Martin, 2005). These previous studies have revealed that the rate and character of nematode succession could vary with ecosystem types, study sites and recovery approaches.

Subtropical evergreen broad-leaved forest of southwestern China is one of the most important vegetation types in East Asia. This forest type possesses unique soil properties and functions and plays an important role in preserving biological diversity (Li, 1983; Qi, 1990; Yan *et al.*, 2007). Primary evergreen broad-leaved forest in Ailao Mountains National Nature Reserve, Yunnan Province, is the largest tract of natural vegetation in China. This forest is classified as a 'temperate rain forest' subtype based on its species composition and the unique environmental characters (abundant rainfall, high humidity and high altitude). Over the past decades, large areas of subtropical evergreen broad-leaved forests in this area were deforested and converted to croplands or grasslands. The loss of natural forests resulted in ecosystem degradation, soil erosion, loss of soil fertility and a decrease in plant diversity (Chen & He, 1995). Since the 1980s, large forest protection areas have been established in this area to aid forest recovery. Natural regeneration occurred following the abandonment of degraded lands to nurture secondary forests. To guide the management of the conservation areas and to facilitate the recovery of these forests to the original state, proper evaluation of the ecological succession and progress of the forest recovery is essential (Wang *et al.*, 2006).

This paper reports the status of soil nematode communities during the natural regeneration after deforestation in the subtropical broad-leaved forest of Ailao Mountains National Nature Reserve in southwestern China. We compared soil nematode communities of two secondary succession stages after deforestation, *i.e.*, shrub-grassland (early successional stage) and secondary forest (late successional stage), with those of virgin forests. By applying nematode community indices, the aims of this study are: *i*) to identify changes in nematode communities during the forest natural regeneration at different time spans; *ii*) to assess the potential of these degraded lands to recover to the state of virgin forest in this area. We presume that the nematode community would develop towards that of virgin forest during the process of natural regeneration, and expect the nematode community in secondary forest to be more similar to that of virgin forest than shrub-grassland.

Materials and methods

STUDY AREA

The study site was at Xujiaba (24°32′N, 101°01′E; altitude 2450 m a.s.l.), which is at the centre of the Ailao Mountains National Nature Reserve, Yunnan Province, in southwestern China (Fig. 1). A detailed description of the site and region is available in Li (1983) and Chen & He (1995). In brief, the mean annual temperature is 11.3°C, with the coldest month (January) at 5.4°C and the hottest month (July) at 16.4°C. Because the mean active accumulative temperature above 10°C is about 3420°C, the temperature of this area resembles that of warm temperate zone. The annual precipitation averages 1932 mm and the annual mean relative humidity is 86%. There are large areas of virgin forest consisting of subtropical evergreen broad-leaved species dominated by *Lithocarpus chintungensis*, *Rhododendron leptothrium*, *Vaccinium ducluoxii*, *L. xylocarpus*, *Castanopsis wattii*, *Schima noronhae*, *Hartia sinensis* and *Manglietia insignsis* (Li, 1983). The soil is acidic yellow-brown loam (Chan *et al.*, 2006). In the 1950s, due to the construction of a reservoir, part of the virgin forest was clear-felled and then developed into shrub-grassland.

Four stations (about 1.5 ha each) at least 200 m apart from each other were set up. At each station, one plot of each of the three vegetation types (about 0.5 ha

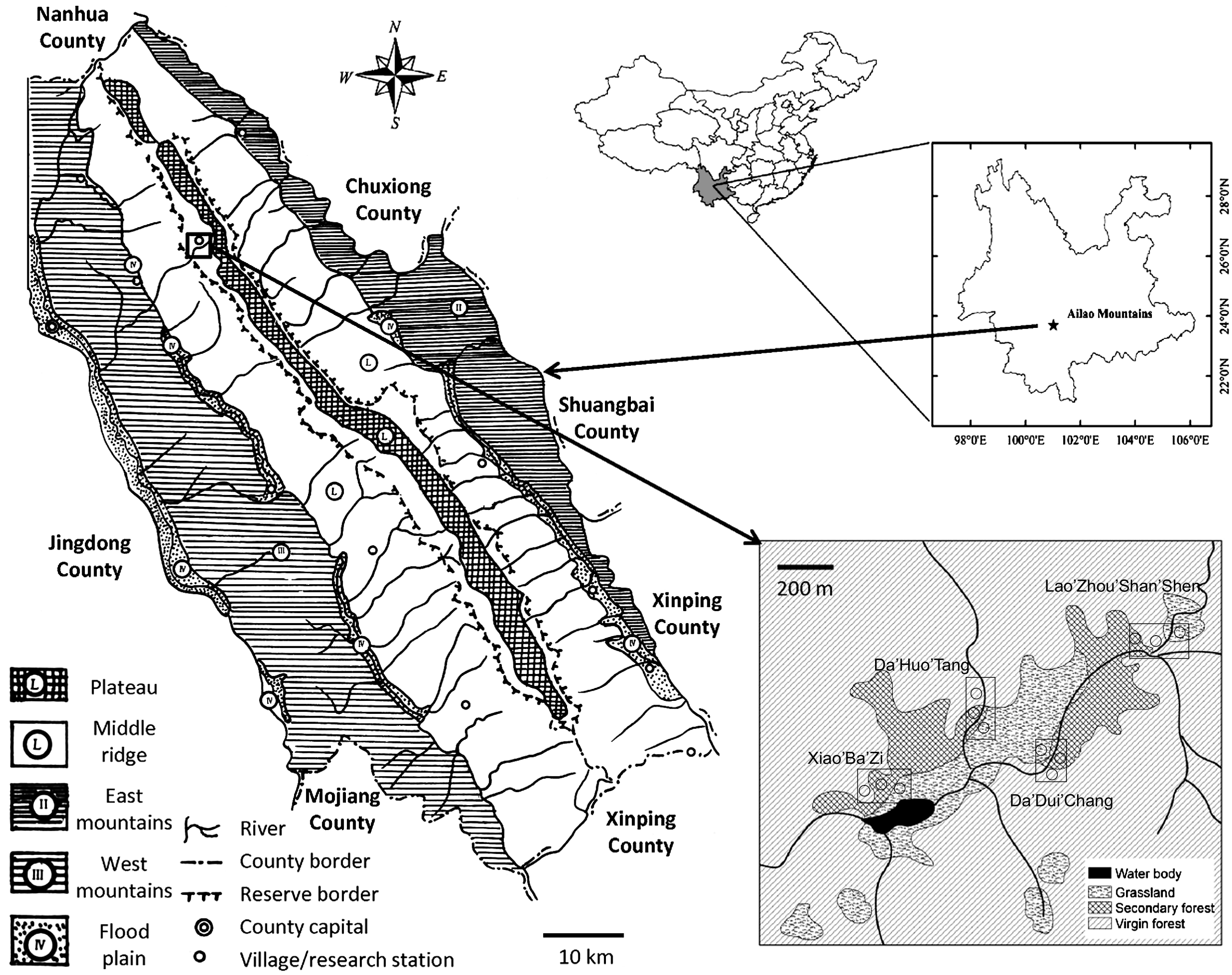

Fig. 1. The map of research site and the distribution of vegetation types. Sampling stations and plots are marked. The map of Ailao Mountains Nature Reserve was modified from Chen & Ye (1988).

each) were selected for sampling: *i*) shrub-grassland, an early succession stage of around 5-8 years after deforestation, which has been lightly grazed, dominated by *Pteridium revolutum* and *Yushannia niitakayamensis*; *ii*) secondary forest, a late succession stage developed from deforestation lands for about 50 years and dominated by tree species *L. jingdongensis* and *Populus bonatii*; and *iii*) virgin forest, dominated by *L. jingdongensis* and *C. wattii*, which served as a reference climax stage (Fig. 1). In each plot, four 20-m-long transects with intervals of 20 m were established with a random starting point. Samples were collected in September 2007. Soil cores were taken by a modified O'Connor split corer (inner diam. 50 mm) to a depth of 10 cm, a common sampling depth in both grassland and forest ecosystems. Litter layer in the sites was generally thin and well decomposed, making it difficult to separate from surface soil, so it was included in the soil core for analysis. The humus layer was a mull-like moder *ca* 7-12 cm deep and could be distinguished from the mineral soil layer (Chan *et al.*, 2006). Four soil cores taken at 5-m intervals along each transect were bulked into a single composite sample to reduce variance associated with the aggregated spatial pattern of soil nematodes. Thus, one composite sample was obtained from each transect. There were a total of 16 composite soil samples for each vegetation type. Each composite sample was then divided into two subsamples; one (*ca* 500 g) was used for soil physicochemical analysis and the other (*ca* 100 g) was fixed in 4% formaldehyde in the laboratory for nematode analysis.

SOIL ANALYSIS

Soil physicochemical properties were determined in September, 2007. Particle size distribution was measured by sedimentation velocity. Soil pH value of the saturated paste was measured in water (1:1) using a glass electrode (Lu, 1999). Soil moisture was determined gravimetrically by oven-drying at 80°C to a constant weight. Soil organic matter content was determined by burning dried soil in a muffle furnace at 550°C for 4 h. Total soil carbon and nitrogen were measured with a Nitrogen and Carbon Soil Analyzer (FlashEA 1112 Series, Thermo Fisher Scientific).

NEMATODE COMMUNITY ANALYSIS

Nematodes were extracted by flotation in Ludox™ in the laboratory (Griffiths *et al.*, 1990). After counting the total number of individuals, nematode specimens were slowly dehydrated in glycerol and prepared on slides. About 100 specimens from each sample were randomly selected and identified to genus, mainly according to Goodey (1963), Siddiqi (1986), Hunt (1993) and Jairajpuri & Ahmad (1992).

The following indices were used to assess the nematode community:

The generic richness is represented by the total number of genera in a sample.

Shannon-Weaver diversity index at generic level (Shannon & Weaver, 1949) was calculated as $H'\text{gen} = -\sum \pi \ln \pi$, where π is the proportion of individuals in the ith taxon.

The Maturity Index (MI) and Plant Parasite Index (PPI) were calculated according to Bongers (1990). MI (or PPI) $= \sum v(i) \times f(i)$, where $v(i)$ is the *c-p* (coloniser-persister) value of free-living (or plant-feeding) nematode taxon i; $f(i)$ is the frequency of free-living (or plant-feeding) nematode taxon i in a sample. The determination of nematode *c-p* value along the *c-p* gradient followed Bongers & Bongers (1998). The MI and PPI were used to assess the successional stage of the free-living and plant-feeding nematode community, with low values indicating disturbance or immature succession stage with dominance of r-strategists.

Nematode channel ratio (Yeates, 2003) was determined as $\text{NCR} = B/(B + F)$, where B and F are the relative contributions of bacterivores and fungivores, respectively, to total nematode abundance.

Trophic diversity index (Freckman & Ettema, 1993) was calculated as $\text{TD} = 1/\sum p_i^2$, where p_i is the proportion of each trophic group i. The nematode genera were classified into five trophic groups according to information on their feeding habits surveyed by Yeates *et al.* (1993): herbivores, bacterivores, fungivores, predators and omnivores.

DATA ANALYSIS

The trial used a nested design. The four stations were blocks and the three succession stages were treatments. Within each treatment of each block, four composite samples were collected. These data were analysed by a linear mixed effects model (ANOVA) with a significance level set at 5%. When there were significant treatment effects, multiple comparison between treatment levels was done using a test for least significant difference (LSD). This analysis was implemented using GenStat 13th Edition (Payne *et al.*, 2010).

Using a ranked similarity matrix based on Bray-Curtis similarity measures, an ordination plot was produced by non-metric multidimensional scaling (nMDS) to intuitively visualise the similarity of nematode communities among three vegetation types. The two-way nested analysis of similarity (ANOSIM) (Clarke & Warwick, 1994) was used to test the vegetation type effects on the nematode community. Similarity percentages (SIMPER) analysis was used to identify nematode genera that contributed most to the average dissimilarity between stations (Clarke, 1993). Nematode generic abundances were $\log(\text{I} + 1)$ transformed to normalise data before conducting the nMDS, ANOSIM and SIMPER analyses. These analyses were implemented using PRIMER 5 (Clarke & Warwick, 1994).

Results

The soil was acidic at all stations. Except pH, which was significantly lower in secondary and virgin forests (approx. 3.6) than that in shrub-grassland (approx. 4.4), there was no significant difference in the other assessed soil physicochemical parameters among the three succession stages (Table 1). In general, the soil of the site was sandy, with high organic matter ($>20\%$) and high total nitrogen ($>0.6\%$).

A total of 51 nematode genera were found in our study (Table 2). Two herbivorous nematodes, *Helicotylenchus* and *Tylenchorhynchus*, were the most abundant genera

Table 1. Soil physicochemical characteristics of each vegetation type. Values are means with ±S.E. in parentheses ($n = 4$). P values of the effect of succession stages are given (ANOVA).

Parameter	Shrub-Grassland	Secondary Forest	Virgin Forest	Effect of succession stage (P value, ANOVA)
Particle size distribution (%)				
Stones (>2 mm)	2.97 (0.89)a	6.70 (1.42)a	10.09 (3.37)a	0.08
Sand (0.2-2 mm)	83.34 (3.25)a	83.12 (2.77)a	82.48 (3.18)a	0.98
Clay and silt (<0.2 mm)	13.69 (2.62)a	10.18 (1.63)a	7.42 (1.44)a	0.13
pH	4.38 (0.17)a	3.64 (0.13)b	3.62 (0.20)b	0.03*
Organic matter (%)	20.73 (1.69)a	24.24 (2.93)a	27.81 (4.56)a	0.10
Total nitrogen (%)	0.63 (0.12)a	0.75 (0.13)a	0.93 (0.14)a	0.39
C/N ratio	14.69 (0.69)a	13.78 (0.26)a	13.70 (0.35)a	0.19

Different letters (a, b) denote significant difference among different vegetation types at $P < 0.05$. *Significant effect, $P < 0.05$.

Table 2. Nematode generic composition and density (individuals (10 g dry soil)$^{-1}$) in each vegetation type. Values are means ± S.E. ($n = 4$). The *c-p* values are also shown.

Nematode taxa	*c-p* value	Vegetation type		
		Shrub-Grassland	Secondary Forest	Virgin Forest
Herbivores				
Criconema	3	5.12 ± 2.44	7.83 ± 2.98	13.13 ± 0.53
Discocriconemella	3	0.00 ± 0.00	9.92 ± 9.92	2.69 ± 1.62
Helicotylenchus	3	71.53 ± 14.23	16.72 ± 4.37	5.27 ± 2.57
Heterodera	3	7.32 ± 4.77	0.35 ± 0.35	1.21 ± 0.68
Longidorus	5	7.74 ± 2.05	2.11 ± 1.18	2.18 ± 0.57
Loofia	3	0.86 ± 0.86	14.93 ± 8.07	0.50 ± 0.50
Ogma	3	2.04 ± 2.04	7.48 ± 3.53	15.78 ± 6.86
Paratylenchus	2	0.22 ± 0.22	1.01 ± 0.62	1.29 ± 0.60
Saevadorella	4	0.27 ± 0.27	0.29 ± 0.29	0.00 ± 0.00
Trichodorus	4	0.13 ± 0.13	0.29 ± 0.29	0.00 ± 0.00
Tylenchina (not identified)	3	0.20 ± 0.20	0.00 ± 0.00	2.42 ± 1.18
Tylenchorhynchus	3	38.83 ± 11.14	6.21 ± 0.94	4.57 ± 2.13
Xiphinema	5	3.74 ± 2.65	7.18 ± 3.00	9.54 ± 3.53
Bacterivores				
Acrobeloides	2	1.89 ± 1.05	5.67 ± 1.86	8.21 ± 2.10
Alaimus	4	4.70 ± 1.19	18.46 ± 5.73	20.00 ± 6.89
Amphidelus	4	4.92 ± 2.93	7.31 ± 2.02	18.42 ± 5.76
Aphanolaimus	3	0.37 ± 0.22	0.81 ± 0.47	5.39 ± 2.65
Bastiania	3	2.34 ± 1.25	6.21 ± 3.25	8.86 ± 1.67
Cervidellus	2	0.44 ± 0.44	0.31 ± 0.31	0.00 ± 0.00
Monhystera	2	0.00 ± 0.00	1.46 ± 0.79	0.92 ± 0.92
Monhystrella	2	0.00 ± 0.00	0.62 ± 0.36	0.00 ± 0.00
Panagrolaimus	1	0.00 ± 0.00	0.00 ± 0.00	0.26 ± 0.26
Plectus	2	0.10 ± 0.10	3.61 ± 1.53	6.16 ± 4.19
Prismatolaimus	3	6.03 ± 2.08	2.25 ± 1.19	1.89 ± 0.79
Rhabditis	1	0.00 ± 0.00	0.70 ± 0.70	0.51 ± 0.51
Fungivores				
Aphelenchoides	2	0.42 ± 0.25	0.23 ± 0.19	2.53 ± 2.00
Boleodorus	2	0.45 ± 0.45	4.44 ± 1.58	0.26 ± 0.26

Table 2. (Continued.)

Nematode taxa	*c-p* value	Vegetation type		
		Shrub-Grassland	Secondary Forest	Virgin Forest
Diphtherophora	3	0.74 ± 0.57	3.47 ± 1.09	5.62 ± 2.34
Imphalenchus	2	1.86 ± 0.54	2.35 ± 0.71	4.15 ± 2.03
Malenchus	2	0.00 ± 0.00	1.35 ± 0.71	7.27 ± 4.67
Neopsilenchus	2	10.14 ± 9.64	1.14 ± 0.49	2.25 ± 1.08
Tylencholaimus	4	8.81 ± 3.04	51.12 ± 21.32	39.57 ± 10.17
Predators				
Aporcelaimellus	5	7.46 ± 1.24	8.96 ± 4.58	6.35 ± 2.77
Clarkus	4	0.00 ± 0.00	1.47 ± 1.47	0.34 ± 0.34
Iotonchus	4	2.92 ± 1.27	1.84 ± 0.57	1.94 ± 0.93
Ironus	4	0.24 ± 0.24	0.00 ± 0.00	0.00 ± 0.00
Mylonchulus	4	0.67 ± 0.37	6.42 ± 3.64	7.15 ± 1.78
Nygolaimus	5	0.14 ± 0.14	0.00 ± 0.00	0.00 ± 0.00
Prionchulus	4	0.00 ± 0.00	0.18 ± 0.18	0.31 ± 0.31
Tripyla	3	9.60 ± 4.46	7.68 ± 2.44	5.49 ± 1.21
Westindicus	5	1.76 ± 1.47	0.20 ± 0.20	0.15 ± 0.15
Omnivores				
Achromadora	3	1.19 ± 0.55	0.29 ± 0.29	0.36 ± 0.36
Amphidorylaimus	4	3.26 ± 2.08	0.87 ± 0.49	0.83 ± 0.32
Axonchium	5	9.40 ± 5.51	1.42 ± 1.04	7.13 ± 1.85
Basirotyleptus	4	28.38 ± 15.19	9.64 ± 4.06	13.19 ± 4.24
Dorylaimellus	5	4.46 ± 1.31	3.27 ± 1.78	4.87 ± 1.84
Dorylaimoides	4	0.69 ± 0.45	0.00 ± 0.00	0.00 ± 0.00
Enchodelus	4	5.39 ± 3.29	2.59 ± 2.18	4.90 ± 2.74
Eudorylaimus	4	30.92 ± 6.73	34.09 ± 9.17	34.36 ± 11.71
Mesodorylaimus	4	11.35 ± 4.04	11.98 ± 3.21	12.49 ± 3.38
Opisthodorylaimus	4	0.55 ± 0.55	1.22 ± 1.22	4.76 ± 1.72

in shrub-grassland, and together represented 37% of total nematode abundance in shrub-grassland. Both the secondary forest and virgin forest had the same dominant genera: fungivorous *Tylencholaimus* and omnivorous *Eudorylaimus*. The total abundance of *Tylencholaimus* and *Eudorylaimus* comprised 30% and 25%, respectively, of the total number of nematode individuals in secondary forest and virgin forest.

Comparing values of soil nematode ecological indices among the three vegetation types, significant differences were found in total nematode diversity, generic richness, MI and TD index but not in total density, PPI index and NCR ratio (Table 3). Shrub-grassland exhibited significantly lower values of total nematode diversity, generic richness, MI and TD index, but no significant differences were found between secondary forest and virgin forest.

Comparing soil nematode community structure among the three vegetation types, significant differences were found between shrub-grassland and virgin forest (ANOSIM pairwise test, $R = 0.885$, $P = 0.03$) and between shrub-grassland and secondary forest (ANOSIM pairwise test, $R = 0.625$, $P = 0.03$), whereas the difference between secondary forest and virgin forest was smallest (Fig. 2) and not significant (ANOSIM pairwise test, $R = 0.234$, $P = 0.06$). Overall, separation of among vegetations types has a low strength, with the stress value of 0.18 (Clarke & Warwick, 1994). The genera that played important roles in the dissimilarities between shrub-grassland and secondary forest were the same as those between shrub-grassland and virgin forest, including *Helicotylenchus*, *Tylencholaimus*, *Tylenchorhynchus*, *Basirotyleptus* and *Eudorylaimus* (Table 4). *Helicotylenchus*, *Tylenchorhynchus* and *Basirotyleptus* were the most abundant in shrub-grassland, while *Tylencholaimus* and *Eudorylaimus* were the least abundant (Table 2). The genera that best explained differences between secondary

Table 3. Soil nematode ecological indices in each vegetation type. Values are means with ±S.E. in parentheses ($n = 4$). P values of the effect of succession stages are presented.

Parameter	Shrub-Grassland	Secondary Forest	Virgin Forest	Effect of succession stage (P value, ANOVA)
Total density	299.61 (48.82)a	277.93 (65.28)a	295.43 (58.25)a	0.88
H'gen diversity index	2.26 (0.11)b	2.58 (0.06)a	2.75 (0.02)a	0.01*
Generic richness	17.37 (0.99)b	20.56 (0.60)ab	22.94 (0.53)a	<0.01*
MI	3.17 (0.07)b	3.44 (0.08)a	3.42 (0.07)a	<0.018
PPI	3.87 (0.09)	3.96 (0.10)	3.85 (0.11)	0.43
NCR ratio	0.55 (0.07)a	0.44 (0.05)a	0.54 (0.04)a	0.37
TD index	2.43 (0.13)b	3.30 (0.21)a	3.43 (0.08)a	<0.01*

Data were log transformed before analysis. Different letters (a, b) denote significant difference among different vegetation types at $P < 0.05$.

* Significant effect, $P < 0.05$.

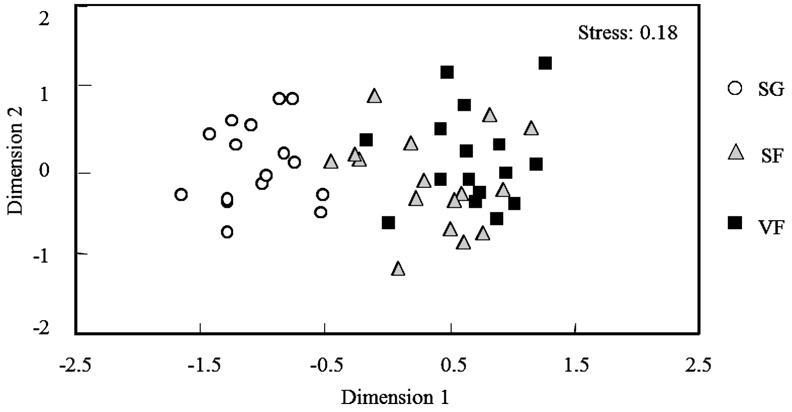

Fig. 2. Non-metric multidimensional scaling ordination of soil nematode communities in different habitats, visualising the similarity of soil nematode communities in three vegetation types. Each dot represents one transaction. SG: Shrub-Grassland; SF: Secondary Forest; VF: Virgin Forest.

forest and virgin forest were *Tylencholaimus*, *Eudorylaimus*, *Alaimus*, *Helicotylenchus* and *Ogma* (Table 4). *Alaimus* and *Ogma* were more abundant in virgin forest than in secondary forest, while *Tylencholaimus* and *Helicotylenchus* were less abundant in virgin forest than in secondary forest (Table 2).

Herbivores were the dominant trophic group in shrub-grassland (46%), while the community shifted to a more bacterivore- and fungivore-dominated status after forest re-established (Table 5). Shrub-grassland also displayed lower herbivore and bacterivore diversity than the forests. Omnivore-predators were abundant in each vegetation type, comprising 40, 33 and 35% of the total number of individuals counted in shrub-grassland, secondary forest and virgin forest, respectively. There was no substantial difference between the secondary forest and virgin forest regarding the relative abundance and diversity of different trophic groups, except that the virgin forest had significantly higher relative abundance of bacterivores.

Among the soil physiochemical properties we addressed, herbivore abundance was positively correlated with soil C/N ratio (Table 6). The abundance of both bacterivores and fungivores was positively correlated with organic matter and total nitrogen, but negatively correlated with pH and clay and silt content. Omnivore-predators abundance was only positively correlated with organic matter and sand content.

Discussion

In our study, after 50 years of secondary succession, the nematode community has recovered to a level close to that of virgin subtropical broad-leaved forest, consistent with our expectation that the nematode community in secondary forest is more similar to virgin forest than shrub-grassland. Additionally, the changes of soil nematodes during the forest recovery process appear trophic group-specific. The system shifted from a herbivore-dominated community in the shrub-grassland to a more microbefeeder-dominated status in the forests.

Table 4. Results of the SIMPER analysis showing five genera that contribute most to the dissimilarity between different vegetation types.

	Av.Diss	Diss/SD	Contrib (%)
Shrub-Grassland *vs* Secondary Forest (mean dissimilarity 68.27)			
Helicotylenchus	9.50	1.35	13.92
Tylencholaimus	7.39	1.30	10.82
Tylenchorhynchus	5.62	1.54	8.24
Basirotyleptus	5.59	0.77	8.19
Eudorylaimus	4.35	1.13	6.37
Shrub-Grassland *vs* Virgin Forest (mean dissimilarity 70.69)			
Helicotylenchus	11.03	1.68	15.61
Tylencholaimus	5.64	1.31	7.98
Tylenchorhynchus	5.63	1.60	7.97
Basirotyleptus	5.24	0.82	7.42
Eudorylaimus	4.21	1.13	5.96
Secondary Forest *vs* Virgin Forest (mean dissimilarity 59.98)			
Tylencholaimus	7.44	1.39	12.40
Eudorylaimus	4.81	1.31	8.02
Alaimus	3.00	1.21	5.00
Helicotylenchus	2.91	1.13	4.85
Ogma	2.72	1.08	4.53

Av.Diss: contribution of the ith genus to the total dissimilarity; Diss/SD: a measure of how consistently individual taxa contribute to the overall dissimilarity; Contrib (%): percentage contribution of the ith genus to the total dissimilarity.

SOIL NEMATODE TAXA COMPOSITION, DIVERSITY AND COMMUNITY STRUCTURE

In our study, the status of nematodes was characterised more by shifts in dominance patterns of autochthonous taxa than by colonisation of new taxa. A total of 37 and 42 genera found in shrub-grassland and secondary

Table 6. Correlation coefficients between nematode trophic groups and soil chemical-biochemical properties.

Soil properties	Hf	Bf	Ff	Om-pr
Particle size distribution (%)				
Stones (>2 mm)	−0.27	0.22	0.34*	−0.24
Sand (0.2-2 mm)	0.23	0.34*	0.18	0.35*
Clay and silt (< 0.2 mm)	0.08	−0.55**	−0.47**	−0.02
pH	0.28	−0.57**	−0.38**	0.02
Organic matter (%)	−0.13	0.71**	0.49**	0.37**
Total nitrogen (%)	0.28	0.57**	0.38**	0.02
C/N ratio	0.31*	−0.26	−0.18	−0.03

Hf: herbivores; Bf: bacterivores; Ff: fungivores; Om-pr: omnivore-predators.

*, ** Correlation coefficients significant at $P < 0.05$ and 0.01, respectively.

Table 5. Relative abundance and diversity indices of soil nematode trophic groups in each vegetation type. Values are means with ±S.E. in parentheses ($n = 4$). P values of the effect of succession stage are presented.

	Shrub-Grassland	Secondary Forest	Virgin Forest	Effect of succession stage (P value, ANOVA)
Relative abundance (proportion)				
Hf	0.46 (0.02)a	0.31 (0.07)b	0.20 (0.03)b	<0.01*
Bf	0.06 (0.01)c	0.16 (0.02)b	0.23 (0.01)a	<0.018
Ff	0.07 (0.02)b	0.20 (0.04)a	0.20 (0.03)a	0.03*
Om-pr	0.41 (0.04)a	0.32 (0.01)a	0.36 (0.03)a	0.16
H'gen diversity index				
Hf	1.10 (0.05)b	1.36 (0.09)a	1.33 (0.04)a	0.03*
Bf	0.97 (0.12)b	1.25 (0.15)ab	1.59 (0.09)a	0.01*
Ff	0.45 (0.09)a	0.67 (0.12)a	0.76 (0.11)a	0.12
Om-pr	1.56 (0.12)a	1.63 (0.09)a	1.83 (0.07)a	0.19

Hf: herbivores, Bf: bacterivores, Ff: fungivores, Om-pr: omnivore-predators. Data were square root transformed. Different letters (a, b, c) denote significant difference among different vegetation types at $P < 0.05$. *Significant effect, $P < 0.05$.

forest also occurred in virgin forest, where they accounted for 84 and 95% of the nematode genera living in virgin forest. Although some genera in the virgin forest, such as *Malenchus*, appeared to be lost after deforestation, most genera in the virgin forest seemed to be able to survive the disturbance. This supports the view that land use might not inevitably lead to taxa loss (Wu *et al.*, 2002). Kardol *et al.* (2005) also found a similar pattern in nematode taxa composition on a chronosequence of 26 ex-arable fields in The Netherlands on loam glacial deposits. Many nematode taxa are able to recover from the stress within a relatively short period (several years) of natural secondary succession (Háněl, 2003). Allochthonous colonisation of nematode taxa composition during secondary succession is probably attributable to their poor dispersal capacity (Ettema & Bongers, 1993; Kardol *et al.*, 2005).

Diversity and maturity of soil nematode communities are greater in the late and climax stages than in the early stages of ecosystem succession (Bongers & Ferris, 1999). This point is supported by our study, which shows that shrub-grassland had the lowest diversity and maturity of nematodes compared with secondary and virgin forests. Additionally, the trophic diversity index in shrub-grassland was significantly lower than that in secondary and virgin forests, which suggests a higher diversity of food source in the forest than in the shrub-grassland. Our results are in contrast to the finding of Háněl (2010), who found that nematode communities were more diverse and ecologically mature beneath relatively early stage compared to late and climax stages during a succession process from abandoned fields to oak forest in the Czech Republic. Háněl’s (2010) finding supported the intermediate disturbance hypothesis (Grime, 1973; Connell, 1978), and was attributable to long-term, continuing disturbance (*e.g.*, predatory mites) that prevents the nematode community from increasing diversity and maturity. The disparity between the results of Háněl (2010) and our work is probably due to the absence of disturbance during forest re-establishment in our site. Alternatively, Panesar *et al.* (2001) reported similar diversity and maturity of nematode communities at four ages (8, 42, 93 and 286 years) of coastal Douglas fir forest in British Columbia, Canada. A high percentage (55%) of omnivore-predators that consistently occur at four ages of this forest appeared to maintain soil food web stability, and, subsequently, soil nematode diversity and maturity during forest aging. Based on the hypothesis of exploitation ecosystems, which predicts that higher trophic levels are maintained in more productive systems (Oksanen *et al.*, 1981; Oksanen & Oksanen, 2000), this observation can be explained by the fact that the productivity of even young Douglas fir forest was high enough to maintain a long soil food chain with high tropic level. These mixed results in line with different ecological theories in various ecosystems suggest that nematode succession is influenced by system-specific environmental and biological factors, *e.g.*, the composition of other soil biota, the disturbance level and ecosystem productivity. Further research is needed to understand the mechanisms that control the patterns of nematode succession in different ecosystems.

This study revealed no distinct difference in diversity and maturity between secondary and virgin forests. The difference in soil nematode community structure between secondary and virgin forests was also small. These results suggest that after a maximum of 50 years of secondary succession, the nematode community has recovered to a level close to that of virgin subtropical broad-leaved forest. This time scale is similar to that found in southern Mississippi woodlands of the USA (Thornton & Matlack, 2002), where the recovery of soil nematode communities after commercial logging required around 50 years.

SOIL NEMATODE TROPHIC STRUCTURE

Trophic structure is a functional classification that contributes to understanding how each trophic group affects the transfer of matter or energy in the ecosystem (Freckman & Ettema, 1993; Armendáriz & Arpin, 1996). In this study, different soil nematode trophic groups changed in different ways during the forest recovery process and the community shifted from herbivore-dominated in the shrub grassland to a more bacterivore- and fungivore-dominated status in the forests.

As primary consumers, herbivores could directly respond to the changes of vegetation succession. Our study displayed a higher relative abundance of herbivores in shrub-grassland than in secondary and virgin forests. This trend is consistent with those found over secondary succession on abandoned fields (Háněl, 2010) and in drained fen peat (Wasilewska, 2006). Possible explanations would be that the plants are more vulnerable to plant-parasites after human disturbance (Bergeson & Ferris, 1986). In our sites, the most abundant genera in shrub-grassland were two herbivorous nematodes, *Helicotylenchus* and *Tylenchorhynchus*, which often dominate in grassland and cultivated field soils (Villenave *et al.*, 2001; Zhi *et al.*, 2009).

Microbe-feeding nematodes could be sensitive indicators of the microbial-related soil processes (Háněl, 2003). During secondary succession, readily available resources become depleted, so that plant communities become dominated by slow-growing species with poorly degradable litter (Bardgett & McAlister, 1999) and the soil nematode communities often change from a bacterivore-dominated to a more fungivore-dominated community (Brzeski, 1995; Armendáriz & Arpin, 1996; Kardol *et al.*, 2005; Neher, 2010). However, our study revealed that both bacterivorous and fungivorous nematodes increased in relative abundance during forest regeneration. Moreover, in our study, bacterivorous and fungivorous nematodes recovered at different time scales during succession. The secondary forest had a significantly lower relative abundance of bacterivores than the virgin forest, but had more or less similar relative abundance of fungivores with the virgin forest, implying that the fungivores recovered from the stress more quickly than the bacterivores. Strong correlations between microbe-feeding nematode abundance, soil organic matter and soil nitrogen suggest that the increment of these trophic groups are due to more abundant food sources, which can be associated with tree inputs into the soil through higher above-ground litter (Eisenhauer & Reich, 2012) and/or below-ground root exudates (Keith *et al.*, 2009).

Omnivore-predators are believed to reflect the complexity of the food web (Polis & Strong, 1996). Panesar (2001) reported that the relative distributions of omnivores and predators (55%) across four successional stages in coastal Douglas fir forest were similar. Kardol *et al.* (2005) also found that the abundance of omni-carnivorous nematodes did not change along a restoration chronosequence. In our study, omnivore-predators displayed no distinguishable differences in the relative abundance or H' diversity index value among the three vegetation types. According to the hypothesis of exploitation ecosystems, higher tropic levels are maintained predominantly in high productive systems (Oksanen *et al.*, 1981; Oksanen & Oksanen, 2000). Therefore, the productivity of the shrub-grassland seemed to be high enough to sustain a long food chain with high trophic levels, so that no substantial changes in soil food web structure was observed during the natural regeneration of this subtropical forest.

Although the changing pattern across the three vegetation types was different among various soil nematode trophic groups, total nematode abundance was similar. It seems that the decrease of herbivore abundance was compensated by the increase of bacterivores and fungivores. This phenomenon matches the observation in a dry pasture recovery process after temporary rye cultivation (Nombela *et al.*, 1999).

RESTORATION OF VEGETATION AND SOIL PROPERTIES *VS* NEMATODE COMMUNITY

We found that after 5-8 years of natural regeneration, significant differences in plant communities and soil nematode communities persisted despite similar soil conditions between the early successional shrub-grassland stage and the virgin forest. This result, together with a few previous studies (Zhang *et al.*, 2010; Piqueray *et al.*, 2011), indicates that the soil habitats could be restored quickly *via* natural regeneration. In particular, our study indicated that the soil conditions were likely to recover prior to the recovery of plant composition and soil biotic communities in the evergreen broad-leaved forest. This may be attributable to two factors. First, deforestation in our site was mainly conducted *via* manual logging, which had limited impact on soil properties. Second, the abandoned land received little disturbance during re-establishment in our site.

In our study, the plant community in the reference virgin forest was dominated by *L. jingdongensis* and *C. wattii*, whereas the regenerated secondary forest (the late succession stage) consisted of trees dominated by *L. jingdongensis* and *P. bonatii*. This suggests that the plant communities clearly developed towards the reference climax stage, although the floristic dissimilarity still exists after 50 years since land abandonment. Except the relative abundance of bacterivorous nematodes, all measured soil properties and most nematode ecological indices were similar between the regenerated secondary and virgin forest. The nMDS and ANOSIM analyses also revealed that the nematode community structures between secondary and virgin forests were most similar. Some studies have shown that the plant and soil nematode communities do not develop in parallel towards the same reference system (Kardol *et al.*, 2005). Our study revealed that, during the forest recovery after deforestation disturbance, soil nematode communities developed towards the original status ahead of the plant community and might have recovered to a level close to that of virgin subtropical broad-leaved forest after up to 50 years.

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