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Soil biota suppress positive plant diversity effects on productivity at high but not low soil fertility

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Summary

1. Plant community productivity commonly increases with increasing plant diversity, which is explained by complementarity among plant species in resource utilization (complementarity effect), or by selection of particularly productive plant species in diverse plant communities (selection effect). Recent studies have also shown that soil biota can drive the positive plant diversity–productivity relationship by suppressing productivity more in low- than in high-diversity plant communities. However, much remains unknown about whether soil fertility plays a role in determining how soil biota affect plant diversity–productivity relationships.

2. We hypothesized that under high soil fertility conditions, negative soil biota effects dominate, which reduces plant monoculture biomass more than that of high-diversity plant communities. Conversely, under low soil fertility conditions, we hypothesized positive soil biota effects dominate, which facilitates plant resource partitioning and enhances community-level biomass in high-diversity plant communities. Hence, we expected positive plant diversity–community productivity relationships under low and high soil fertility conditions but caused by different mechanisms.

3. We tested these hypotheses using woody seedlings and set up plant assemblages with four species richness levels (one, two, four and eight species), and grew them in sterilized and unsterilized (sterilized soil + living soil inoculum) soils at two nutrient levels (low versus high fertility).

4. We found that at high fertility negative soil biota effects dominated and suppressed plant community biomass more in high-diversity plant communities than in monocultures, resulting in reduced complementarity effects of diverse plant communities and a non-significant plant species richness–community biomass relationship in unsterilized soil. Whereas at low fertility soil biota had net neutral to positive effects on plant community biomass but the beneficial effects did not increase with increasing plant species richness. Instead, soil biota neutrally affected the positive plant species richness–community biomass relationship, presumably due to non-specific effects of beneficial soil biota.

5. *Synthesis.* Soil biota and soil fertility interactively determine plant species richness–community biomass relationships. Moreover, soil biota modulate the complementary resource use among plant species. These findings suggest that environmental context plays an important role in determining whether and how soil biota generate the biodiversity–productivity relationship. Future studies would benefit from revealing the mechanisms underlying the interactive effects of soil biota, soil fertility, and plant diversity on ecosystem functioning.

Key-words: biodiversity effect, complementarity effect, plant diversity–productivity relationships, plant–microbe interactions, soil biota, soil fertility, subtropical forest

Introduction

Many empirical studies conducted under more or less constant environmental conditions have documented positive plant diversity–productivity relationships (Tilman *et al.* 2001; van Ruijven & Berendse 2005; Tilman, Reich & Isbell 2012), which has been explained by complementarity and selection effects (Loreau & Hector 2001). The complementarity effect refers to niche differentiation or facilitation among plant species, resulting in more complete utilization of resources and

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thus higher overall productivity in high-diversity plant communities (Tilman *et al.* 2001; Lambers *et al.* 2004; Fargione *et al.* 2007). In contrast, the selection effect is caused by an increased probability of diverse plant communities to contain competitive plant species that become dominant and disproportionately contribute to community productivity (Huston 1997; Loreau & Hector 2001). These two mechanisms are based on resource partitioning and competition. However, it is becoming increasingly clear that soil biota can also drive the positive plant diversity–productivity relationships (van der Heijden, Bardgett & van Straalen 2008; Maron *et al.* 2011; Schnitzer *et al.* 2011). Moreover, soil biota are likely to act in concert with niche-based processes, because they may influence plant niche partitioning (Reynolds *et al.* 2003; Bever *et al.* 2010), plant–plant facilitation (Rodríguez-Echeverría *et al.* 2013) and competition (van der Putten & Peters 1997; De Deyn *et al.* 2003; Casper & Castelli 2007; Petermann *et al.* 2008; Hodge & Fitter 2013). Yet many questions remain about whether and how soil biota influence complementarity and selection effects in determining plant diversity–productivity relationships under different soil nutrient conditions.

Soil nutrient availability affects plant–microbe interactions (van der Putten & Peters 1997; Wardle 2002; Reynolds *et al.* 2003; De Deyn, Raaijmakers & van der Putten 2004; Kardol *et al.* 2013). In low-nutrient soils plants benefit most from mycorrhizal mutualisms, whereas fertilization reduces mycorrhizal colonization (Johnson *et al.* 2003; Treseder 2004; Grman & Robinson 2013; Liu *et al.* 2015), or reduces plant benefits from the association, leading to neutral or even parasitic mycorrhizal effects (Hoeksema *et al.* 2010; Johnson 2010). On the contrary, fertilization tends to increase the negative effects of soil pathogens on plants (Solomon, Tan & Oliver 2003; Walters & Bingham 2007). Therefore, under different soil nutrient conditions, the relative strength of positive and negative soil biota effects on plant growth may change.

Both positive and negative plant–microbe interactions can affect plant diversity–productivity relationships (Klironomos *et al.* 2000; Maron *et al.* 2011; Schnitzer *et al.* 2011). Species-specific soil pathogens are more effective in low-diversity plant communities, thus negative plant–microbe interactions may reduce plant productivity more in low- than in high-diversity plant communities. This has been thought to drive the positive plant diversity–productivity relationship in some cases (Maron *et al.* 2011; Schnitzer *et al.* 2011; Kulmatiski, Beard & Heavilin 2012; Hendriks *et al.* 2013). In contrast, positive plant–microbe interactions may increase community productivity at high levels of plant diversity. Mycorrhizae are commonly known as positive soil microbes as they can improve plant nutrient uptake (Jakobsen, Abbott & Robson 1992; van der Heijden *et al.* 1998, 2006; Smith & Read 2010). In species rich plant communities, mycorrhizae may thus reduce overlap of resource niches among plants, reducing interspecific plant competition and increasing complementarity between plant species and increasing plant community productivity (Wagg *et al.* 2011). Taken together, both positive and negative soil biota effects may change with plant diversity levels, while the relative importance of them may change with soil nutrient levels. Consequently, plant diversity–productivity relationships may result from the interactive effects between soil nutrient availability and soil biota. To our knowledge, no biodiversity experiment has manipulated soil fertility, the presence/absence of soil biota, and plant diversity simultaneously.

We hypothesized that soil fertility plays an important role in determining how soil biota affect plant species richness–community biomass relationships. Specifically, we expected that under high fertility conditions, negative soil biota effects dominate and increase the steepness of the positive plant species richness–community biomass relationship by reducing plant productivity to a greater extent in low- than in high-diversity plant communities. Conversely, under low fertility conditions, we expected positive soil biota effects to dominate, which increases the steepness of the positive plant species richness–community biomass relationship by facilitating resource partitioning in high-diversity plant communities.

To test these hypotheses, we assembled plant communities at four species richness levels (one, two, four and eight species) in a greenhouse experiment. Each assemblage was grown in four soil treatments, namely low and high fertility crossed with sterilized and unsterilized (sterilized soil + living soil inoculum) soils, to test how soil biota affect plant species richness–community biomass relationships under different soil fertility conditions. We determined biodiversity effects of mixed plant communities grown under each soil condition to test how soil biota affect the complementarity, selection and biodiversity net effects.

Materials and methods

STUDY SITE, SPECIES SELECTION AND SEED COLLECTION

The greenhouse microcosm experiment was conducted at Heishiding Nature Reserve (111°53′E, 23°27′N; 150–927 m altitude) in Guangdong Province, China. The reserve has a subtropical moist monsoon climate. Mean annual temperature is 19·6 °C, with the lowest mean monthly temperature of 10·6 °C in January and the highest of 28·4 °C in July.

We chose eight co-occurring woody species based on seed availability: *Canarium album* Raeusch. (Burseraceae), *Castanopsis fissa* Rehd. Et Wils (Fagaceae), *Cryptocarya concinna* Hance (Lauraceae), *Engelhardtia fenzlii* Merr. (Juglandaceae), *Lithocarpus litseifolius* Chun (Fagaceae), *Ormosia pachycarpa* Champ. (Fabaceae), *Schima superba* Gardn. et Champ. (Theaceae), *Choerospondias axillaris* Burtt et Hill. (Anacardiaceae). Specially, *O. pachycarpa* is a nitrogen-fixing species. We collected seeds of all focal species during autumn and winter 2012. We surface-sterilized (70% ethanol for 1 min, 2·625% NaOCl for 3 min, 70% ethanol for 1 min, and sufficiently rinsed with distilled water) the seeds and stored them at 4 °C until March 2013. From March to April, all seeds were germinated in plastic boxed filled with sterilized sand.

BACKGROUND SOIL CHARACTERISTICS

Clay loam soil from the field site was mixed with sand (1: 1 v/v) and sterilized by gamma radiation (25 kGy) to be used as background

soil. A high sand content was used to reduce the nutrient availability of the background soil, which helped in generating the soil fertility gradient with the subsequent nutrient treatment. In the background soil, the total N content was 0·625 g kg^{-1}, the total P content 0·141 g kg^{-1}, the total K content 35·9 g kg^{-1}, and the percentage organic matter was 1·29%.

EXPERIMENTAL SET-UP

Each pot (20 cm in diameter, 25 cm in height) was filled with 2900 g of the background soil. Eight newly germinated seedlings were transplanted into each pot. Plant communities were assembled into pots at four species richness levels (one, two, four and eight species). Specifically, each of the eight species was planted as a monoculture (richness level of one) and was replicated twice (16 replications of monocultures in total). The two- or four-species mixtures were created by separate random draws from the eight-species pool. There were 16 random draws for each of the two- and four-species richness levels. Each randomly drawn species composition was considered as one replication. The mixture of all eight-species was replicated 16 times. All species mixtures were planted with the species in equal portions and the same total density as the monocultures (substitutive design).

To study the effects of soil biota, soil fertility and their interaction on plant species richness–community biomass relationships, we used a full-factorial design with the factors nutrient treatment (low versus high fertility) crossed with soil biota treatment (sterilized versus unsterilized soil, i.e. sterilized soil + living soil inoculum) crossed with plant species richness. This resulted in a total number of 4 richness levels × 2 soil biota treatments × 2 nutrient treatments × 16 replications = 256 pots and 256 × 8 = 2048 individuals. All pots were placed randomly in the experimental area within the glasshouse. Seedlings were watered between nutrient treatments.

SOIL BIOTA TREATMENT

Two weeks after transplantation, each experimental unit received unsterilized or sterilized soil treatments. We collected living soils beneath adults of all focal species from 24 sites (8 focal species × 3 adults) in the field. The nutrient availability across the field is that the total N content ranges from 0·2 to 3·3 g kg^{-1}, the total P content ranges from 0·028 to 0·173 g kg^{-1}, and the total K content ranges from 1·87 to 50·08 g kg^{-1}. All living soils were then mixed thoroughly and divided into two halves. The first half was sterilized by gamma radiation and the second half was used as living soil inoculum source. For the unsterilized soil treatment, we added 50 g of living soil onto the background soil in each pot, covered by another 50 g of sterilized soil to prevent cross-infection among pots. For the sterilized soil treatment, we added 100 g of sterilized soil into each pot as a layer on top of the background soil. Together with the original 2900 g of background soil, each pot contained 3000 g of soil in total. Though it is possible that soil sterilization inoculum had increased mineral nutrient availability as compared to living soil inoculum (Troelstra *et al.* 2001), the 59:1 ratio of sterilized soil to inoculum is expected to strongly dilute this effect.

NUTRIENT TREATMENT

The nutrient addition treatment was started 4 weeks after the planting of seedlings. Every month each experimental unit received 150 mL of water (low fertility treatment) or half-strength Hoagland nutrient solution (high fertility treatment).

PLANT BIOMASS

Seedlings were allowed to grow for 16 months. At the end of the experiment, we harvested the seedlings and determined dry weight for each individual (separately for shoots and roots).

STATISTICAL ANALYSIS

Plant species richness–community biomass relationships under different nutrient and soil biota treatments

To explore how plant species richness, soil fertility and soil biota influenced plant community biomass, we first applied a linear mixed-effects model with plant species richness, nutrient and soil biota treatments, as well as interactions among them as fixed terms. *Ormosia pachycarpa* was the only nitrogen-fixing species in the experiment and thus its presence was included as a covariate to account for nitrogen-fixing effects (Schmid *et al.* 2002; Zuppinger-Dingley *et al.* 2014). This may help explain the remaining variation in community biomass that was unexplained by plant species richness. Species composition and its interaction with nutrient and soil biota treatments were used as random terms. Second, we analysed plant community biomass with different nutrient and soil biota treatments separately using mixed-effects models. Plant species richness was included as a fixed term and *O. pachycarpa* presence was included as a covariate. Again, species composition and its interactions with nutrient and soil biota treatments were used as random terms. In all of the above models the log-transformed species richness was used as continuous explanatory variable and community biomass was log-transformed to improve normality and homoscedasticity of residuals.

Effects of nutrient and soil biota treatments on plant biodiversity effects

To calculate biodiversity effects for mixed plant communities we used the additive partitioning method (Loreau & Hector 2001), which partitions biodiversity net effects into complementarity and selection effects. The biodiversity net effect is the difference between the mixture and the average of the monocultures of the species making up the mixture. A large complementary effect reflects that different species contribute similarly to mixture biomass. A large selection effect reflects that a few or a single species dominates the mixture biomass.

Plant biodiversity effects (complementarity, selection and biodiversity net effects) were assessed using a linear mixed-effects model with nutrient treatment, soil biota treatment and interaction between them as fixed terms. Plant species richness was included as a covariate to control for the potential differences in biodiversity effects among plant communities with different richness. In particular, when analyzing the selection effect, we also included the presence of *O. pachycarpa* as a covariate to test whether changes in selection effects in response to soil fertility and soil biota would also occur for the remaining species. Again, species composition and its interaction with nutrient and soil biota treatments were included as random terms. In addition, we used t-tests to examine whether biodiversity effects significantly differed from zero and differed between sterilized and unsterilized soils.

Effects of nutrient and soil biota treatments on individual plant species performances

To reveal how individual plant species in mixed communities responded to the nutrient and soil biota treatments, we analysed the species-specific biomass in eight-species mixtures of all plant species in response to soil biota and soil fertility using redundancy analysis (RDA). The significance of the canonical axes was investigated by partial Monte Carlo permutation tests, using nutrient treatment as factor and soil biota treatment as cofactor and vice versa. Treatment effects on the biomass of individual plant species were analysed by a multivariate general linear models.

Linear mixed-effects models were run using the ASReml software for R (VSN International Ltd., Herts, UK). The RDA was performed using the R package 'VEGAN'. All data processing and analyses were performed in R 3.2.5 (R Core Team 2015).

Results

PLANT SPECIES RICHNESS–COMMUNITY BIOMASS RELATIONSHIPS IN RESPONSE TO SOIL BIOTA AND SOIL FERTILITY

Community biomass increased with increasing plant species richness (Table 1; $P = 0{\cdot}031$). More notably, nutrient and soil biota treatments concurrently affected the slopes of the species richness–community biomass relationships (Table 1; plant species richness × nutrient treatment × soil biota treatment interaction; $P = 0{\cdot}017$) even after we excluded the effects of the nitrogen-fixing species *O. pachycarpa*. Sterilized and unsterilized soils did not differ in nutrient availability at the end of the experiment (see Table S1, Supporting Information), as expected since the soil inoculum that distinguished the unsterilized from the sterilized soil represented a minor amount of the total soil per pot. Under high fertility conditions, soil sterilization changed the plant species richness–community biomass relationship: significant positive species richness–community biomass relationship existed in sterilized soil ($P = 0{\cdot}013$), but this relationship was not present in unsterilized soil ($P = 0{\cdot}927$; Fig. 1a; Table S2). Moreover, under high soil fertility the average monoculture biomass in unsterilized and sterilized soils were not significantly different ($P = 0{\cdot}639$); whereas the average biomass of eight-species mixtures increased by 26·7% from 11·6 ± 0·72 g per pot in unsterilized soil to 14·7 ± 1·14 g

Table 1. Effects of mixed-effects models for the log-transformed community biomass (numDF: degrees of freedom of term, denDF: degrees of freedom of error term [which can be fractional in REML analysis], F: variance ratio, *P*: error probability, VC: variance component, s.e.: standard error of variance component, the numbers in bold indicate significant effects)

Fixed terms	numDF	denDF	*F*	*P*
Species richness (SR)	1	36·9	5·02	**0·031**
Nutrient treatment: infertile versus fertile (N)	1	104·7	8·23	**0·005**
Soil treatment: sterilized versus unsterilized (S)	1	104·7	0·01	0·911
SR × N	1	55·4	0·11	0·741
SR × S	1	55·4	4·42	**0·040**
SR × N × S	1	78·8	6·00	**0·017**
Ormosia pachycarpa	1	38·1	22·80	**<0·001**
Random terms	**VC**	**s.e.**		
Species composition (Sp.com)	0·343	0·087		
Sp.com × N × S	0·053	0·021		
Residual	0·102	0·014		

The random effect term (Sp.com × N) was bound in the final model and therefore excluded.

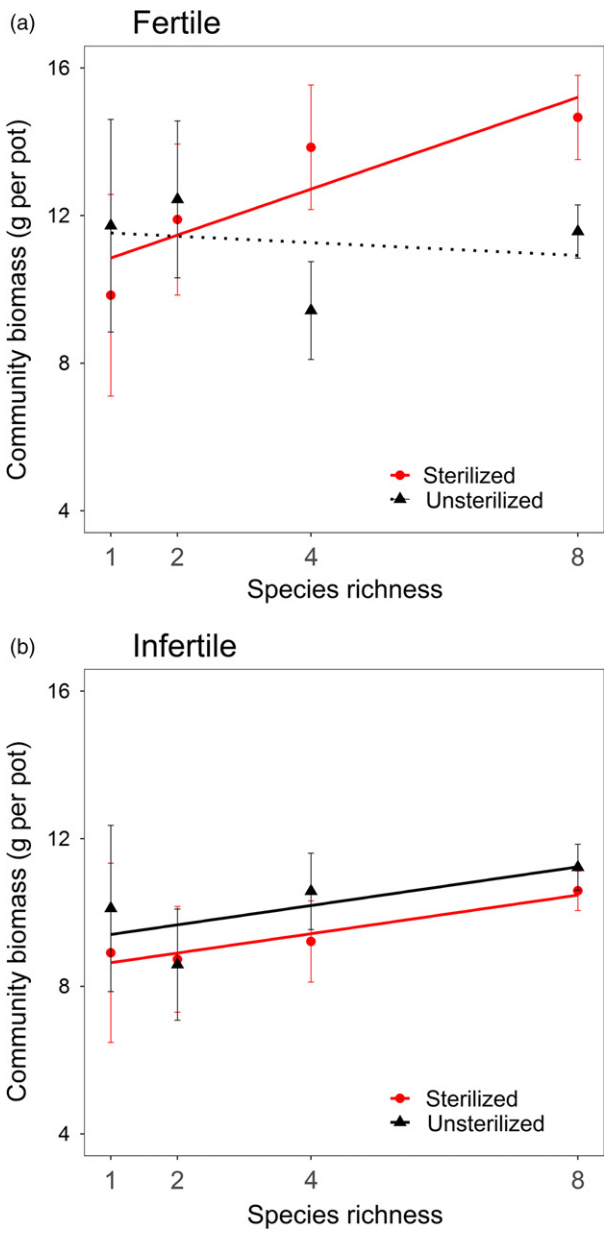

Fig. 1. Relationships between plant species richness and community biomass under (a) fertile and (b) infertile conditions, treated with sterilized (sterilized) or unsterilized soil inoculum (unsterilized). Solid line indicates significant ($P < 0{\cdot}05$) relationships and dotted line indicate insignificant ($P > 0{\cdot}05$) relationship between plant species richness and community biomass (see Table S2). [Colour figure can be viewed at wileyonlinelibrary.com]

per pot in sterilized soil ($P = 0{\cdot}030$). Thus, living soil inoculum resulted in the non-significant species richness–community biomass relationship by reducing the community biomass at the high end of the plant species richness gradient. Conversely, under low soil fertility the relationship between plant species richness and plant community biomass was not affected by the presence of living versus sterilized soil inoculum (Fig. 1b). Under this condition of low soil fertility, plant community biomass increased similarly with increasing plant species richness in both sterilized and unsterilized soils (Table S2; $P \leq 0{\cdot}043$ for both of them), whereas the biomass tended to be higher in unsterilized than in sterilized soil.

COMPLEMENTARITY AND BIODIVERSITY NET EFFECTS IN RESPONSE TO SOIL BIOTA AND SOIL FERTILITY

The soil biota treatment affected the complementarity effect, and interacted with soil fertility in influencing the biodiversity net effect (Table 2; $P = 0{\cdot}014$ and $P = 0{\cdot}001$, respectively). In soil with fertilizer for four- and eight-species mixtures, the complementarity effect and biodiversity net effect were greater in soil with sterilized than that in soil with living soil inoculum (Fig. 2a,b). In fertile sterilized soil, four- and eight-species mixtures had significant positive biodiversity net effect (Fig. 2a; $P = 0{\cdot}003$ and $P < 0{\cdot}001$, respectively), and eight-species mixtures had significant positive complementarity effect (Fig. 2b; $P < 0{\cdot}001$). In fertile unsterilized soil, mixed communities generally did not have significant complementarity and biodiversity net effects, except that the eight-species mixtures had significant positive biodiversity net effect (Fig. 2a; $P = 0{\cdot}019$). Therefore, at high soil fertility unsterilized soil as compared to sterilized soil resulted in reduced complementarity and biodiversity net effects of diverse plant communities. Whereas at low soil fertility, biodiversity effects (net, complementarity and selection effects) did not differ between unsterilized and sterilized soils (Fig. 2d–f). Overall high fertility tended to increase the selection effect ($P = 0{\cdot}008$), whereas soil sterilization did not affect the selection effect ($P = 0{\cdot}167$; Table 2; Fig. 2c,d). The nitrogen-fixing species *O. pachycarpa* did not significantly influence the selection effect ($P = 0{\cdot}110$; Table 2).

Table 2. Results of mixed-effects models for the biodiversity net effect, the complementarity effect, and the selection effect (numDF: degrees of freedom of term, denDF: degrees of freedom of error term [which can be fractional in REML analysis], F: variance ratio, *P*: error probability, VC: variance component, s.e.: standard error of variance component, the numbers in bold indicate significant effects)

Fixed terms	numDF	denDF	*F*	*P*
Net effect				
Species richness (SR)	1	9·8	1·29	0·283
Nutrient treatment: infertile versus fertile (N)	1	118·8	22·94	**<0·001**
Soil treatment: sterilized versus unsterilized (S)	1	23·8	1·43	0·243
N × S	1	118·8	9·84	**0·002**
Random terms	VC	s.e.		
Species composition (Sp.com)	0·894	1·624		
Sp.com × S	2·224	2·157		
Residual	12·098	1·574		
Complementarity effect				
SR	1	6·6	1·08	0·335
Nutrient treatment: infertile versus fertile (N)	1	143·1	0·64	0·425
Soil treatment: sterilized versus unsterilized (S)	1	6·6	5·81	**0·048**
N × S	1	142·5	1·21	0·273
Random terms	VC	s.e.		
Species composition (Sp.com)	2·939	2·588		
Sp.com × S	0·065	1·469		
Residual	26·382	3·131		
Selection effect				
SR	1	4·6	0·92	0·387
Nutrient treatment: infertile versus fertile (N)	1	150·9	7·43	**0·007**
Soil treatment: sterilized versus unsterilized (S)	1	150·9	1·91	0·170
N × S	1	150·9	1·28	0·259
Ormosia pachycarpa	1	29·6	2·72	0·110
Random terms	VC	s.e.		
Species composition (Sp.com)	1·446	1·202		
Residual	21·710	4·659		

The random effect term (Sp.com × S) was bound in the final models for selection effect and the term (Sp.com × N) was bound in all models and therefore excluded.

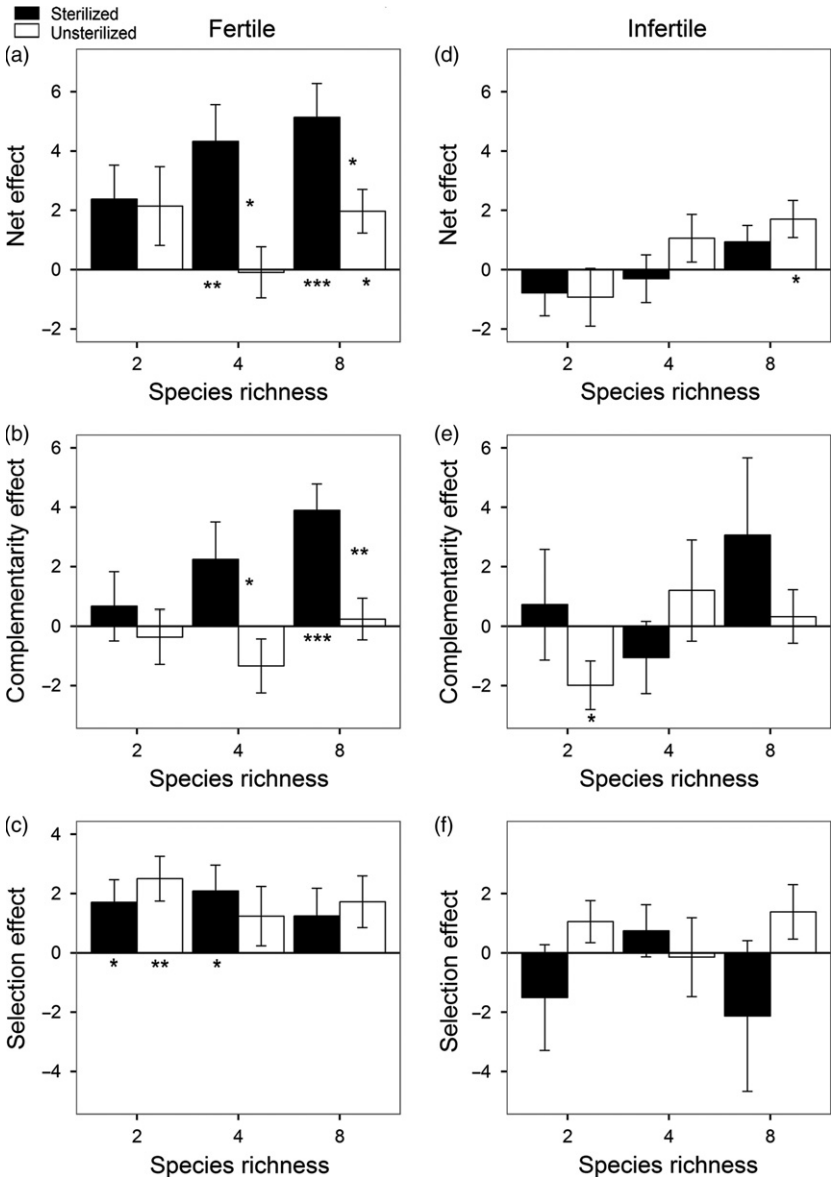

Fig. 2. Net effect (a), complementarity effect (b) and selection effect (c) of plant mixtures measured under different nutrient (infertile versus fertile) and soil (sterilized versus unsterilized) treatments. Asterisks between two bars indicate significant differences between sterilized and unsterilized soils at the same richness levels. Asterisks below bars indicate significant differences from zero. ***$P < 0{\cdot}001$; **$P < 0{\cdot}01$; *$P < 0{\cdot}05$. Data are mean values ± SE.

INDIVIDUAL PLANT SPECIES IN RESPONSE TO SOIL BIOTA AND SOIL FERTILITY IN MIXED PLANT COMMUNITIES

Overall the different plant species in the eight-species plant communities responded significantly to the soil biota and nutrient treatments (Fig. 3). The soil biota treatment explained 23·0% of the variation in the plant species-specific biomass along the first canonical axis (CA1: unsterilized versus sterilized), whereas the fertilizer treatment (CA2: infertile versus fertile) accounted for 17·8% of the variation in the plant biomass responses of the species in the eight-species mixtures (partial Monte Carlo permutation tests, $F = 6{\cdot}81$ for soil biota treatment and $F = 4{\cdot}82$ for nutrient treatment, $P < 0{\cdot}05$ for both of them). In the eight-species communities, the plant species *S. superba*, *C. album* and *C. axillaris* performed well with the presence of soil biota whereas in sterilized soil the plant species *C. fissa* and *E. fenzlii* were most productive. The effect of soil fertility on the plant community was most notable for *O. pachycarpa* which performed well in infertile soil but declined in fertilized soil, whereas all other species (apart from *E. fenzlii*) responded positively to soil fertility and especially *C. concinna* (Table S3).

Discussion

We aimed to experimentally test whether soil biota acted in concert with plant resource-based processes (complementarity or selection effects) to drive different plant species richness–community biomass relationships under different soil nutrient conditions. We found that with decreasing soil fertility, the net effects of soil biota on plant growth changed from negative to neutral and tending towards being positive. Correspondingly the relationship between plant species richness and community productivity changed from non-significant in

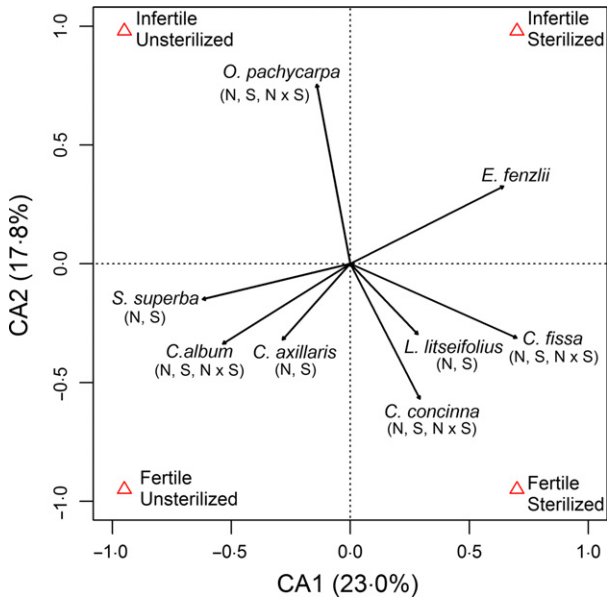

Fig. 3. Multivariate redundancy analysis (RDA) of individual plant species' response to nutrient and soil biota treatments in the eight-species mixtures. The first canonical axis (CA1) significantly separates the species in unsterilized versus those in sterilized soil ($F = 6{\cdot}81$, $P < 0{\cdot}01$), while the second canonical axis (CA2) significantly separates the species in low or high soil fertility ($F = 4{\cdot}82$, $P < 0{\cdot}01$). Letters between brackets denote significant ($P < 0{\cdot}05$) effects of nutrient treatment (N), soil biota treatment (S) and interaction (S × F) on the biomass of the individual species. Species are: *C. album* = *Canarium album*, *C. axillaris* = *Choerospondias axillaris*, *C. concinna* = *Cryptocarya concinna*, *C. fissa* = *Castanopsis fissa*, *E. fenzlii* = *Engelhardtia fenzlii*, *L. litseifolius* = *Lithocarpus litseifolius*, *O. pachycarpa* = *Ormosia pachycarpa*, *S. superba* = *Schima superba*. [Colour figure can be viewed at wileyonlinelibrary.com]

non-sterilized fertilized soil to positive in non-sterilized unfertilized soil. Those changes were not caused by the presence of the nitrogen-fixing species *O. pachycarpa* in the mixed plant communities (as shown in our models), although *O. pachycarpa* promoted plant community biomass, which is not surprising given its nitrogen-fixing properties (Lambers *et al.* 2004; Fargione *et al.* 2007).

The context dependency of plant species richness–community productivity relationships was most likely attributed to fertilization induced shifts in soil microbial community functioning, because accumulating evidence indicates that soil fertility influences plant–microbe interactions. At low soil fertility, plants rely on mycorrhizae for nutrient acquisition (Johnson *et al.* 2008). Moreover, mycorrhizal symbionts can protect plants from pathogenic soil biota (Newsham, Fitter & Watkinson 1995; Borowicz 2001; Bennett, Alers-Garcia & Bever 2006; Morris *et al.* 2007; Sikes, Cottenie & Klironomos 2009; Liang *et al.* 2015). We suspect that under low soil fertility conditions, the counteraction between positive and negative soil biota effects may result in the net neutral to positive soil biota effects in our case. These soil biota effects in non-sterilized unfertilized soil, however, did not alter the positive plant species richness–community biomass relationship, indicating that these net biotic effects were not very specific. Consistently, Cortois *et al.* (2016) found that beneficial soil biota appear to be less species-specific than pathogenic soil biota as both species that accumulate negative or positive soil biota, grew better with soil biota from plant species mixtures. Whereas as nutrient availability increases, pathogen loads of individual plants tend to increase (Solomon, Tan & Oliver 2003; Walters & Bingham 2007; Whitaker, Rúa & Mitchell 2015), favouring pathogens but disfavouring mycorrhizae (Johnson *et al.* 2008). This may result in the negative overall effects of soil biota in non-sterilized fertilized soils.

Under high fertility conditions, negative soil biota effects dominated and suppressed complementarity effects of high-diversity plant communities, whereas complementarity effects were clearly apparent in sterilized soil. This suppression of complementarity effects resulted in a non-significant plant species richness–community biomass relationship in unsterilized and fertilized soil. Our findings are inconsistent with results showing that negative soil biota effects decrease and community productivity increases with increasing plant diversity in grasslands (Maron *et al.* 2011; Schnitzer *et al.* 2011). In previous studies, the decrease in negative soil biota effects in high-diversity plant communities is based on the premise that the effects of soil pathogens are species-specific and density-dependent (Maron *et al.* 2011; Schnitzer *et al.* 2011). Unfortunately, those previous studies, as well as ours, did not directly test for the host specificity of soil biota. However, it is known that pathogenic fungi can be very variable in their host range (Augspurger & Wilkinson 2007) and that many pathogens have a broad host range (Gilbert 2002; Augspurger & Wilkinson 2007; Gilbert *et al.* 2012). In our experiment, live soil inoculum was a mixture of soils collected from beneath eight focal plant species. It is possible that in plant mixtures, the presence of a second host species can increase infection in a focal host species (Bowers & Begon 1991; Begon *et al.* 1992), whereas the second host species may be the most competent reservoir for the pathogen (Ostfeld & Keesing 2000; Schmidt & Ostfeld 2001). Consequently, disease severity could increase with increasing host diversity (Nguyen *et al.* 2016). We found that different plant species had different response to soil biota under high nutrient conditions where some species (e.g. *C. fissa*) even suffered more strongly from negative soil biota effects in eight-species mixtures than that in monocultures (Fig. 3; Table S3). These results suggest that increased plant diversity did not reduce the negative soil biota effects in our case, which is likely to occur when soil pathogens are not strongly host-specific. Instead, increased plant diversity might provide more possible host species for soil pathogens that have a broad host range, increasing the negative effects of soil biota. The negative soil biota effects could also be caused by arbuscular mycorrhizal fungi (AMF), as fertilization tends to increase the parasitic effects of mycorrhizal fungi (Hoeksema *et al.* 2010; Johnson 2010). However, it is less well-known how the parasitic effects of AMF may change with plant diversity.

We acknowledged that our study had some limitations. First, all replicates of the highest plant richness treatment had the same community composition. This may limit our abilities to infer how soil biota mediate the plant diversity–community productivity relationship in communities assembled by different sets of plant species. Second, our experiment has a

relatively short duration (i.e. 16 months). The complementarity among plant species is likely to increase over time (Cardinale *et al.* 2007; Fargione *et al.* 2007; Reich *et al.* 2012) and the effects of soil biota on plants may have a time-lag (Eisenhauer, Reich & Scheu 2012). Our study may thus have underestimated the impacts of plant diversity and soil biota on productivity. Third, though nutrient levels in our treatments were expected to be in the range of the nutrient availability in natural environments from which we collected soil samples for soil inoculums, soil biota from different sites may prefer different nutrient conditions. Therefore, we could not fully exclude the possibility that soil biota may be 'mismatched' to the environment in our experiment, which may affect the effectiveness of soil biota and its influence on the plant diversity–community productivity relationship. Also note that the difference between fertility treatments was much smaller than the natural range of nutrient availability, our study thus represents a conservative estimate of how soil nutrients influence the effects of soil biota on plant diversity–productivity relationships.

Conclusions

Our study shows that soil biota and soil fertility are key interacting factors in determining the complementarity effects in plant mixtures and the plant species richness–community biomass relationship. Under high soil fertility conditions, the expected positive relationship between plant species richness and community productivity was only found when soil biota were not present: soil biota negated the positive complementarity effects in high richness plant communities. Under low fertility conditions, soil biota did not alter the positive relationship between plant species richness and community productivity. These findings indicate that environmental context plays an important role in determining how soil biota influence the plant diversity–productivity relationship. Our study is an important first step and may stimulate further researches to better understand the interactive roles of soil biota, soil nutrient availability and plant resource-based processes in determining biodiversity–ecosystem functioning relationships in natural environments.

Authors' contributions

S.L. designed the experimental procedure with advice from S.X.Y., and carried out the experiment with the help of B.J.; S.L. and G.B.D.D. analysed the data; S.L. wrote the first draft of the manuscript, and all authors discussed the results and contributed substantially to revisions.

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Data accessibility

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.p8t61 (Luo *et al.* 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Table S1. Soil nutrient availability at the end of the experiment in the sterilized and unsterilized soil with different nutrient treatments (data are mean values ± SE; $n = 20$).

Table S2. Effects of mixed-effects models for the log-transformed community biomass assessed separately for different environmental conditions.

Table S3. Proportional biomass of individual plant species in response to soil treatment (unsterilized versus sterilized) treatment under (a) fertile and (b) infertile soil conditions in communities with different richness levels (one, two, four and eight species).

Appendix S1. Supporting analyses.