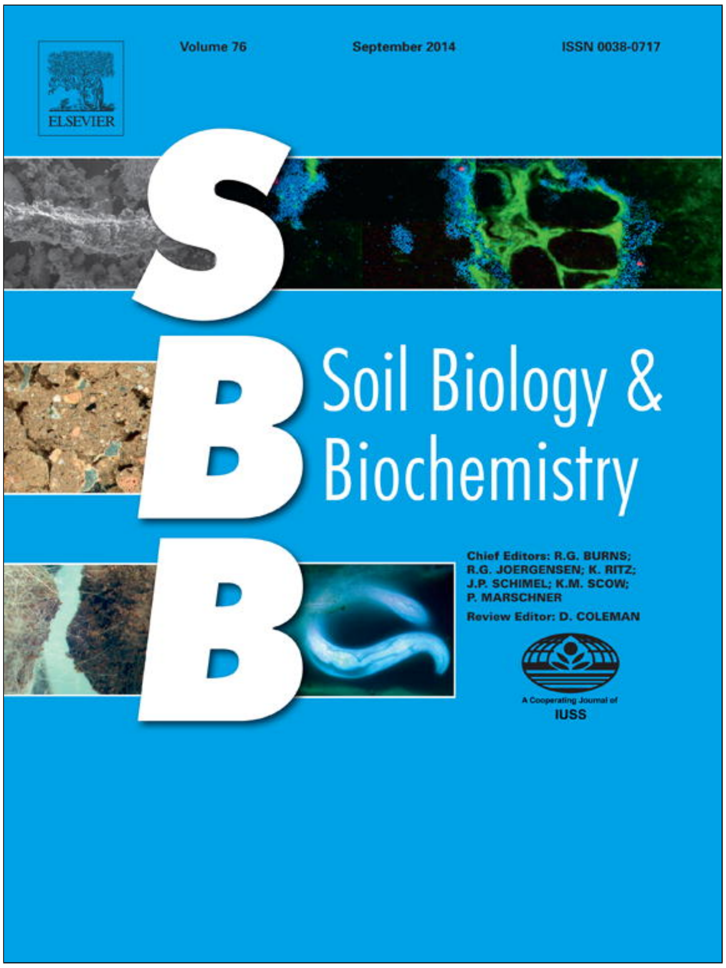
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Intensive rubber cultivation degrades soil nematode communities in Xishuangbanna, southwest China

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ABSTRACT

Fifty years after the introduction, rubber monoculture now covers more than 400,000 ha of previously tropical seasonal rainforest, representing 20% of the land in Xishuangbanna, southwest China. However, little is known about effects of this widespread rubber monoculture on soil ecosystems. Here, we used soil nematodes as indicator species to assess effects of different rubber plantation types on soil ecosystems. Four land-use types (rubber monoculture, rubber and tea mixture, rubber polyculture and natural forest) at three sites were selected to compare soil nematode communities. Nematode communities were significantly different among the four land-use types. Natural forest had highest nematode abundance and taxa richness, followed by rubber polyculture, rubber and tea mixture and rubber monoculture. Compared to natural forest, rubber monoculture after 15–20 years reduced nematode taxa richness by as much as 33%. This was accompanied by reduced soil C and N, indicating loss of soil nutrients and ecological functioning. Nematode ecological indices (H', MI and PPI) suggested a common pattern that natural forest was the most stable and undisturbed ecosystem, followed by rubber polyculture, rubber and tea mixture and rubber monoculture. Nematode trophic groups and SI indicated that food-web structures changed from complex in natural forest to much more simple in rubber monoculture. Finally, based on our results, two protective measures have been proposed to local government and farmers for rubber plantation and management in Xishuangbanna: 1. plant various cash crops such as tea, coffee, and cocoa into rubber monocultures; 2. decrease the management intensity and adjust strategies to restore surface vegetation, and ultimately convert rubber monoculture to rubber polyculture.

1. Introduction

Rubber (*Hevea brasiliensis*), an economic forest species suitable for low latitudes and elevations, is indigenous to the tropical Amazon Basin (Xu, 2006; Sturgeon and Menzies, 2008). It was introduced to Xishuangbanna, one of the three remaining rainforest regions, Yunnan province of China in 1950s (Xu, 2006; Yi et al., 2013). As rubber prices have tripled over the past decade, rubber plantations provide considerable income for local residents (Qiu, 2009), and this directly drives local people to convert forested areas to rubber cultivation. The majority of natural forests including primary and secondary forests have thus been converted to monoculture rubber plantations (Li et al., 2008). Rubber monoculture now covers more than 400,000 ha, or 20% of land in Xishuangbanna (Qiu, 2009).

The conversion of both primary and secondary forests to monoculture rubber plantations threatens biodiversity, results in reduced total biomass carbon stock (Qiu, 2009; Ziegler et al., 2009) and has negative hydrological consequences (Qiu, 2010; Tan et al., 2011). Previous studies demonstrated that, compared to primary tropical forests, rubber plantations significantly decrease diversity of plant species (Zhou et al., 2012), birds (Aratrakorn et al., 2006), bats (Phommexay et al., 2011), insects (Meng et al., 2012) and spiders (Zheng et al., 2009). However, there are few studies on the effects of rubber plantation on soil (Li et al., 2012), particularly soil biota. Thus, the assessment of the impact of rubber plantation on soil ecosystems is an urgent need.

Soil nematode communities are useful biological indicators of soil health (Bongers, 1990; Bongers and Bongers, 1998; Ferris et al.,

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2001). First, nematodes are a dominant group of soil organisms and live in a wide variety of soils including those chemically contaminated (Yeates, 2003). Second, they represent key links in soil food-webs (as herbivores, bacterivores, fungivores, omnivores and carnivores) and their trophic structure is closely linked with soil ecosystem processes (Yeates et al., 1993; Yeates, 2010). Third, nematodes have short generation times and they are sensitive to environmental changes (Bongers and Ferris, 1999). We compared nematode communities among four different land-use types with increasing plant diversity. They were rubber monoculture; rubber and tea mixture; rubber polyculture, which is a diversified system derived from swidden cultivation, in which man-made forests with a high density of rubber trees replace fallows (Gouyon et al., 1993), and natural forest at three different sites. We used the following ecological indices to assess soil conditions and ecosystem changes: Shannon–Weaver diversity, maturity index, plant parasite index, enrichment index, structure index and Channel Ratio. They have been applied to monitor environmental changes (Bongers and Ferris, 1999; Yeates, 2003; Chen et al., 2007).

The main difference among these four land-use types is the aboveground vegetation diversity, which increases from rubber monoculture to natural forest. The establishment of rubber plantation initially decreases aboveground vegetation diversity by clearing and burning, and this is maintained by weeding and herbicides (Qiu, 2009). Nematode communities are influenced both by plant diversity and identity (Porazinska et al., 2003). Some studies found plant identity to be more important than plant diversity for soil biological diversity (De Deyn et al., 2004; Viketoft et al., 2009; Sohlenius et al., 2011; Cesarz et al., 2013). Other studies showed that resource diversity at the base of the soil food-web is also highly relevant for population dynamics and trophic complexity, and thus consumer diversity that influences ecosystem functioning (De Deyn et al., 2008; Gessner et al., 2010; Eisenhauer et al., 2011). Nevertheless, our understanding of simplification of plant community structures on belowground processes in tropical regions is still incomplete. The large area of rubber plantations in Xishuangbanna established over recent decades provides natural study sites to explore this issue.

As plant diversity increased from rubber monoculture, rubber and tea mixture, rubber polyculture, to natural forest, quality and quantity of plant litter and roots were different. We tested the hypothesis that nematode abundance was increased by plant litter and root quantity and nematode diversity by plant diversity. In addition, that nematode community structure would be degraded by rubber cultivation. Our objectives were (1) investigate nematode community in response to increased plant diversity in the field after long-term modifications (2) assess soil health level after rubber plantation for decades, (3) provide some suggestions for rubber management, with the goal of working towards a balance between direct economic benefit and ecological health.

2. Materials and methods

2.1. Study areas

The study was carried out in Xishuangbanna (21°08′–22°36′ N, 99°56′–101°50′E; 19,150 km^2), Yunnan Province, southwest China, which includes three counties (Jinghong, Menghai and Mengla), and borders Laos to the south and Myanmar to the southwest (Fig. 1). Elevation ranges between 475 and 2430 m with a mean annual temperature of 21.8 °C (data from local meteorological station). It receives a mean annual precipitation of approximately 1500 mm, of which 80% occurs in the rainy season (May–October; Li et al., 2012). The sites used in this study were selected based on similarities in physical characteristics, soil parent material, rubber

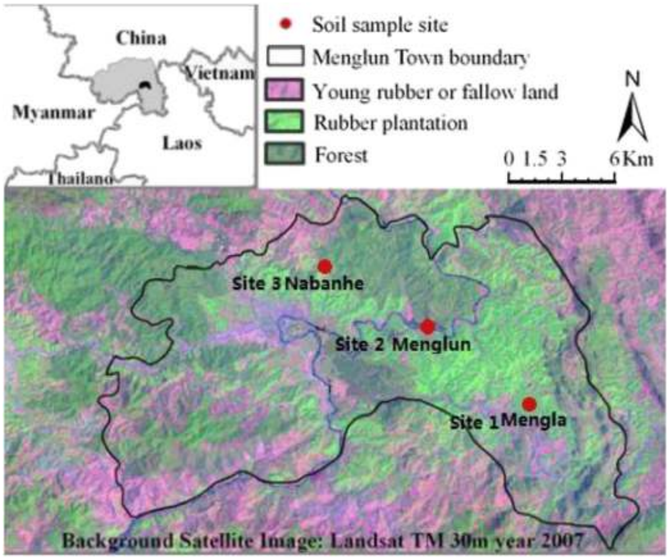

Fig. 1. Study area and land-use sites in this study in Yunnan Province, China (Li et al., 2012).

age (we chose sites planted with rubber 15–20 years ago and rubber tree diameters about 15–20 cm) and similar management practices. The soils are classified as laterites (Oxisols) developed from arenaceous shale sediments (Wang et al., 1996; Li et al., 2012).

2.2. Sampling design

Three sites (Site 1, Mengla; Site 2, Menglun; Site 3, Nabanhe) were selected to sample soil in May 2012 (Fig. 1). Each site has four land-use types: rubber monoculture (NPK fertilizer applied irregularly); rubber and tea mixture (NPK fertilizer applied irregularly); rubber polyculture (not fertilized), and natural forest (Fig. S1). Rubber was absent only from the natural forest. In each land-use type, we established five 10 × 10 m squared plots, spaced apart by 10 m. All the plant species in the understory vegetation in the squared plots were recorded (Table S1). In each plot, we placed five circular frames of 20 cm diameter in the middle, and in the four corners. Then, plant litter was collected from each frame and combined. After collecting the litter, soil samples were taken from 0 to 15 cm depth with a 5 cm diameter soil corer and these soils were also combined as independent replicates. Plant litter was oven dried at 80 °C to constant weight. Each replicate of soil was passed through a 2-mm diameter mesh and the roots were collected. Since some plant feeders live inside the roots, these collected roots were also used to extract nematodes together with the soil samples. Then, those roots were oven dried to constant weight. The soil was divided into two parts. One part was used for physical and chemical properties (Soil moisture, total C, N and pH) analysis and the other was used for nematode community analysis.

2.3. Isolation and identification of nematodes

Nematodes were extracted from 100-g soil samples from each pot via a modified cotton–wool filter method (Liang et al., 2009), and were counted and identified under a dissecting microscope. Nematodes were grouped according to feeding habit: (1) bacterial-feeding nematodes (Ba), (2) fungal-feeding nematodes (Fu), (3) plant-feeding nematodes (Pl), and (4) omnivores and carnivores (Om&Ca) (Yeates et al., 1993). Additionally, several ecological indices were calculated to assess nematode community diversity and structure. These included the Shannon–Weaver diversity index

$H' = -\sum p_i (\ln p_i)$, where p_i is the proportion of individuals in the ith taxon (Yeates and Bongers, 1999); maturity index (MI) = $\sum(v_i)\cdot(f_i)$, where (v_i) is the cp value of taxon i according to their r and K characteristics (Bongers, 1990), and (f_i) is the frequency of taxon i in a sample; plant parasite index (PPI) which was determined in a similar manner for plant–parasitic genera (Bongers, 1990); Nematode Channel Ratio (NCR) = Ba/(Ba + Fu) where Ba and Fu are, respectively, the relative contributions of bacterial-feeding and fungal-feeding nematodes to total nematode abundance (Yeates, 2003); enrichment index EI = $100 \times (\sum k_e n_e / (\sum k_e n_e + \sum k_b n_b))$, where k_b is the weight assigned to guilds Ba_2 and Fu_2, and n_b represents the abundance of nematodes in guilds Ba_2 and Fu_2, which indicate basal characteristics of the food-web (Ferris et al., 2001; Li et al., 2009). k_e is the weight assigned to guilds Ba_1 and Fu_2, n_e is the abundance of nematodes in these guilds (indicating an enriched condition of the food-web); structure index SI = $100 \times (\sum k_s n_s / (\sum k_s n_s + \sum k_b n_b))$, k_s is the weight assigned to guilds Ba_3–Ba_5, Fu_3–Fu_5, Om_4–Om_5, and Ca_2–Ca_5; and n_s is the abundance of nematodes in these guilds, representing the structural condition of the food-web (Ferris et al., 2001).

2.4. Data analyses

Two-way MANOVA was used to detect significant effects of site and land-use type on soil nematode number of genera in each feeding type. Two-way ANOVA was used for effects of site and land-use type on nematode abundance, taxa richness and ecological indices. The Mantel test was used to determine which factors (C, N, plant diversity, pH, soil moisture, root quantity and litter quantity) were significantly correlated with the nematode community structure. These factors were used to construct a soil property and plant diversity matrix for redundancy analysis (RDA) in the vegan package (Oksanen et al., 2010) of R v. 1.17-3 project (R Development Core Team, 2010). Detrended correspondence analysis (DCA) indicated that axis lengths were less than 3, so redundancy analysis (RDA) was the appropriate method to analyze the relationship between nematode communities and environmental factors. Duncan's test was employed to determine if differences were significant, with the significance level set at $P < 0.05$. ANOVA and linear regressions were performed in SPSS 13.0 software. Linear regression was used to analyze relationships between plant litter quantity and nematode abundance and between root quantity and nematode abundance.

3. Results

3.1. Nematode communities

In this study, a total of 28, 31, 39, and 42 nematode genera were found in rubber monoculture, rubber and tea mixture, rubber polyculture, and natural forest, respectively. *Cephalobus*, *Filenchus* and *Tylenchus* were dominant throughout (Table 1). Two-way MANOVA showed that both land-use types and sites significantly affected nematode community structure (Df = 3, $F_{\text{land-use type}} = 16.668$, $P < 0.01$; Df = 2, $F_{\text{site}} = 10.300$, $P < 0.01$), with a significant interaction between the two factors ($Df_{\text{land-use type*site}} = 6$, $F_{\text{land-use type*site}} = 3.627$, $P < 0.01$). Land-use types had significant impact on the nematode abundance. Site had significant impacts on nematode taxa richness. Significant interactions between land-use type and site were observed on nematode taxa richness (Table 2). Nematode taxa richness increased from rubber monoculture to natural forest (Tables 1 and 3). The RDA showed that RDA1 explained 56.85% and RDA2 explained 6.85% variation among nematode communities (Fig. 2). The strongest separation occurred between nematode communities in rubber monoculture

Table 1
Nematode genera (%), ordered by feeding type and colonizer-persister value, and number of genera in each feeding type present in four land-use types at three sites ($n = 5$). Site 1 = Mengla, site 2 = Menglun and site 3 = Nabanhe. ± represent standard deviation.

Feeding types	Rubber monoculture			Rubber and tea mixture			Rubber polyculture			Natural forest		
	Site1	Site2	Site3	Site1	Site2	Site3	Site1	Site2	Site3	Site1	Site2	Site3
Ba_1												
Brevibucca	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.40 ± 0.55	0 ± 0	0.31 ± 0.43	1.25 ± 1.00
Diploscapter	0 ± 0	0.20 ± 0.44	0 ± 0	0 ± 0	0.30 ± 0.21	0 ± 0	0.85 ± 0.58	0.58 ± 0.53	0.82 ± 0.46	0 ± 0	0.93 ± 0.85	1.28 ± 0.54
Mesorhabditis	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.37 ± 0.51	0 ± 0	0 ± 0	0 ± 0	0.78 ± 1.24	0 ± 0	0 ± 0	1.43 ± 1.16
Panagrobelus	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.75 ± 0.64	0 ± 0	0.82 ± 1.02	0.79 ± 0.85	1.62 ± 0.82	1.67 ± 1.31	1.56 ± 1.31	0.71 ± 0.73
Panagrolaimus	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1.66 ± 1.33	1.54 ± 1.27	2.06 ± 0.76	0 ± 0	0.47 ± 0.69	1.84 ± 0.72
Protorhabditis	1.79 ± 1.07	1.56 ± 0.92	0 ± 0	1.93 ± 1.08	0 ± 0	0.39 ± 0.53	1.14 ± 0.90	0 ± 0	0 ± 0	1.54 ± 0.75	1.27 ± 0.89	0.54 ± 0.50
Rhabditis	0 ± 0	0 ± 0	1.54 ± 0.85	0 ± 0	1.04 ± 0.64	3.17 ± 1.13	1.17 ± 1.29	0.79 ± 0.85	1.45 ± 0.59	0.81 ± 0.98	0.93 ± 1.00	1.27 ± 0.49
Ba_2												
Acrobeles	0 ± 0	0.95 ± 0.66	0 ± 0	0 ± 0	1.52 ± 0.85	0 ± 0	0 ± 0	3.59 ± 1.15	0 ± 0	1.76 ± 0.98	1.63 ± 0.53	1.46 ± 0.52
Acrobeloides	0 ± 0	0 ± 0	0.95 ± 0.67	0.80 ± 0.84	0.99 ± 0.69	1.27 ± 0.40	1.70 ± 0.61	1.72 ± 1.07	1.03 ± 0.75	0.47 ± 0.44	0.62 ± 0.38	1.28 ± 0.84
Anaplectus	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1.20 ± 1.34	1.45 ± 0.97	0.71 ± 1.23	0.99 ± 0.98	1.28 ± 0.84
Cephalobus[a]	16.34 ± 1.32	15.11 ± 1.77	15.11 ± 2.17	7.52 ± 1.93	9.04 ± 1.38	7.92 ± 1.40	6.11 ± 2.52	6.53 ± 2.28	6.57 ± 1.56	5.05 ± 1.65	5.18 ± 1.55	6.88 ± 1.03
Chiloplacus	2.14 ± 0.74	0 ± 0	0 ± 0	2.83 ± 0.87	0 ± 0	0 ± 0	1.34 ± 0.72	1.38 ± 1.17	1.45 ± 0.62	0 ± 0	1.63 ± 0.73	1.27 ± 1.00
Eucephalobus	2.97 ± 0.83	4.61 ± 1.31	6.21 ± 1.77	1.78 ± 1.47	5.35 ± 0.94	5.69 ± 1.40	2.74 ± 1.40	3.56 ± 0.80	4.08 ± 0.88	3.83 ± 0.61	3.92 ± 0.97	3.61 ± 0.76
Paraphanolaimus	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.36 ± 0.49
Plectus	1.94 ± 1.12	0 ± 0	0 ± 0	1.09 ± 0.70	0.98 ± 0.66	1.09 ± 0.75	2.85 ± 0.89	2.77 ± 1.25	3.28 ± 1.53	2.33 ± 1.84	2.24 ± 1.68	2.91 ± 1.36
Tylocephalus	1.52 ± 1.05	1.91 ± 0.94	1.16 ± 0.44	0.69 ± 0.67	3.20 ± 1.46	2.48 ± 1.60	3.45 ± 1.58	3.59 ± 2.31	4.12 ± 2.12	3.18 ± 1.02	2.01 ± 1.00	3.67 ± 1.98

(continued on next page)

Table 1 (*continued*)

Feeding types	Rubber monoculture			Rubber and tea mixture			Rubber polyculture			Natural forest		
	Site1	Site2	Site3	Site1	Site2	Site3	Site1	Site2	Site3	Site1	Site2	Site3
Ba_3												
Prismatolaimus	6.10 ± 1.84	6.88 ± 1.08	7.51 ± 1.69	7.00 ± 1.46	0 ± 0	0 ± 0	4.75 ± 1.08	3.78 ± 0.80	3.73 ± 1.68	7.18 ± 3.02	8.12 ± 1.95	3.29 ± 1.43
Rhabdolaimus	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.72 ± 0.78	0.30 ± 0.41	1.64 ± 1.22
Ba_4												
Alaimus	8.06 ± 1.57	6.71 ± 0.96	5.65 ± 2.04	8.01 ± 1.02	7.91 ± 1.55	7.65 ± 2.01	1.70 ± 0.61	7.60 ± 1.44	7.00 ± 1.45	7.43 ± 1.15	6.25 ± 0.38	4.58 ± 1.33
Fu_2												
Aphelenchoides	7.46 ± 0.70	4.04 ± 0.89	4.03 ± 1.13	7.12 ± 1.10	4.68 ± 1.76	4.80 ± 0.97	2.30 ± 1.60	4.20 ± 1.38	3.94 ± 1.63	2.69 ± 1.33	3.53 ± 1.01	5.12 ± 1.94
Aphelenchus	4.13 ± 0.87	2.31 ± 1.13	2.48 ± 1.37	2.40 ± 0.38	3.80 ± 1.39	3.58 ± 1.02	4.32 ± 2.65	2.60 ± 1.80	3.66 ± 1.73	1.81 ± 0.98	2.32 ± 0.68	3.77 ± 1.48
Fu_4												
Leptonchus	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.65 ± 0.68	0 ± 0	0 ± 0	3.81 ± 0.86	2.28 ± 1.04	0.93 ± 0.69
Pl_2												
Filenchus[a]	11.73 ± 2.36	4.78 ± 1.52	5.21 ± 1.01	10.72 ± 2.54	5.00 ± 1.76	4.61 ± 1.36	12.95 ± 1.13	7.16 ± 1.84	7.20 ± 1.68	6.93 ± 1.61	9.54 ± 3.01	6.53 ± 1.72
Paratylenchus	0 ± 0	0.77 ± 0.80	0.76 ± 0.81	0 ± 0	1.30 ± 0.99	1.65 ± 0.68	0 ± 0	1.35 ± 0.72	1.84 ± 0.86	1.15 ± 0.87	1.51 ± 1.16	0.88 ± 0.87
Tylenchus[a]	13.53 ± 3.33	23.36 ± 3.45	22.62 ± 4.07	17.24 ± 5.13	18.58 ± 1.45	22.00 ± 3.33	8.02 ± 2.27	12.66 ± 3.20	8.60 ± 1.76	4.06 ± 1.41	4.75 ± 0.74	7.24 ± 1.30
Pl_3												
Criconema	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1.54 ± 1.35	1.04 ± 1.25	1.60 ± 1.54	1.36 ± 1.13	1.83 ± 0.94
Dolichodorus	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	3.79 ± 1.34	3.20 ± 1.45	0.90 ± 1.13
Helicotylenchus	5.34 ± 1.23	5.59 ± 1.57	5.21 ± 1.01	3.10 ± 1.51	9.17 ± 0.66	8.11 ± .0.71	1.81 ± 1.25	4.79 ± 1.29	3.50 ± 1.20	4.59 ± 1.19	2.84 ± 0.98	2.51 ± 1.11
Hirschmanniella	4.94 ± 1.43	2.31 ± 0.89	2.32 ± 0.87	4.07 ± 0.94	3.89 ± 1.64	3.52 ± 1.49	3.40 ± 0.70	1.98 ± 0.98	2.26 ± 0.87	3.02 ± 1.35	2.90 ± 1.81	2.91 ± 1.21
Pratylenchus	1.36 ± 0.88	0 ± 0	0 ± 0	1.64 ± 1.20	0 ± 0	0 ± 0	2.69 ± 1.01	1.20 ± 1.34	1.66 ± 0.98	1.47 ± 0.99	1.14 ± 0.99	1.63 ± 0.72
Rotylenchus	0 ± 0	6.13 ± 1.88	6.21 ± 1.23	0 ± 0	5.18 ± 2.09	5.09 ± 2.46	3.47 ± 2.45	3.00 ± 1.41	3.05 ± 1.32	4.14 ± 0.96	4.67 ± 1.12	3.27 ± 1.72
Tylenchorhynchus	0 ± 0	0.96 ± 1.21	1.37 ± 0.93	0 ± 0	1.51 ± 0.74	1.53 ± 0.97	0 ± 0	1.76 ± 1.55	2.27 ± 1.59	1.45 ± 0.87	1.47 ± 0.62	2.02 ± 0.82
Pl_5												
Xiphinema	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.21 ± 0.47	0.47 ± 0.44	0.85 ± 0.63	0.53 ± 0.78
$Om\&Ca_4$												
Aporcelaimus	2.38 ± 1.14	2.09 ± 1.19	2.52 ± 1.09	6.81 ± 0.78	2.89 ± 0.77	2.41 ± 1.05	8.69 ± 3.11	3.01 ± 0.79	4.11 ± 0.72	3.47 ± 0.66	3.62 ± 0.64	3.64 ± 1.42
Dorylaimus	3.15 ± 1.30	3.64 ± 0.37	3.09 ± 0.81	8.78 ± 1.21	3.42 ± 1.84	3.12 ± 1.38	8.78 ± 2.5	5.99 ± 2.28	5.69 ± 1.89	6.46 ± 1.31	5.68 ± 1.38	4.34 ± 1.52
Eudorylaimus	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1.18 ± 1.09	0.61 ± 0.55	0.14 ± 0.32	0 ± 0	1.27 ± 0.51
Mesodorylaimus	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1.01 ± 0.83	0 ± 0	0.22 ± 0.49	0.62 ± 0.92	0 ± 0	0 ± 0	0.36 ± 0.49
Mononchus	2.53 ± 1.06	1.34 ± 0.50	2.32 ± 1.31	2.99 ± 1.25	2.91 ± 0.81	2.82 ± 1.05	2.20 ± 0.93	3.95 ± 0.40	4.11 ± 0.72	2.59 ± 1.18	2.33 ± 0.90	3.09 ± 1.02
Mylonchulus	0 ± 0	0.57 ± 0.52	0.59 ± 0.54	0 ± 0	0 ± 0	0.75 ± 0.84	0.50 ± 0.75	0.44 ± 0.98	0.63 ± 0.94	0.85 ± 0.84	0.30 ± 0.41	0.90 ± 0.64
Prionchulus	0 ± 0	0.77 ± 0.83	0 ± 0	0 ± 0	1.08 ± 1.14	1.82 ± 0.85	0.67 ± 0.69	1.37 ± 1.05	1.24 ± 1.17	1.83 ± 0.58	1.09 ± 0.43	1.26 ± 1.02
Prodorylaimus	2.56 ± 0.55	3.42 ± 1.33	3.10 ± 1.28	3.49 ± 0.35	4.18 ± 1.33	3.52 ± 0.67	1.02 ± 0.70	2.21 ± 1.33	3.71 ± 1.42	6.99 ± 0.90	5.85 ± 1.52	4.15 ± 1.55
$Om\&Ca_5$												
Belondira	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.21 ± 0.48	0 ± 0	0.19 ± 0.43	0.37 ± 0.51

[a] Indicates the dominant genera. Ba_x, Fu_x, Pl_x, $Om\&Ca_x$, where subscript x from 1 to 5 represents the nematode functional guilds: Bacterial-feeding nematodes, Fungi-feeding nematodes, Plant-feeding nematodes, and Omnivores and Carnivores, respectively; and x represents the colonizer−persister (*cp*) value according to their *r* and *K* characteristics following Bongers (1990).

Table 2
Summary of two-way analysis of variance (ANOVA) significant effects of land-use type, site and interactions on nematode abundance, taxa richness, diversity and ecological indices.

	Abundance	Taxa richness	H′	MI	PPI	EI	SI	NCR
Land use type	**	**	**	**	*	**	**	ns
Site	ns	**	**	*	**	ns	*	ns
Site * Land use type	ns	*	**	ns	ns	ns	ns	ns

Note: H′ is the Shannon–Weaver diversity; MI is the maturity index; PPI is the plant parasitic index; EI is the enrichment index; SI is the structure index; NCR is the nematode channel ratio. Symbols ** and * indicate significance at $P < 0.01$ and $P < 0.05$, respectively, statistical difference among treatment groups according to Duncan's test; ns indicates no significant difference.

and natural forest, related to differences in plant diversity, root quantity, soil moisture and C and N content. The second strongest separation occurred between nematode communities in rubber monoculture and rubber and tea mixture, corresponding to differences in pH and litter quantity. Sites of the other land-use pairs showed some degree of overlap (Fig. 2). Mantel test also showed a significant correlation between nematode community and all the environmental factors except for a marginally significant correlation with litter quantity (Table S2). Linear regression showed that nematode abundance significantly increased with plant litter quantity (Fig. 3). However, no significant correlation was observed between root quantity and nematode abundance (Fig. S2).

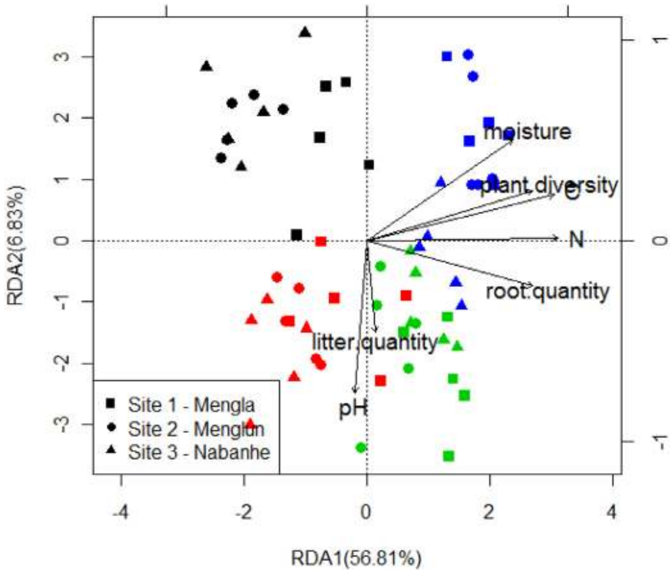

Fig. 2. Redundancy analysis (RDA) of the nematode communities with symbols coded by study sites in Yunnan Province, China. Black indicates rubber monoculture; red indicates rubber and tea mixture; green indicates rubber polyculture; blue indicates natural forest. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.2. Nematode trophic groups

Comparing nematode trophic groups among the four land-use types (Fig. 4) showed that Ba and Pl were the dominant groups in this study. They comprised about 70% of nematodes. The proportions of Ba and Fu were slightly affected by different rubber planting patterns and natural forest. The proportion of Ba was significantly lower in rubber and tea mixture than in rubber monoculture at site 1 (Df = 3, $F = 4.947$, $P = 0.013$) and it was significantly lower than other land-use types at site 3 (Df = 3, $F = 8.201$, $P < 0.01$). The proportion of Pl was significantly lower in rubber polyculture and natural forest than in rubber monoculture and rubber and tea mixture at site 2 (Df = 3, $F = 15.764$, $P < 0.01$) and site 3 (Df = 3, $F = 29.454$, $P < 0.01$). Compared to rubber monoculture, proportions of Om&Ca were significantly higher in rubber polyculture and in natural forest.

Ba and Pl richness in rubber polyculture and natural forest were significantly higher than in rubber monoculture and rubber and tea mixture at all three sites (Fig. 5). Compared to rubber monoculture, Ba and Pl richness observed in natural forest was almost twice as high. In addition, Fu richness was slightly higher in natural forest, and Om&Ca richness was higher in natural forest at sites 1 and 3.

3.3. Nematode ecological indices

Two-way ANOVA showed that land-use types had significant impacts on MI, PPI, SI and EI. However, the effect of land-use type on H′ differed among sites (Tables 2 and 3, S3). In the order from rubber monoculture to natural forest, values of MI gradually increased while PPI gradually decreased. At site 1, H′ was significantly higher in natural forest than in the rubber plantations, and it was also significantly higher in rubber polyculture than in rubber monoculture at site 1. At sites 2 and 3, H′ was consistently higher in rubber polyculture and natural forest than in rubber monoculture and rubber and tea mixture (Table S3). MI at site 1 was significantly higher than at site 3 (Table 3). PPI at site 2 and 3 were significantly higher than at site 1. SI showed the same result with MI. The value of MI in rubber monoculture and rubber and tea mixture was significantly lower than in other land-use types. PPI in rubber monoculture was significantly higher than in natural forest. EI was highest in rubber monoculture but lowest in rubber and tea mixture. SI was lowest in rubber monoculture with no significant differences among the other three land-use types (Table 3).

4. Discussion

4.1. Nematode communities

We studied effects of rubber plantation types on nematode communities at three different sites. We used spatial patterns instead of temporal sequences assuming that local site conditions before rubber planting were similar. Nematode communities were distinctly different among the four land-use types and significantly correlated with all the examined environmental factors except

Table 3
Effect of sites and of land-use types on nematode abundance, MI, PPI, EI and SI (mean ± sd). MI is maturity index; PPI is plant parasite index; SI is structural index; EI is enrichment index. Site 1 = Mengla, site 2 = Menglun and site 3 = Nabanhe.

	Nematode abundance	MI	PPI	EI	SI
Site1	740 ± 156.34a	2.81 ± 0.15a	2.34 ± 0.11b	41.35 ± 9.45a	75.34 ± 6.94a
Site2	799.5 ± 138.29a	2.71 ± 0.13 ab	2.42 ± 0.07a	40.35 ± 7.30a	73.41 ± 5.01 ab
Site3	821.3 ± 159.59a	2.69 ± 0.15b	2.41 ± 0.07a	43.73 ± 7.32a	70.90 ± 4.46b
Rubber monoculture	707.2 ± 68.20b	2.64 ± 0.11b	2.43 ± 0.09a	50.03 ± 5.19a	64.35 ± 5.24b
Rubber and tea mixture	710.73 ± 96.16b	2.67 ± 0.13b	2.41 ± 0.06 ab	33.41 ± 4.82c	74.78 ± 4.74a
Rubber polyculture	752.33 ± 75.79b	2.82 ± 0.16a	2.38 ± 0.12 ab	41.96 ± 6.56b	76.29 ± 4.98a
Natural forest	977.47 ± 160.94a	2.82 ± 0.13a	2.34 ± 0.06b	41.84 ± 5.82b	77.44 ± 4.77a

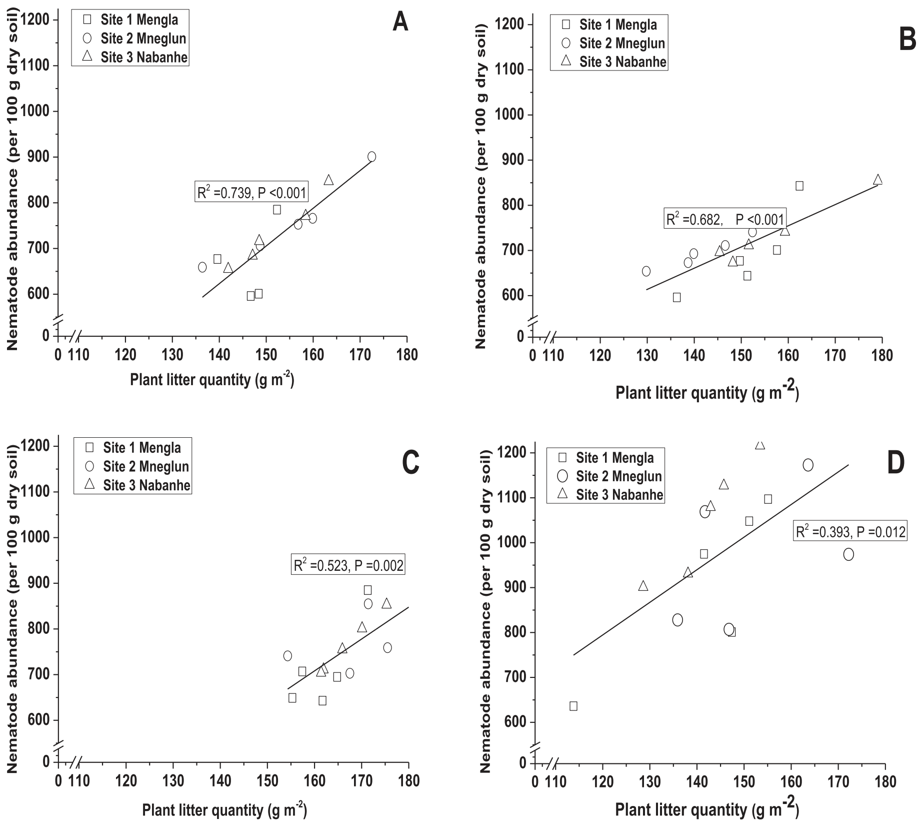

Fig. 3. Relationship between plant litter quantity and nematode abundance in A) rubber monoculture, B) rubber and tea mixture C) rubber polyculture D) natural forest in Yunnan Province, China. Note the breaks on both axes.

litter quantity, which suggested that rubber management practices significantly affected soil C, N, pH, soil moisture and vegetation (including plant diversity and quantity of plant litter and roots) and thus affected soil nematode communities. This result was consistent with many previous studies' finding that plant species richness could result in soil nematode community structure change (De Deyn et al., 2004; Viketoft et al., 2009; Eisenhauer et al., 2011; Sohlenius et al., 2011; Cesarz et al., 2013). Patterns of soil C, N and vegetation were consistent with Li et al. (2012) and Yi et al. (2013) respectively. Unfortunately, abiotic and biotic soil conditions before establishing the rubber plantations were not known, but it is likely that differences in nematode communities were caused by management practices including spraying glyphosate and weeding.

Significant effects on nematode abundance and taxa richness by rubber management also may result in ecological impacts. Low nematode abundance and taxa richness in rubber plantations may decrease soil nutrient turnover and finally limit nutrient supplies. Soil nematodes are important especially in nitrogen mineralization (Ingham et al., 1985; Griffiths, 1994; Ferris et al., 1998), and thus provide more rapid nutrient return to plants. Also, as biodiversity can enhance ecosystem functioning (Maestre et al., 2012), decreased nematode richness may diminish it. In total, 28 nematode genera were found in rubber monoculture and 42 were found

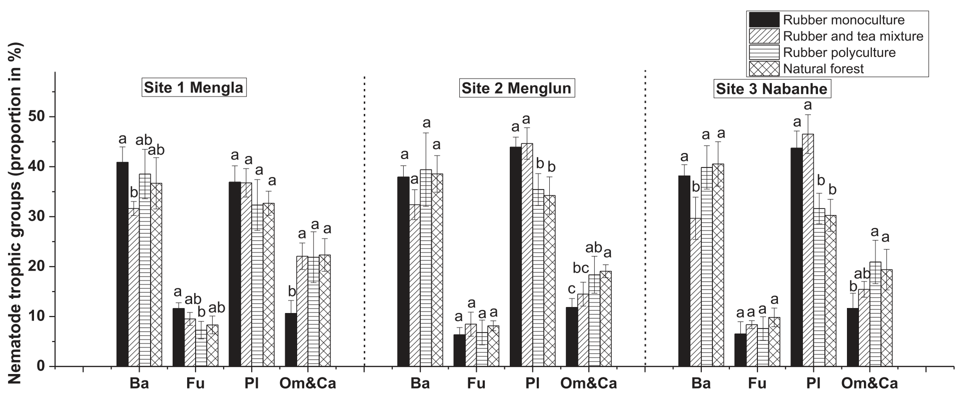

Fig. 4. Nematode trophic groups (proportion in %) among four land-use types at three sites in Yunnan Province, China. Ba, Fu, Pl, Om&Ca represent the nematode functional guilds: Bacterial-feeding nematodes, Fungi-feeding nematodes, Plant-feeding nematodes, and Omnivores and Carnivores, respectively. Error bars represent standard deviation ($n = 5$). Lower case letters indicate significant differences ($P < 0.05$, Duncan's test) among land-use types within each site.

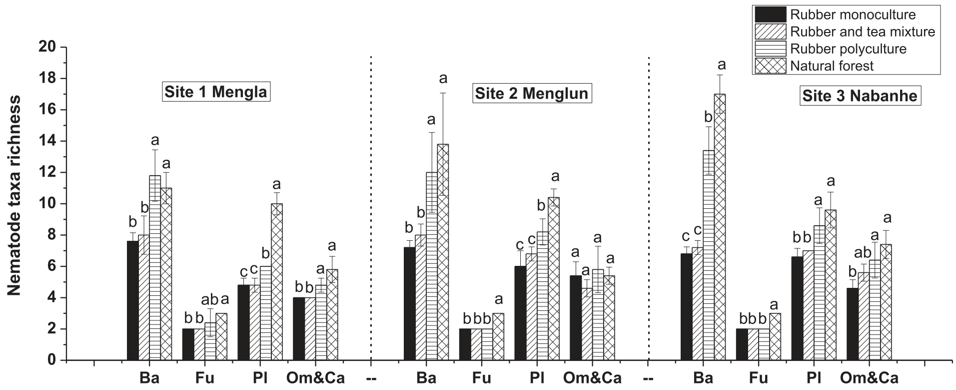

Fig. 5. Nematode taxa richness among four land-use types at three study sites in Yunnan Province, China. Ba, Fu, Pl, Om&Ca represent the nematode functional guilds: Bacterial-feeding nematodes, Fungi-feeding nematodes, Plant-feeding nematodes, and Omnivores and Carnivores, respectively. Error bars represent standard deviation ($n = 5$). Lower case letters indicate significant differences ($P < 0.05$, Duncan's test) among land-use types within each site.

in natural forest in this study, so 33% of nematode taxa richness was lost 15–20 years after conversion of natural forest to rubber monoculture. This may indicate that long-term rubber monoculture can severely degrade soil ecological functions. Therefore, simplification of rubber plantations may ultimately decrease production due to reduced soil nutrients and other functions (An et al., 2005).

Highest nematode and plant diversity both occurred in the natural forests. Nematode abundance also showed significant positive correlations with litter quantity in each land-use type, indicating that resource input into soil has important effects on nematode abundance. These are consistent with our hypothesis, and were observed at each of the three sites. However, the hypothesis related to root quantity was not supported by our observations. In Xishuangbanna, the decomposition rate of litter in natural forest is significantly higher than in man-made rubber plantations (Tang et al., 2010). Thus, the resource turnover in natural forest soils is faster than in rubber plantations. This is consistent with higher nematode populations of bacterial feeders, fungal feeders, omnivores and predators in natural forest. In addition, rubber loses its leaves in a sudden pulse (January to February), while natural forest has litterfall in all months. This provides the soil community in natural forest with a continuous food supply. Therefore, the nematode community in the natural forest may be more stable throughout the year, whereas nematode communities in the rubber plantations may show larger temporal variations. Absence of rubber plants in natural forest may also contribute to significant difference of nematode communities in natural forest compared with rubber plantations because of different chemical composition of the leaves and roots between these vegetation types.

4.2. Nematode trophic groups and nematode ecological indices

Decreased proportion (not quantitative value) of Pl due to reductions in the dominant *Tylenchus* (*cp*-2) and increased proportion of Om&Ca (*cp*-4 or -5) was observed in rubber polyculture and natural forest than in rubber monoculture and rubber and tea mixture in support of our hypothesis. This was similar to Eisenhauer et al. (2011) who found that in complex plant communities the nematode community shifted in favour of predators, thereby reducing the relative abundance of plant feeders. More *K*-strategist nematodes with a higher cp-value occur in rubber polyculture and natural forests, indicating that these two land-use types provide more stable soil environments than do rubber monoculture and rubber and tea mixtures (Bongers and Ferris, 1999; Ferris et al., 2001). In this study, the appearance of the free-living nematode *Belondira* (*cp*-5) in rubber polyculture and natural forest provided strong evidence that these soil ecosystems were more stable.

Bongers (1990) proposed MI directly reflects nematode succession and extent of soil disturbance, and that PPI was a useful index of plant-management effects. In this study, as with H', MI gradually increased with deceasing management intensity, indicating that natural forests have the most stable soil ecosystems, with rubber monoculture the least. This result was consistent with Wasilewska (1995) who found that MI increased with farming method, from monoculture to mixed cropping. We found an inverse relationship between MI and PPI, as has been previously observed (Bongers, 1990; Bongers and Korthals, 1995; Bongers et al., 1997; Li et al., 2009).

High EI values indicate predominantly enrichment with nitrogen as well as basal food-web conditions while high SI values indicate structured food-web conditions (Ferris et al., 2001; Liang et al., 2009). High EI is associated with greater abundance of Ba_1, Ba_2 and Fu_2 (Ferris et al., 2001). These nematode types are in lower trophic levels and often dominate in enriched soil environments (Ferris and Matute, 2003). High SI corresponds to high omnivorous and predatory nematode populations, which are sensitive to disruption and need more time to establish compared to more rapidly growing fungi- and bacteria-feeding nematodes (Ferris et al., 2001; Liang et al., 2009). In this study, EI decreased but SI increased, from rubber monoculture to natural forest, suggesting that nematode food-web structures were changed from basal food-web conditions to more complex structured food-web conditions, consistent with Ferris et al. (2001).

Composition of bacterial feeders and fungal feeders is affected by soil C/N (Griffiths, 1994; Ferris et al., 2001). High soil C/N ratios increase the rate of succession from bacterial-feeding to fungal-feeding nematodes, which indicate a shift from bacterial to fungal decomposition channels (Ferris et al., 2001; Ferris and Matute, 2003). That no significant soil C/N differences were observed among land-use types in this study may be reflected in unchanged NCR values. Values of NCR above 0.5 indicated that all four land-use types had bacterial-based decomposition pathway (Yeates, 2003).

5. Conclusions

In this study, four land-use types (rubber monoculture, rubber and tea mixture, rubber polyculture, natural forest) at three sites were selected to compare soil nematode community. Gradually increased nematode abundance, taxa richness, soil C and N were observed in this sequence. Inverse relationships between the extent of soil disturbance and nematode food-web conditions also were observed among these land-use types. Our results provided evidence to the local government and plantation managers that vegetation diversity has positive effects such as relatively high soil nutrient (N) levels and biodiversity in rubber plantations. However, large areas of rubber monoculture and high-intensity management have already been established in Xishuangbanna for half a century (Yi et al., 2013). Based on these results, local government and plantation managers were advised to: 1. plant various cash crops such as tea, coffee, and cocoa into rubber monocultures, which is consistent with the local government recently proposing environmentally friendly rubber plantations; 2. decrease the management intensity and adjust strategies to restore surface vegetation, and ultimately convert rubber monoculture to rubber polyculture. These actions can increase soil nematode abundance and diversity; nutrient turnover, and thus may provide more nutrients to rubber and increase soil sustainability.

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Author contributions

Hai F. Xiao and Xiao D. Yang contributed to experimental design. Hai F. Xiao and Yao H. Tian performed experiments and wrote the manuscript. D.A. Schaefer provided technical support. Hui P. Zhang and Xiang S. Ai discussed the results and commented on the manuscript.

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Appendix A. Supplementary material

Supplementary material related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2014.05.012.

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