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Subordinate plants sustain the complexity and stability of soil micro-food webs in natural bamboo forest ecosystems

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Summary

1. Subordinate plants have a significant impact on soil organisms in primary successional floodplains and grassland ecosystems, but their role in subtropical forest ecosystems remains unclear.

2. An experiment was conducted in a subtropical forest to test the hypothesis that removal of shrubs or subordinate arbour tree species would reduce the complexity and stability of the soil micro-food web. Principal response curves (PRCs) were performed to assess the responses of soil microbial and nematode communities to plant removal compared with a control through time. The effect of plant removal on complexity and stability in the soil micro-food web was assessed using a suite of indices including ratio of omnivorous-predatory to herbivorous nematode abundance (OP : H ratio), nematode diversity, resistance and resilience. Furthermore, increments of bamboo productivity among treatments were estimated.

3. Soil microbial community structure changed in response to plant removal in 2009, but recovered in 2010, and the only change observed was increased soil fungal biomass. In contrast, plant removal had greater impact on soil nematode community composition in 2010 than 2009. Subordinate arbour tree species removal (with or without shrubs) decreased the values of nematode richness, evenness, diversity, ratio of microbial-feeding to herbivorous nematode abundance (M : H ratios), OP : H ratios and resistance indices in 2010, but only decreased OP : H ratios in 2009 and increased the values of nematode dominance in 2010. Although increments in bamboo productivity were statistically similar among treatments, there was a trend decreasing progressively from control to shrub removal + selective-cutting of subordinate arbour tree species, shrub removal, and selective-cutting of subordinate arbour tree species treatments.

4. *Synthesis and applications*. Subordinate plants help sustain the complexity and stability of soil micro-food webs in subtropical bamboo forest ecosystems. Therefore, protection of subordinate plants and maintaining high plant diversity are important parts of a responsible management strategy in subtropical bamboo forests.

Key-words: complexity, plant removal, soil micro-food web, soil nematodes, stability, subordinate plants, subtropical forest

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Introduction

Bamboo is an economically important and fast-growing non-timber forest resource that is native to tropical and subtropical regions, with a few species found in temperate and polar latitudes. Moso bamboo *Phyllostachys pubescens* is the most prevalent bamboo species with high economic value in China (Gui *et al.* 2007). The world bamboo market is expected to double in 5 years (Woodridge 2012). Currently, bamboo grows on 31·3 million hectares distributed across 21 countries in the world. The majority of that land occurs in Asia, and 70% of this area is naturally regenerated (Lobovikov *et al.* 2005). There are 5·38 million hectares of bamboo in China (SFA 2009). Bamboo species are versatile, rapidly regenerate and have long been used as an important substitute for timber. The rapid growth rates (75–1000 mm per day in peak growing periods) suggest that bamboo can be harvested more frequently than comparable short-rotation silviculture species (e.g. *Eucalyptus*, an exotic species to China) (Kumar & Sastry 1999; Buckingham *et al.* 2011). In the last 20 years, ownership and control over natural resources is increasingly shifting from state governments to local communities and the private sector – and to individual households in many countries (FAO 2006). As a result, people have certain rights to manage forest resources to obtain economic benefits. Generally, plant communities are diverse in subtropical natural bamboo forest ecosystems. Although the relative abundance of bamboo in natural forests is about 77·5%, shrub removal and selective-cutting of subordinate arbour tree species are still common management practices. The goal is to increase bamboo productivity in the studied region (Li 2008; Lou, Li & Buckingham 2008), but the effects of management on forest sustainability are often ignored.

According to the 'mass ratio hypothesis' (Grime 1998), dominant plant species are considered important in ecosystems because of their substantial biomass. Subordinate species can also have significant impacts by altering soil microbial or nematode communities in primary successional floodplain or grassland ecosystems (Peltzer *et al.* 2009; Mariotte *et al.* 2013a), and enhancing community resistance against drought in grassland ecosystems (Mariotte *et al.* 2013b). The 'subordinate insurance hypothesis' suggests that subordinate species may compensate for the loss of dominant species on ecosystem functions (Mariotte 2014). Although forests generally display greater biological and structural complexity than primary successional floodplain or grassland ecosystems, most of the species diversity of forests occurs in the herb layer (Gilliam 2006). The role of subordinate plant species in subtropical forest ecosystems is poorly understood.

Soil micro-organisms are the basal components of detritus food webs, playing important roles in soil formation, nutrient cycling, regulating plant productivity (Wardle 1998) and influencing plant evolutionary processes (Lau & Lennon 2011). Subsequently, microbial consumers, such as soil nematodes, influence soil micro-organisms (Fu *et al.* 2005). Based on life-history strategy, nematode families can be classified on a colonizer–persister (c-p) scale (from 1 to 5). Nematodes with a low c-p value are relatively tolerant to disturbance in contrast to those nematodes with high c-p values (Bongers 1990; Bongers & Bongers 1998; Bongers & Ferris 1999). Moreover, many herbivorous nematodes have net negative effects on ecosystem services because they can decrease primary productivity of the plants by feeding on plant root or root hairs (Ferris & Bongers 2006; Neher 2010). When consuming their prey, bacterial- and fungal-feeding nematodes excrete *N* that is in excess of their structural and metabolic needs, which will increase the nutrient supply for the plant (Ingham *et al.* 1985). The ratio of microbial-feeding to herbivorous nematodes (M : H ratio) can indicate effects of soil food webs on plant growth (Wasilewska 1997; Thakur *et al.* 2014). Omnivorous-predatory nematodes are sensitive to environmental disturbance (Bongers & Bongers 1998), and their relative abundance can reflect the strength of top-down control and the complexity of the soil food web (Neher 2010; Thakur *et al.* 2014), which can, in turn, influence the feedback effects of lower trophic-level nematodes on plant growth.

Understanding plant–soil interactions is necessary to predict the complexity and stability of a soil food web under disturbance (Bezemer *et al.* 2013). Plant species identity and species and functional group diversities are key players in determining the abundance, diversity and trophic levels of soil biota (Wardle 2002; De Deyn *et al.* 2004; Milcu *et al.* 2006). *P. heterocycla* is the dominant arbour species and shrub representing the greatest variety of plant functional types in the studied forest (Li 2008). Moreover, even though subordinate tree species and understorey vegetation represent low biomass, they contribute to plant diversity and are, thus, intimately linked with soil organisms through the rhizosphere. Considering the importance of subordinate plant species and the potential of soil microbes and soil nematodes for the assessment of environmental disturbance, we conducted an experiment to evaluate removal of shrubs or subordinate arbour tree species in a subtropical natural bamboo forest to assess the responses of soil microbial and nematode communities. Hereafter, we refer to the soil microbial-nematode-based food web as soil micro-food web and the combination of subordinate arbour tree species and shrubs simply as subordinate plant species due to their low biomass in the plant community. Our primary objective was to evaluate the current management practices and to promote responsible management practices in subtropical natural bamboo forests. We hypothesized that removal of shrubs or subordinate arbour tree species would reduce the complexity and stability of the soil micro-food web.

Materials and methods

SITE DESCRIPTION AND SOIL SAMPLING

This experiment was conducted in Yanling County (N26°30′ E113°59′), Hunan Province, China. The climate is subtropical monsoon. The mean annual temperature is 13·9°. The mean annual precipitation is 2109 mm; distinct rainfall occurs mainly from April to June, accounting for 42% of the total annual rainfall. The soil is classified as Ultisol developed from sandstone (Li 2008). Naturally regenerated, mixed bamboo forests are widespread in this region.

Experimental sites were established in natural mixed bamboo forests in November 2007. The dominant plant species was *P. heterocycla* (relative abundance is 77·5%). In sum, a total of 73 families, 122 genera and 161 species of plants occurred in the study site. There are 34 tree species and the main families in the tree layer included *Lauraceae*, *Fagaceae, Theaceae*, *Euphorbiaceae* and *Rosaceae*.

The experiment was designed as a randomized complete block design with three blocks arranged contour to slope. Four plant community treatments were assigned randomly to four equal-sized plots (20 × 20 m = 400 m^2) within each block. Plant community treatments were as follows: (i) control without treatment (CK), (ii) shrub removal (SR) (all the shrubs were removed), (iii) selective-cutting of subordinate arbour tree species (SCST) (40–50% of subordinate arbour tree species were uniformly and randomly removed) and (iv) shrub removal + selective-cutting of subordinate arbour tree species (SR + SCST). All treatments were applied at the start of the experiment (end of November 2008). However, the regrowth of shrubs was removed again in late November 2009 under SR and SR+SCST treatments. All the plant remains were removed from the experimental plot.

The arboreal tree and bamboo species composition was recorded within each plot. Furthermore, one subplot of 10 m × 10 m was established to investigate shrubby plant species composition, and three subplots of 2 m × 2 m were established to investigate herbaceous plant species composition. The mean number of tree, shrub and herb species were seven, nineteen and five per plot, respectively. *Rubiaceae*, *Smilacaceae*, *Compositae*, *Rosaceae*, *Sabiaceae*, *Myrsinaceae* and *Araliaceae* were the dominant families found in the understorey vegetation (Li 2008).

A pretreatment survey of the general soil properties showed that soil physico-chemical characteristics (pH, total *N*, soil organic carbon) were similar among treatments before treatment application (data not shown). Similarly, we conducted simple analyses for soil microbial and soil nematode communities to provide background information of soil microbes and soil nematodes prior to treatment application. Soil sampling was conducted in May 2009 and March 2010 after treatment application. A composite sample for each plot was collected using a stratified random design. Specifically, each plot was divided into strata demarcated by positions on the slope. Within each stratum, three cores (5-cm depth, 5-cm diameter) were collected and combined into a single composite sample (3 cores × 3 slopes = 9 cores) from each plot. As a result, 12 samples (four treatments × three replicate blocks) were taken in each sampling time. Litter was removed from soil surface before soil samples were taken. Visible roots in the soil samples were removed as quickly as possible.

SOIL ANALYSES

Phospholipid fatty acids (PLFAs) were quantified by gas chromatography (Bossio & Scow 1998). Lipids were extracted from 8 g of dry-weight-equivalent fresh soil using a chloroform : methanol : phosphate buffer (1 : 2 : 0·8). Phospholipids were then separated into neutral, glyco- and phospho-lipids using solid-phase extraction columns by eluting with $CHCl_3$, acetone and methanol, respectively. Subsequently, phospholipids were subjected to a mild-alkali methanolysis to recover fatty acid methyl esters. Samples were then redissolved in 200 ml hexane containing nonadecanoic acid methyl ester (19 : 0) as an internal standard and were analysed using an Agilent 6890 gas chromatograph (Agilent Technologies, Palo Alto, CA, USA) equipped with an Ultra 2-methylpolysiloxane column. A 2-μl injection with a 1 : 50 split was analysed at an oven temperature of 260 °C, a flame ionization detector temperature of 300 °C and pressure 10·7 PSI at a constant flow rate of 0·4 ml min^{-1}. Peaks were identified using bacterial fatty acid standards and MIDI peak identification software (MIDI, Inc., Newark, DE, USA). Concentrations of each PLFA were standardized using a 19 : 0 internal standard. The biomass of bacteria was estimated by summing fatty acids, *iso* 15 : 0, *anteiso* 15 : 0, 15 : 0, *iso* 16 : 0, 16 : 1ω9c, *iso* 17 : 0, 17 : 0, *anteiso* 17 : 0, 17 : 0cy, 18 : 1ω5c and 19 : 0cy. The biomass of fungi was estimated as the sum of 18 : 1ω9c, 18 : 2ω6c and 18 : 3ω6c. The biomass of arbuscular mycorrhizae was determined by 16 : 1ω5c (Olsson *et al.* 1995; Bossio *et al.* 1998; Mikola & Setälä 1998; Kowalchuk *et al.* 2004). Evenness of soil microbial PLFAs was calculated using a Shannon evenness index (De Vries *et al.* 2012).

For each composite soil sample, nematodes were extracted from 50 g of fresh soil using Baermann funnels (Barker 1985). Nematodes were preserved in 4% formalin solution, counted under an inverted microscope, and the first 100 individuals encountered were identified to genus or family, and classified into five trophic groups (herbivores, bacterivores, fungivores, predators and omnivores) (Yeates *et al.* 1993) and into 16 nematode colonizer-persistent (c-p) and trophic group combinations (H2, H3, H4, H5, Ba1, Ba2, Ba3, Ba4, Fu2, Fu3, Fu4, P3, P4, P5, Om4 and Om5) representing five trophic groups (herbivore, bacterivore, fungivore, predator, omnivore) and c-p values (Bongers 1990; Bongers & Bongers 1998). Nematode diversity indices (Shannon–Wiener index H', Evenness J', Richness SR, Dominance λ) at the genus level were calculated (Yeates & Bongers 1999; Neher & Darby 2006).

Two trophic group ratios based on the relative abundance of different trophic groups of nematodes were calculated. First, a ratio of microbial-feeding (fungal-feeding plus bacterial-feeding) to herbivorous nematode abundance (M : H ratio) was computed to indicate soil feedback effects on plant growth (Thakur *et al.* 2014). Values of M : H ratios exceeding 1·0 indicate positive effects of soil nematodes on plant productivity (relative decline in herbivorous nematodes), whereas values <1·0 represent negative effects on plant productivity (Wasilewska 1997; Thakur *et al.* 2014). Second, a ratio of omnivorous-predatory to herbivorous nematode abundance (OP : H ratio) was computed as a measure of food web complexity. A greater ratio value of predatory to herbivorous nematode abundance indicates a stronger control of predatory nematodes on herbivorous nematodes (top-down control) or vice versa (Wasilewska 1997; Eisenhauer *et al.* 2011; Thakur *et al.* 2014). Because genera designated as the predatory

trophic group were found infrequently in our experiment, we combined omnivorous and predatory nematodes for calculating this ratio. Furthermore, a nematode resistance index was calculated as RS (t_0) = 1-(2|D_0|)/(c_0 + |D_0|), where c_0 is the value of the control at the end of the disturbance and |D_0| is the absolute difference between the control and the disturbed soil. A nematode resilience index was calculated as RL (t_x) = (2|D_0|)/(|D_0| + |D_x|) − 1, where |D_x| is the absolute difference between the control and the disturbed soil at time x. Both the index of resistance and resilience are bounded by −1 and +1, with a value of +1 for resistance index showing that disturbance had no effect (maximal resistance), and lower values showing stronger effects (less resistance). A value of 1 for resilience index at the time of measurement indicates full recovery (maximal resilience), and lower values indicate a slower rate of recovery (Orwin & Wardle 2004). In this study, we assumed a value of 1·0 for both nematode resistance and resilience indices in control soil.

ESTIMATION OF INCREMENTS OF BAMBOO PRODUCTIVITY

The diameter at breast height (d.b.h.) of *P. pubescens* prior to treatment application in 2008 and the basal diameter of *P. pubescens* in 2011 were measured. Basal diameter was converted to d.b.h. using published equations for *P. pubescens* (Zhong 2007):

$y = (x - 0 \cdot 5683)/1 \cdot 1258$ where x is the basal diameter of *P.pubescens*.

The estimation of bamboo productivity based on published allometric equations for *P. pubescens* is (Hao *et al.* 2010) as follows:

$y = 2 \cdot 7255x - 10 \cdot 168$ where x is the d.b.h. of *P.pubescens*.

STATISTICAL ANALYSIS

Two-way ANOVA (treatment and year as main factors, replicate block as error term) was employed to compare the effects of treatment, year and their possible two-way interaction on soil microbes and soil nematodes. One-way ANOVA was employed to compare the effect of treatment on the increment of bamboo productivity (replicate block as error term). Levene's test was performed to test for homogeneity of variance. Tukey (Tukey's honestly significant difference) tests were used to compare the effects of treatment on soil microbes and soil nematodes for each sampling event and the effects of treatment on the increment of bamboo productivity (replicate block as error term). Statistical significance was determined at $P < 0{\cdot}05$. ANOVAs were performed using SPSS 18.0 software (SPSS Inc., Chicago, IL, USA). The principal response curves (PRCs) method was used to determine the temporal trends of multivariate microbial community (represented by PLFAs biomarkers) and soil nematode community (represented by functional guilds) composition for each treatment using CANOCO 4.5 (Ithaca, NY, USA). PRC is based on redundancy analysis (RDA). The result is a diagram showing the first principal component of the variance explained by treatment on the y-axis along the sampling periods on the x-axis. The control treatment is treated as a zero baseline (the horizontal line). Treatment effects are represented by the deviation of each fluctuating line (i.e. SR, SCST and SR+SCST) from the zero baseline through time. Combined with the species weights, the PRC can be used to interpret the effect of treatments relative to the control based on the abundance of individual species (Lepš & Šmilauer 2003). A single microbial PLFA or nematode functional guild can be estimated by the following equation: the abundance of a PLFA biomarker/nematode functional guild relative to the control = EXP (the PRC score for each of the 'treatments' through time × value of PLFAs biomarkers/nematode functional guild score on the first RDA axis). If the relative abundance is smaller than 1, it indicates the treatment decreased the abundance of the PLFA biomarkers/nematode functional guild or vice versa. Both environmental class variables (treatments) and covariables (sampling times) were coded as nominal 0 or 1 variables (Lepš & Šmilauer 2003). Monte Carlo permutation tests were applied to compute statistical significance (n = 499).

Results

SOIL MICROBIAL AND NEMATODE COMMUNITIES

Principal response curves eigenvalues of first canonical axis were 6·5% (F = 9·106, P = 0·024) for the soil microbial community and 13·6% (F = 4·425, P = 0·018) for the soil nematode community (Fig. 1). Soil microbial community structure changed in response to plant removal in 2009 (1 year after treatments) but soon recovered in 2010. Shrub removal and selective-cutting of subordinate tree species changed the soil microbial community more than shrub removal or selective-cutting of subordinate tree species alone. Generally, the relative abundance of 13 of 15 major soil PLFAs increased in response to the SR+SCST treatment in 2009. However, the trend was nearly the opposite in the SR treatment. In contrast, based on nematode genera, temporal dynamics of soil nematode community composition within SR, SCST and SR+SCST treatments were similar (Fig. 1). Specifically, the effect of SR+SCST treatment was more pronounced on soil nematode community composition than SR treatment and SCST treatment, and SR+SCST treatment increased the herbivorous nematode communities belonging to the c-p3 guild (H3) but decreased the omnivorous nematode communities belonging to the c-p5 guild (Om5) (Fig. 1).

COMPLEXITY AND STABILITY INDICES OF SOIL MICRO-FOOD WEBS

Soil bacterial biomass, biomass of arbuscular mycorrhizal (AM) fungi, total PLFA biomass and soil PLFA evenness were similar among treatments, but differed between years (see Appendix S1 in Supporting Information). Soil fungal biomass increased after removal of subordinate plants (P = 0·038, Fig. 2). Soil nematode diversity indices responding to plant removal occurred mainly in 2010. Specifically, SCST and SR+SCST treatments decreased the values of nematode richness (Fig. 3a); and the SR+SCST treatment decreased the values of nematode evenness (Fig. 3b) and diversity (Fig. 3c), but increased the values of nematode dominance in 2010 (Fig. 3d). The SCST and SR+SCST treatments decreased the nematode M : H ratios in 2010 (P = 0·004, Fig. 4a) and OP : H ratios both in 2009 and 2010 (P = 0·001, Fig. 4b). The

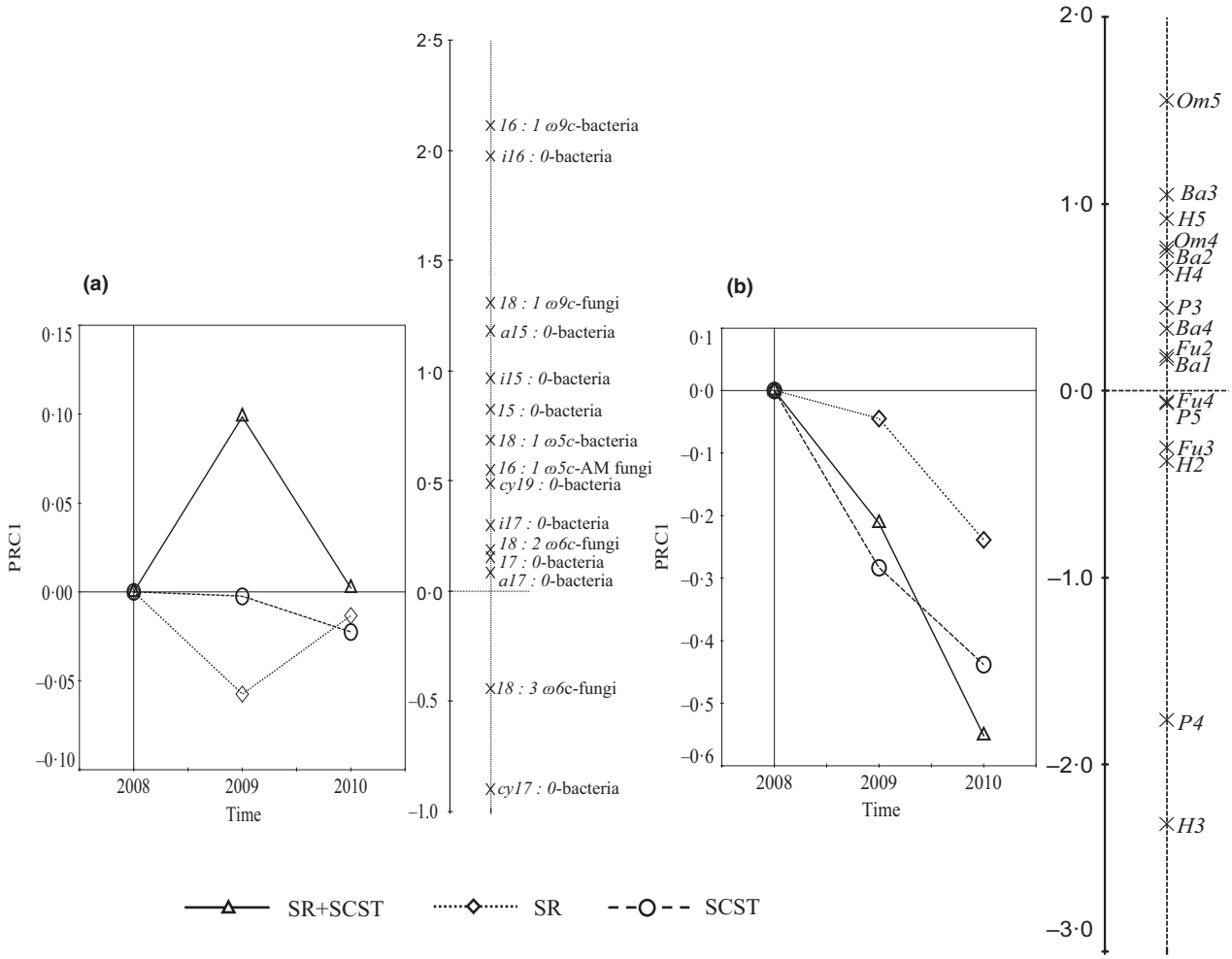

Fig. 1. Principal response curves (PRCs) with phospholipid fatty acids (PLFA) biomarker weights (a) and weights of relative abundance of each soil nematode functional guild (b) under control (CK), shrub removal (SR), selective-cutting of subordinate arbour tree species (SCST), and shrub removal + selective-cutting of subordinate arbour tree species (SR+SCST). The proportion of variability explained by the first response curves was 6·5% (F = 9·106, P = 0·024) for the soil microbial community, and 13·6% (F = 4·425, P = 0·018) for the soil nematode community. The horizontal axis represents the control treatment, and the vertical axis on the right represents PLFA biomarker weights (a) and weights of relative abundance of each soil nematode functional guild (b). Soil nematode functional guild designation is the composite of trophic group and c-p value. Ba, bacterivore; Fu, fungivore; P, predator; Om, omnivore; He, herbivore. Each nematode family/genus is assigned a value on a scale of c-p1 (short life cycle, large number of eggs, resistant to environmental perturbation, r-strategists) to c-p5 (long life cycle, low number of eggs, sensitive to environmental perturbation, k-strategists). All the nematodes were classified into 16 nematode colonizer-persistent (c-p) groups (H2, H3, H4, H5, Ba1, Ba2, Ba3, Ba4, Fu2, Fu3, Fu4, P3, P4, P5, Om4 and Om5) in five trophic groups from c-p1 to c-p5 (Bongers 1990; Bongers *et al.,* 1991; Bongers & Bongers 1998).

SR+SCST treatment decreased the nematode resistance indices in 2010 (P = 0·015, Fig. 4c).

INCREMENT OF BAMBOO PRODUCTIVITY

Although no significant differences of increments in bamboo productivity occurred among treatments, there was a trend decreasing progressively from CK to SR+SCST, SR, and SCST treatments (Fig. 5).

Discussion

Plant–soil interactions are important not only for understanding the performance and population dynamics of plants (Reynolds *et al.* 2003; Kardol, Bezemer & van der Putten 2006), but also for soil biodiversity and corresponding structure and functioning of terrestrial communities (Wardle 2006). Recent studies suggest that subordinate species may have a greater influence on ecosystem functioning than their relative abundance suggests (Mariotte *et al.* 2013a,b; Mariotte 2014). Investigating interactions between subordinate plant species and soil biota is crucial for a better understanding of plant–soil interactions and assessing the management practices of economically important forest resources. In the present study, we employed a plant removal approach to explore the interactions between subordinate plants and the complexity and stability of soil micro-food webs in a subtropical forest. Subordinate plant removal is a common management practice that alters the response of soil micro-food webs.

Our study demonstrates that the response of soil microbial and nematode communities to plant removal varies through time. Microbial community structure is affected sooner than nematode community indicators, which is proportional to their generation time. The effects on microbial communities are relatively short-lived. Saprophytic fungal components (Zak *et al.* 1996; Zelles 1997; Olsson 1999) responded quickly, indicating that subordinate plant species are an important input of detritus resources to soil organisms. Removal of subordinate plant species results in a large increase of root death and a corresponding increase of fungal biomass. The main effect of treatments occurred at relatively high positions in the food chain, such as in omnivorous nematodes (Bongers & Bongers 1998). Given that omnivorous nematodes are typically sensitive to disturbance (Bongers & Ferris 1999), this implies that plant removal created soil disturbance. A second type of nematode response was an increase in plant–parasitic nematode abundance after removal of subordinate plants, perhaps because these were rare plants and had the unintended consequence of increasing host density (Klironomos 2002). The significant increase in the abundance of herbivorous nematodes might result from compensatory growth of understorey plants after removal of subordinate arbour tree species (McGuire *et al.* 2001). Additionally,

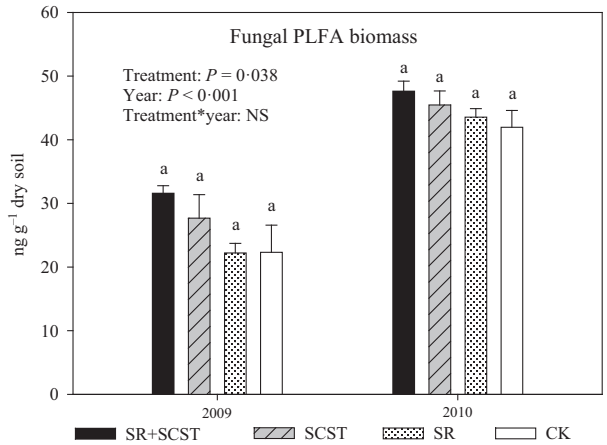

Fig. 2. Soil fungal biomass characteristics. Data are means + SE (n = 3). Treatment and year effects from the two-way ANOVA were provided for each panel. Bars in a particular sample time sharing the same superscript letter were not significantly different at P = 0·05 (Tukey).

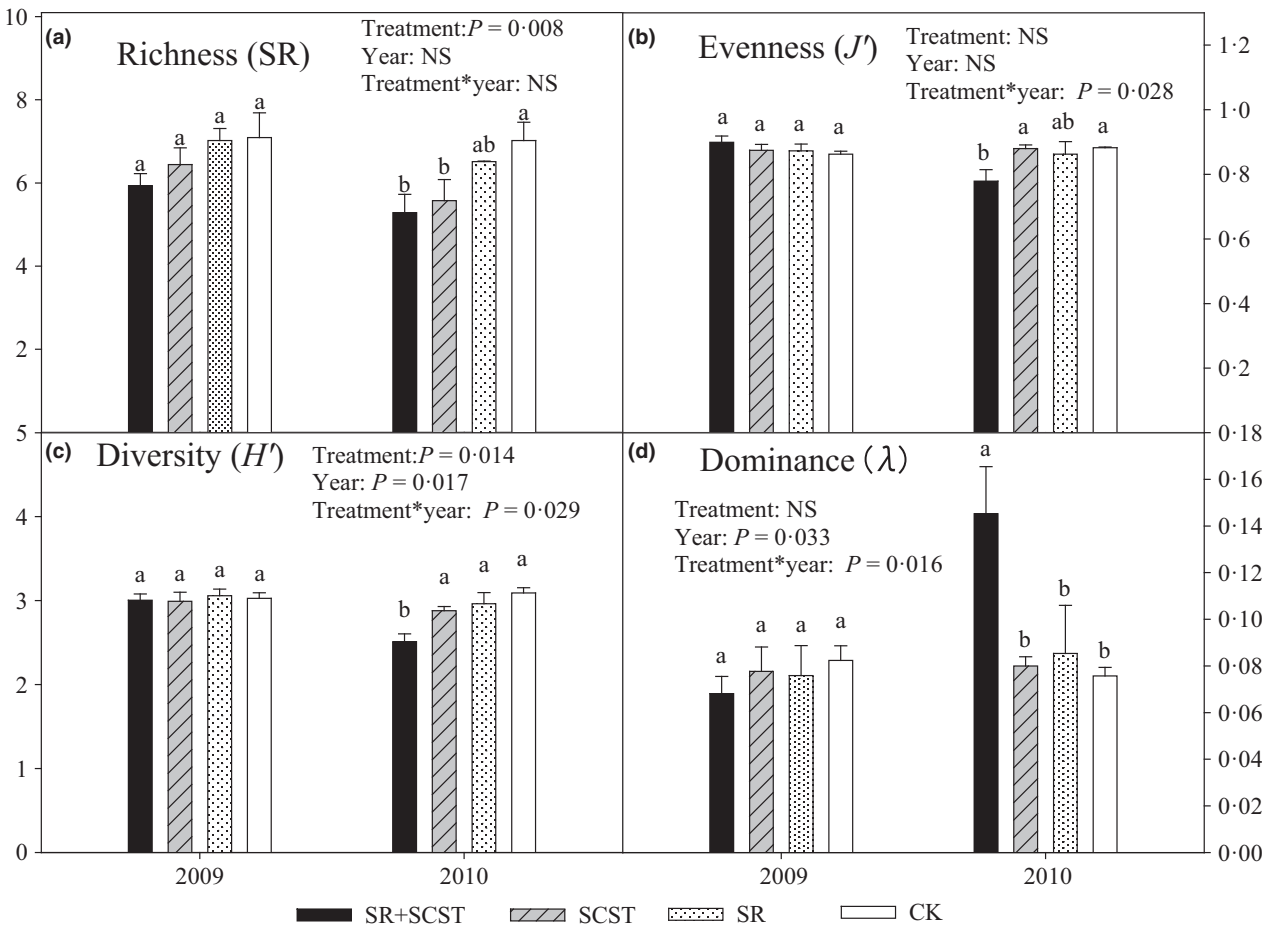

Fig. 3. Diversity indices of nematodes for different treatments. Data are means + SE (n = 3). Treatment and year effects from the two-way ANOVA were provided for each subfigure. Bars in a particular sample time sharing the same superscript letter were not significantly different at P = 0·05 (Tukey).

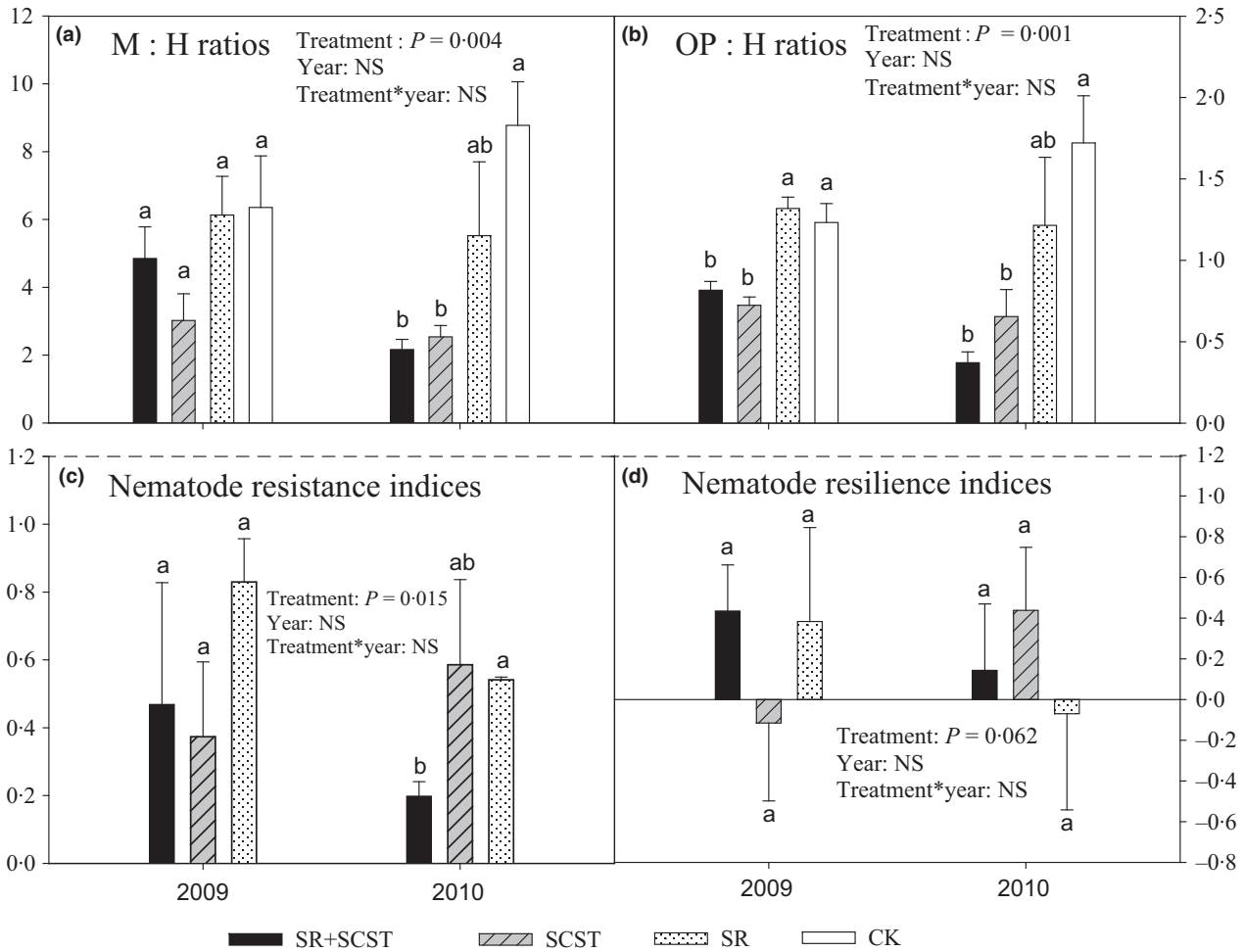

Fig. 4. The nematode trophic group ratio and resistance and resilience indices. M : H ratios – the ratio between the microbial-feeding (M) and herbivorous (H) nematode abundances. OP : H ratios: the ratio between the omnivorous-predatory (OP) and herbivorous (H) nematode abundances. Data are means + SE (n = 3). Treatment and year effects from the two-way ANOVA were provided for each subfigure. Bars in a particular sample time sharing the same superscript letter were not significantly different at P = 0·05 (Tukey). For nematode resistance and resilience indices, the dashed line represents the control treatment.

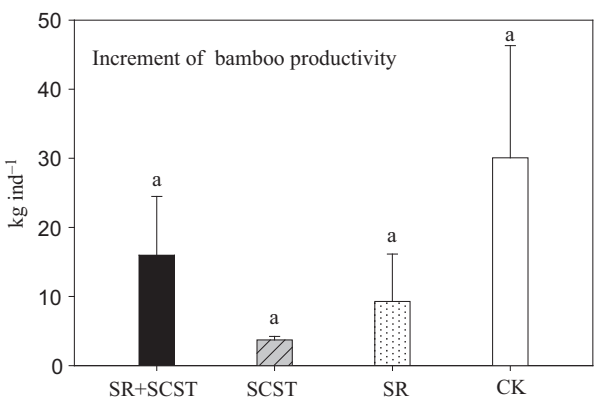

Fig. 5. Increment of bamboo productivity. Data are means + SE (n = 3). Treatment effects from the one-way ANOVA were provided. Bars sharing the same superscript letter were not different significantly at P = 0·05 (Tukey).

plant–parasitic nematodes have species-specific relationships with plant hosts, which is less true for other nematode trophic groups (Neher 2010).

A small proportion of variation was explained by PRC results, suggesting there are additional sources of variation not quantified in the experiment. First, we sampled only two points in time after plant removal which do not encompass all temporal dynamics of soil microbes and nematodes after treatments. Secondly, soil processes are less dynamic temporally than above-ground processes and the symptoms of damage to soils and soil organisms take longer to detect than damage incurred above-ground (Amundson, Guo & Gong 2003).

In the present study, we studied the response of the complexity and stability indices of soil micro-food webs to plant removal. Complexity would imply greater richness of species, species interactions, or more functional groups. Stability would imply some consistency through time; either species or functional group richness, or resilience or resistance to loss even under perturbation (Neutel *et al.* 2007).

Overall, the results support our hypothesis that subordinate plant removal reduces the complexity and stability of

soil micro-food webs. There was a cascade of response in the present study, whereby removal of subordinate arbour tree species or shrubs reduced the diversity of above-ground vegetation, which eventually reduced the complexity of soil micro-food webs. Nematode community index values of richness, diversity, resistance and resilience decreased in response to the disturbance created by removal of subordinate plants. Collectively, disturbance reduced the complexity and stability of soil micro-food webs. Therefore, subordinate plants may be important for maintaining complex and stable soil micro-food webs in subtropical forests.

Our study increases the understanding of how the complexity and stability of soil micro-food web structure changes with plant removal. The abundance and diversity of one group of soil organisms depend on other groups. For example, bacterivorous and fungivorous nematodes graze on soil bacteria and fungi, respectively, but they are eaten subsequently by higher order consumers (such as predacious nematodes and mites) (Fu *et al.* 2005; Scheu, Ruess & Bonkowski 2005). Omnivorous-predatory nematodes link several levels of food chains, establishing interconnections among trophic groups within the soil food web (Coleman, Reid & Cole 1983). Nonetheless, omnivores are common in soil (Moore, Walter & Hunt 1988; Walter, Kaplan & Permar 1991), and some predators are likely to feed on other predators (Polis 1991), thereby increasing the complexity of soil micro-food webs.

Generally, the ratio of microbivorous (bacterivorous and fungivorous) to herbivorous nematode abundance (M : H ratio) reflects the contribution of nematodes to plant productivity. For example, small M : H ratio values indicate negative effects of nematodes on plant productivity (Wasilewska 1997; Thakur *et al.* 2014). In the present study, the SCST and SR+SCST treatments may have intensified the negative effects of nematodes on plant productivity. Subsequently, this would reduce the resource input to soil organisms and exacerbate the negative effects of plant removal on soil micro-food webs.

Plants can affect soil organisms in ways that alter subsequent plant growth, which is often referred to as 'plant–soil feedback' (Kulmatiski *et al.* 2008). In the present study, subordinate plant removal did not increase bamboo productivity, but there was a trend for decreased increments of bamboo productivity from CK progressively to SR+SCST, SR and SCST treatments, suggesting that subordinate plants facilitate rather than compete with bamboo productivity. Therefore, subordinate plant removal should not be considered as an appropriate management practice.

Our results highlight the important ecological role of subordinate plants in subtropical forest ecosystems. Unfortunately, the current management practice that removes subordinate plants reflects a short-term economic gain, but results in losing ecosystem service value in the long term. Policymakers do not perceive this long-term damage. Instead, they focus on the great economic value in developing livelihoods in subtropical and tropical regions of the world where bamboo grows (Buckingham, Wu & Lou 2014). Because of the versatile uses of bamboo, there are many opportunities for management advancement to benefit the natural bamboo forests: we recommend that managers of subtropical forests employ a holistic framework that includes both above- and below-ground biodiversity, which will facilitate a better mechanistic understanding of the plant–soil interactions. Longer term experiments are needed to validate the role of subordinate plants in subtropical forest ecosystems on bamboo productivity and the complexity and stability of soil micro-food webs. Specifically, we recommend implementing treatments that (i) identify a suitable proportion of bamboo and individuals of other arbour tree species by selective harvesting, and (ii) attempt to incorporate native subordinate plants to enhance both economic value and increase the plant diversity. Ultimately, some weighted indices considering both ecological and socio-economic values based on theory-driven work should be developed for policymakers (Knoke *et al.* 2014). Ecological indicators should represent an integrated assessment of the effects of management practices on bamboo productivity and soil micro-food webs to develop management practices that optimize sustainability of subtropical natural bamboo forests. For example, we propose development of management practices that increase beneficial free-living nematodes and/or bamboo productivity, but suppress harmful plant parasitic nematodes. Socio-economic parameters should include labour costs and the potential economic return per unit area under contrasting forest management practices such as removal of subordinate plants, selective harvesting of bamboo species, and regulating the soil fertility (Hernández-Barrios, Anten & Martínez-Ramos 2015). Finally, bridging information gaps between farmers, policymakers and researchers is necessary to promote management of natural bamboo forests and achieve sustainable harvesting. Nevertheless, we believe that the present study provides empirical evidence to persuade farmers and government officials of the long-term trade-offs between socio-economic gains and ecological consequences of sustainable forest management.

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Data accessibility

The data are available at the Dryad Digital Repository doi:10.5061/dryad.5gf59 (Shao *et al.* 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Soil bacterial, AM fungal, total PLFA biomass and PLFA evenness.