



# Initial community evenness increases the light resource use complementarity and sampling effects on species richness

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## Abstract

Although evenness has been proved to affect the effect of species richness on ecosystem processes, the potentially affected mechanism has still rarely been studied directly. In this study, different species richness levels (1, 2, 4, 8 and 12) were manipulated in low- and high-evenness plots, and light interception efficiency (LIE) of the plots was measured to determine light resource use. The results showed that there was a positive relationship between species richness (SR) and LIE in the high-evenness plots during two years of this experiment. However, the positive relationship disappeared in the low-evenness plots. Only in the high-evenness plots, the values of transgressive overyielding ( $D_{\max}$ ) were positively correlated with the complementarity effect, which increased with SR. Moreover, most of 12-species mixtures had positive  $D_{\max}$  ( $D_{\max} > 0$ ) which further confirmed the complementarity effect on LIE. The presence of *Phytolacca americana* or *Macleaya cordata* significantly increased LIE in the high-evenness plots but did not increase LIE in the low-evenness plots. Moreover, the dominance of superior (*P. americana* or *M. cordata*) was positively correlated with the selection effect. Our results suggest that high initial evenness will increase the complementarity and sampling effects of SR on light interception and may be an important mechanism that can influence the effect of SR on ecosystem processes, such as biomass production.

## Zusammenfassung

Wenn auch gezeigt worden ist, dass die Evenness den Effekt des Artenreichtums auf Ökosystemprozesse beeinflusst, so sind die potentiell betroffenen Mechanismen selten direkt untersucht worden. In dieser Untersuchung richteten wir bei unterschiedlichem Artenreichtum (1, 2, 4, 8 und 12) Beete mit geringer und hoher Evenness ein und maßen die Lichtaufnahmeeffizienz (LIE) der Beete um die Lichtnutzung zu bestimmen. Es gab eine positive Beziehung zwischen Artenreichtum und LIE in den Beeten mit hoher Evenness in diesem zweijährigen Experiment. Indessen verschwand die positive Beziehung auf den Beeten mit geringer Evenness. Nur auf den Beeten mit hoher Evenness war das "transgressive overyielding ( $D_{\max}$ )" positiv mit dem Komplementaritätseffekt korreliert, der mit dem Artenreichtum zunahm. Die meisten der 12-Arten-Mischungen hatten ein positives  $D_{\max}$ , was zusätzlich den Komplementaritätseffekt auf die LIE bestätigt. Die Anwesenheit von *Phytolacca americana* oder *Macleaya cordata* steigerte die LIE signifikant in den Beeten mit hoher Evenness, aber nicht in den Beeten mit geringer Evenness. Die Dominanz überlegener Konkurrenten (*P. americana* oder *M. cordata*) war positiv mit dem Selektionseffekt

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verknüpft. Unsere Ergebnisse legen nahe, dass hohe anfängliche Evenness die Komplementaritäts- und Probenahmeeffekte des Artenreichtums auf die Lichtaufnahme erhöht und ein wichtiger Mechanismus sein könnte, der den Einfluss des Artenreichtums auf Ökosystemprozesse wie die Biomasseproduktion beeinflusst.

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**Keywords:** Species richness; Evenness; Complementarity effect; Sampling effect; Light interception efficiency

## Introduction

Many experiments have shown positive relationships between species richness and ecosystem processes, especially for biomass production (Hooper et al., 2005; Spehn et al., 2005; van Ruijven & Berendse, 2009; Šimová, Li, & Storch, 2013). Two general mechanisms have been suggested to explain the positive relationship: the complementarity effect states that niche differences among species, such as interspecific differences in resource use, should lead to a more efficient acquisition of limiting resources (Loreau, 2000; Loreau & Hector, 2001) and the sampling effect suggests that species richness effects are caused by the increased success of one or a few dominant species with particular traits (Huston, 1997; Tilman, Lehman, & Thompson, 1997). However, some experiments showed that species richness did not always have positive effects on ecosystem processes (Fukima & Morin, 2003; Pfisterer, Joshi, Schmid, & Fisher, 2004). Although evenness may affect the effect of species richness on ecosystem processes (Wilsey & Potvin, 2000; Roscher et al., 2005; Isbell, Losure, Yurkonis, & Wilsey, 2008; Schmitz, Flynn, Mwangi, Schmid, & Scherer-Lorenzen, 2013), the potentially affected mechanism has still rarely been studied directly.

The complementarity effect of species richness is mainly attributed to complementary resource use (Tilman et al., 1997; Hooper, 1998; Dimitrakopoulos & Schmid, 2004; Matthew, Bracken, & Stachowicz, 2006; Schultz, Bouchard, & Frey, 2012). It has been reported that complementary resource use is directly linked to interspecific trait differences that are associated with resource use (Petchey & Gaston, 2002; Petchey & Gaston, 2006). The complementarity among species is only expressed in relation to the touch of interspecific neighbors (Tilman et al., 1997) and complementary species suffer less competition from interspecific neighbors than from conspecific neighbors (Loreau, 1998). Variations in evenness will affect the number of physical contacts between different species, which changes the expression of interspecific interactions (Wilsey & Polley, 2004). This means that variations in evenness will change the complementarity effect on species richness.

The sampling effect has been thought to be an important mechanism which leads to the positive effect of species richness on biomass production (Tilman et al., 1997; Mouquet, Moore, & Loreau, 2002). However, Jiang, Pu, and Nemergut (2008) suggested that the sampling effect is likely to operate only on ecosystem processes, such as biomass production,

where the competitive ability of a species is a good indicator of the magnitude of its functional impact. However, if the initial abundance of a species in a community is low, its high competitive ability will not have a large functional impact (Polley, Wilsey, & Derner, 2002). Accordingly, negative selection effects should be common when superior competitors contribute little to ecosystem processes (Jiang et al., 2008). Consequently, the initial abundance of superior competitors probably positively affects the sampling effect on species richness.

Complementary use of light could be an important mechanism that may improve the positive effects of species richness on plant biomass production (Naeem, Thompson, Lawler, Lawton, & Woodfin, 1994). Moreover, light interception among different species is a good indicator of interspecific interactions and differences in competitive ability among species (Vojtech, Loreau, Yachi, Spehn, & Hector, 2008; Zhang, Chen, & Reich, 2012). To explore the potential mechanism of evenness affecting the effect of species richness on ecosystem processes, we focus on the interactive effects of evenness and species richness on the light interception of communities. The effects of species richness and evenness on the light interception efficiency of communities were measured in a controlled grassland experiment manipulating species richness (1, 2, 4, 8 and 12) and evenness (two levels) in a factorial design. As the light interception proportions of individual species in the mixtures cannot be measured directly, the complementarity and selection effects were indirectly calculated using the biomass data. We tested the following hypotheses: (i) high evenness will promote the complementarity effect on the light interception; and (ii) the initial abundance of superior competitors probably positively affects the sampling effect on the light interception.

## Materials and methods

### Experimental design

An arable field near Taizhou University, Linhai city, Zhejiang Province, China (121°53'26.26"E, 28°09'51.13"N) was ploughed in April 2010. In October 2010, square flower beds were built using bricks. The volume of each flower bed was 1 m<sup>3</sup> (1 m × 1 m × 1 m) and these beds were then used as experimental plots. The experimental plots were separated by 1.0 m walkways. A water-osmosis plastic

membrane was placed at the bottom of the plots and then they were filled with fully mixed mountain yellow soil (organic matter:  $1.44 \pm 0.19 \text{ g kg}^{-1}$ , total P:  $0.13 \pm 0.03 \text{ g kg}^{-1}$ , total N:  $0.62 \pm 0.17 \text{ g kg}^{-1}$ ). During the study period, the experimental field was surrounded by rice fields. The region has a semitropical climate with an annual rainfall of 1800 mm, which occurs mostly during spring and summer. The annual average temperature is  $19.5^\circ\text{C}$ . The photosynthetically active radiation (PAR, 11:00–14:00) ranges from 1300 to  $1800 \mu\text{mol m}^{-2} \text{ s}^{-1}$  at the experimental site.

Two treatments were assigned to each experimental plot. The treatments had five species richness levels (1, 2, 4, 8 and 12) and two evenness levels (high and low). All 16 species in our species pool were planted in monoculture without replication. The species pool contained *Antenoron filiforme* (Thunb.) Rob. et Vaut., *Setaria viridis* (Linn.) Beauv., *Plantago asiatica* Linn., *Lysimachia fortunei* Maxim., *Inula japonica* Thunb., *Pterocypselia formosana* (Maxim.) Shih., *Achyranthes bidentata* Blume., *Phytolacca americana* Linn., *Digitaria sanguinalis* (Linn.) Scop., *Macleaya cordata* (Willd.) R. Br., *Polygonum perfoliatum* Linn., *Acalypha australis* Linn., *Talinum paniculatum* (Jacq.) Gaertn., *Reynoutria japonica* Houtt., *Mirabilis jalapa* Linn. and *Tubocapsicum anomalum* (Franch. et Sav.) Makino. Except of *S. viridis* and *D. sanguinalis*, all other species are biennial or perennial, and all 16 species are common native species in the mountain area around Linhai city. The reason for selecting many biennial or perennial species was that the relative abundance of the species could be manipulated more accurately during the study period. Twenty mixtures, containing different plant compositions, were established at four levels of species richness. The species assigned to each mixture were chosen by a separate random draw of the appropriate number of species from the species pool. For each random draw, we assigned equal relative abundance among species to create high evenness treatment. As the grassland communities in the mountain area around Linhai city are usually dominated by a single species, and the dominance (calculated using the number of plants) ranged from 47.2% to 78.4%, we mainly manipulated the dominance (3:1 in 2-species, 8:2:1:1 in 4-species, 12:2:2:2:2:2:1:1 in 8-species and 12:2:1:1:1:1:1:1:1:1:1 in 12-species mixtures) to create low-evenness treatment. The corresponding evenness values (calculated as  $E_{1/D}$ ; Smith & Wilson, 1996) are 0.80, 0.51, 0.43 and 0.30 for the 2-species, 4-species, 8-species and 12-species mixtures, respectively.

Seeds of the 16 species were collected from the plants growing on the mountain area around Linhai city. The seeds were sown in plastic containers (64 cm  $\times$  42 cm  $\times$  27 cm) in November 2010. In May 2011, the young seedlings were transplanted into the plots about one month after germination. Each plot consisted of 48 seedlings. The plant density was similar to natural densities (40–60 plants  $\text{m}^{-2}$ ) of plant communities in the mountain area around Linhai city. In each plot, the number of seedlings transplanted for each species followed the experimental treatment designs. Seedlings of the same species were not transplanted adjacently and the

48 seedlings were evenly distributed in each plot. Ten days after transplantation, the dead seedlings were removed and replaced with new seedlings of the same species in order to maintain the original species abundance distribution.

## Data collection

The photosynthetically active radiation was measured using a PAR ceptometer (GLZ-C, Zhejiang Top Instrument Co., Ltd, China). In order to avoid edge effects, three points were randomly selected in the central area (0.5 m  $\times$  0.5 m) of each plot and the electronic fisheye sensor was covered with black cloth. The top 1 cm was left uncovered. We took measurements between 11:00 and 14:00 when the sun almost vertically irradiated the plot. On cloud free days (October 1–4, 2012 and October 7–10, 2013), the PAR above the community canopy and the PAR at ground level were measured at each of the three points. The light interception efficiency (LIE) of the plot was estimated as follows:

$$\text{LIE} = \frac{(\text{PAR}_{\text{above}} - \text{PAR}_{\text{ground}})}{\text{PAR}_{\text{ground}}}$$

The average LIE of the three points was used as the LIE for each plot.

In October 2013, the biomass was harvested. Instead of estimating belowground biomass by sampling soil cores in many prior studies (Bessler et al., 2009), we separated the roots from the soil and washed, care taken to recover as many of the fine roots as possible. All the samples were sorted to species level and any dead plant material was removed. The biomass (aboveground and underground biomass) was dried to constant mass at  $80^\circ\text{C}$  for 48 h. As LIE of the plots were positively correlated with the biomass (see Appendix A: Fig. 1), the effect of dominance on LIE was analyzed by using the biomass proportion of each species in the mixtures. If the mixtures had both *P. americana* and *M. cordata*, the dominance was determined as the species with more biomass proportion.

The naturally established seedlings were surveyed every week. Newly established seedlings (including the seedlings of unplanted species and reestablished seedlings of planted species) were removed so that they did not influence the original transplanted seedlings. The species richness treatment was successful as indicated by a positive correlation between planted species richness and observed species richness of 2013 ( $r=0.921$ ,  $n=176$ ,  $P<0.001$ ). Based on the biomass data of 2013, evenness was calculated using the index  $E_{1/D}$  (Smith & Wilson, 1996), and it was found that the high-evenness plots ( $0.529 \pm 0.022$ ) still had a higher evenness level ( $t=2.758$ ,  $n=158$ ,  $P=0.006$ ) than the low-evenness plots ( $0.437 \pm 0.023$ ). We acknowledge that the degree of evenness and species composition will probably change during the course of the experiment. However, this study aimed to test the effect of the initial community evenness on the

richness effects, regardless of any further shifts in community structure.

## Data analysis

$D_{\max}$  assesses the degree to which transgressive overyielding occurs:

$$D_{\max} = \frac{O_T - \max(M_i)}{\max(M_i)}$$

where  $O_T$  is the observed LIE of a given mixture and  $\max(M_i)$  is the maximum monoculture LIE of the species found in that mixture.  $D_{\max} > 0$  indicates the transgressive overyielding (Loreau, 1998).  $D_{\max}$  is an appropriate measure if one is interested in whether complementarity is occurring because the sampling effect alone cannot give a significantly positive  $D_{\max}$  (Huston et al., 2000; Tilman et al., 2001).

We used the biomass data and the additive partitioning method (Loreau & Hector, 2001) to quantify the selection and complementarity effects. The complementarity effect for a specific number of species  $N$  is  $N\Delta\overline{RYM}$ , where  $\Delta\overline{RY}$  is the average change in relative yield for all species in the mixture and  $\overline{M}$  is the average monoculture yield. The selection effect  $N_{\text{cov}}(\Delta\overline{RY}, M)$  was calculated as the covariance between the monoculture yield of species  $M$  and their change in relative yield in the mixture  $\Delta\overline{RY}$  multiplied by  $N$  of the mixture.

The data of biomass were log-transformed and the data of complementarity and selection effects (absolute value) were sqrt-transformed and then the data sign was reinstated (i.e.  $\pm$ ). Data analyses were executed by R 2.12.0 software. The data of LIE was analyzed with general linear models (Schmid et al., 2002). For LIE (see Table 1), we fitted the following terms in sequential order: (1) year, (2) evenness, (3) species richness, (4) species composition (the mixtures with different species composition) within species richness, (5) interactions of the previous terms and (6) the presence of each species within species richness. The dependence of LIE and  $D_{\max}$  on SR, the dependence of  $D_{\max}$  on the complementarity effect and the dependence of the dominance of *P. americana* or *M. cordata* on SR were analyzed using simple regression. The difference of LIE among plots with different species compositions (plots without *P. americana* and *M. cordata*, with the presence of *P. americana*, with the presence of *M. cordata* and with the presence of *P. americana* and *M. cordata*) were analyzed using the general linear model (ANOVA). The dominance difference between the high- and low- evenness mixtures was analyzed using the paired-sample  $T$  test.

## Results

The difference in species composition among plots explains the most variance of light interception efficiency (LIE, Table 1). Species richness and evenness

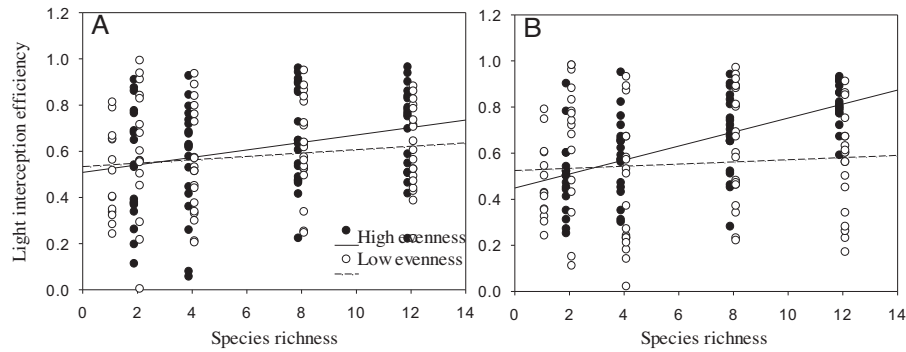
**Table 1.** Analyses of variance for light interception efficiency per plot. Each line represents a term fitted by the multiple regression, allowing mixing of multilevel factors and continuous variables in sequence.

Line	Source of variation	df	Light interception efficiency (%SS)
1	Year	1	0.01
2	Evenness	1	1.09*
3	Richness (SR)	1	4.12***
4	Species composition within SR	52	23.94***
5	Year $\times$ evenness	1	0.35
6	Year $\times$ SR	1	0.18
7	Year $\times$ composition	52	16.15***
8	Evenness $\times$ SR	1	2.67**
9	Evenness $\times$ species composition within SR	51	13.29***
10	<i>M. cordata</i> presence within SR	1	1.72*
11	<i>P. americana</i> presence within SR	1	3.42***
12	Residuals	136	25.86

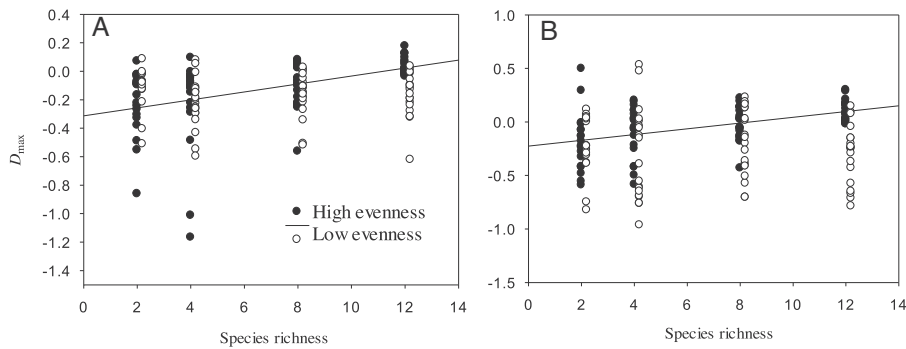
Listed are numbers (line) and names (source of variation) of terms, degrees of freedom (d.f.), and % sum of squares (% SS) indicating increases in multiple  $R^2$  (explained variance) due to the addition of this term to the model. Significant terms are indicated by asterisks (\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ). All other species were not significant, explaining 7.15% of the total variance, and were not included in the table. Note that the full model explains more than 74% of the total variance (% SS residual <26).

had a significant interactive effect on LIE (see evenness  $\times$  s.r. interaction in Table 1): species richness had a significantly positive effect in the high-evenness plots (Fig. 1; 2012:  $\text{LIE} = 0.325\text{SR} + 0.494$ ,  $F = 8.766$ ,  $P = 0.004$ ; 2013:  $\text{LIE} = 0.613\text{SR} + 0.446$ ,  $F = 44.484$ ,  $P < 0.001$ ) but had no significant effect in the low-evenness plots (2012:  $\text{LIE} = 0.139\text{SR} + 0.533$ ,  $F = 1.685$ ,  $P = 0.198$ ; 2013:  $\text{LIE} = 0.075\text{SR} + 0.524$ ,  $F = 0.492$ ,  $P = 0.485$ ). Moreover, LIE of high-evenness plots was higher than that of low-evenness plots (Table 1;  $t = 2.178$ ,  $df = 318$ ,  $P = 0.030$ ). The effect of evenness or SR on LIE did not significantly change over the years (nonsignificant interaction between  $E$  and year, and between SR and year in Table 1).

$D_{\max}$  of the high-evenness plots significantly increased as SR rose and was greater than zero in most of the 12-species mixtures (Fig. 2; 2012:  $D_{\max} = 0.445\text{SR} - 0.313$ ,  $F = 18.306$ ,  $P < 0.001$ ; 2013:  $D_{\max} = 0.239\text{SR} - 0.184$ ,  $F = 4.498$ ,  $P = 0.037$ ). However, in the low-evenness plots,  $D_{\max}$  had no significant relationship with SR. In the high-evenness plots,  $D_{\max}$  had a positive relationship with the complementarity effect (Fig. 3; 2012:  $r = 0.325$ ,  $n = 78$ ,  $P = 0.004$ ; 2013:  $r = 0.318$ ,  $n = 78$ ,  $P = 0.005$ ), which also increased with SR (Complementarity effect =  $0.374\text{SR} - 6.028$ ,  $F = 12.014$ ,  $P = 0.001$ ). However, the complementarity effect had



**Fig. 1.** The dependence of light interception efficiency on species richness in the high- and low-evenness plots from 2012 (A) to 2013 (B). Lines represent regression slopes from the statistical model.



**Fig. 2.** The dependence of  $D_{\max}$  on species richness in the high- and low-evenness plots from 2012 (A) to 2013 (B). Lines represent regression slopes from the statistical model.

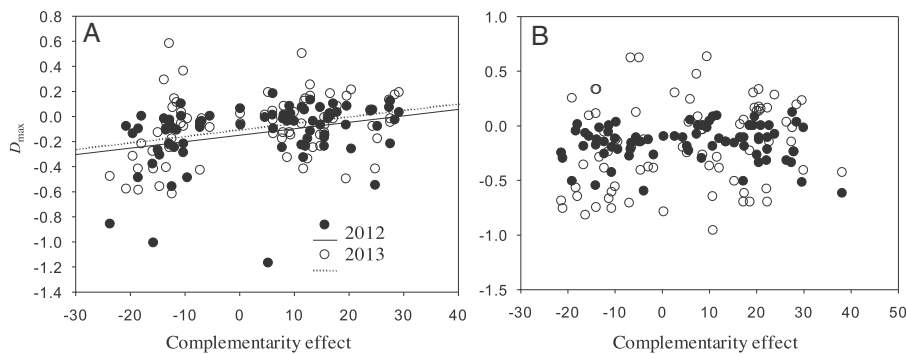
no significant relationship with SR (Complementarity effect =  $0.196SR - 1.738$ ,  $F = 3.014$ ,  $P = 0.071$ ) in the low-evenness plots.

In the high-evenness plots, the presence of *P. americana* or *M. cordata* significantly increased LIE (Table 1, Fig. 4), while it did not increase LIE in the low-evenness plots. The dominance of *P. americana* or *M. cordata* in the high-evenness plots in which any one of them occurred positively correlated with SR (Fig. 5; Dominance =  $0.379SR + 0.412$ ,  $F = 6.703$ ,  $P = 0.013$ ), and also positively correlated with the selection effect (Dominance =  $0.464$  selection effect +  $0.536$ ,

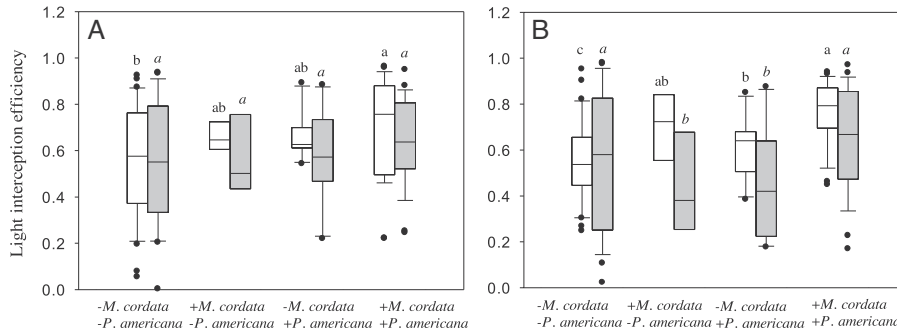
$F = 10.955$ ,  $P < 0.001$ ). However, these positive relationships disappeared in the low-evenness plots. Moreover, the dominance of *P. americana* or *M. cordata* in the high-evenness plots was higher than that in the low-evenness plots ( $t = 6.243$ ,  $df = 80$ ,  $P < 0.001$ ).

## Discussion

In this study, the effects of species richness (SR), evenness and the presence of superior on light interception efficiency



**Fig. 3.** The relationships between  $D_{\max}$  and the complementary effect in the high- (A) and low- (B) evenness plots from 2012 to 2013. Lines represent regression slopes from the statistical model.



**Fig. 4.** The light interception efficiency of plots with different species composition in high- (open rectangles) and low- (solid rectangles) evenness plots for 2012 (A) and 2013 (B).—indicates absence from the plot, +indicates presence in the plot. Bars with different letters indicate significant differences (LSD test,  $P < 0.05$ ; test results are for comparisons within evenness treatments).

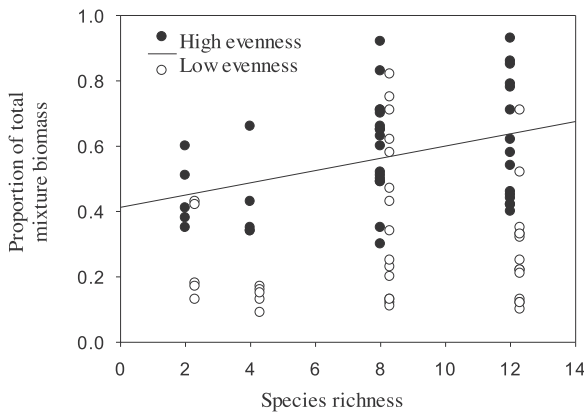
(LIE) were explored. In the high-evenness plots, SR had a positive effect on LIE, which should be related to the increasing complementarity effect with SR. However, this positive effect disappeared in the low-evenness plots. *P. americana* and *M. cordata* had high light interception efficiency in the monocultures (see Appendix A: Fig. 2) and their presence significantly increased LIE of the high-evenness mixtures but did not increase LIE in the low-evenness mixtures. Moreover, the dominance of *P. americana* and *M. cordata* in the high-evenness plots in which any one of them occurred was positively correlated with the selection effect, which also increased with SR (data not shown). Consequently, in the high-evenness plots, the positive effect of SR on LIE should be ascribed to the complementarity and sampling effects.

The overyielding of LIE increased with the complementarity effect in the high-evenness plots. Moreover,  $D_{max}$  values for most of the 12-species plots were greater than zero, which further confirmed the increasing complementarity effect of SR on light interception (Huston et al., 2000; Tilman et al., 2001). Wilsey and Potvin (2000) found that resource partitioning among species (variance in plant heights) increased light interception and that this was promoted by an increase in evenness. Although plant height was not directly measured in mixtures, the increasing complementarity effect with SR

may also indirectly confirm the complementary use of light by the species. However, the increasing complementarity effect with SR disappeared in the low-evenness plots. We speculate that low evenness most likely decreases the touching opportunities for interspecific plants, which restrains the functional complementarity for light interception (Tilman et al., 1997; Loreau, 1998).

Although the complementarity effect of SR was present only in the high-evenness plots, LIEs of most of the mixtures were lower than the monocultures of the best-performing component species ( $D_{max} < 0$ ). This indicates that the sampling effect should be the dominant mechanism, which leads to the positive relationship between SR and LIE (Tilman et al., 1997; Mouquet et al., 2002). *P. americana* and *M. cordata* had high LIEs in the monocultures and their presence was a good indicator of high LIEs in the high-evenness mixtures. Jiang et al. (2008) postulated that in communities where the competitive ability of a species is a good indicator of the functional impact of ecosystem processes are likely to be communities where the positive effect of species richness may be the dominant sampling effect. Moreover, we did find the dominance of *P. americana* or *M. cordata* was positively correlated with the selection effect in the high-evenness plots. However, in the low-evenness plots, the sampling effect did not operate. Here, the dominance of *P. americana* and *M. cordata* was lower than in the high-evenness plots. In the low-evenness mixtures with low initial abundance of *P. americana* or *M. cordata*, they were generally not the dominants in the end, which may indicate that species with high competitive abilities do not have a large functional impact when they had a low initial abundance. Consequently, we suggest that the hypothesis of Jiang et al. (2008) should be modified, in that the positive effect of SR should depend not only on the ecosystem processes, but also on the initial abundance of the superior competitors.

Although evenness had a positive effect on LIE, the positive effect of evenness is not obvious in the 2-species and 4-species mixtures, which may be related to the contribution of *A. filiforme* to light interception. *A. filiforme* also had high light interception efficiency in the monocultures (see Appendix A: Fig. 2) but contributed little to light interception



**Fig. 5.** The dependence of dominance of *P. americana* and *M. cordata* on species richness in the high- and low-evenness plots that included *P. americana* or *M. cordata*.

in the high-evenness plots. However, in some of 2-species and 4-species low-evenness mixtures, high initial abundance of *A. filiforme* increased light interception. In 8-species and 12-species low-evenness mixtures, *A. filiforme* still contributed little to light interception for the competition of *P. americana* or *M. cordata* which present in most of these mixtures.

LIE positively determined biomass in both the high- and low-evenness plots (see Appendix A: Fig. 1). Consequently, the effect of SR on biomass production should mainly depend on the effects of SR on LIE, which is consistent with the results of Naeem et al. (1994). Controlled experiments usually attempt to create communities in which the initial abundances of all the component species are similar (Tilman, 1996; Loreau & Hector, 2001; Hector et al., 1999; Mulder, Uliassi, & Doak, 2001). Consequently, high evenness most likely lead to a positive relationship between SR and LIE, which lead to the positive relationship between SR and biomass being usually found in the controlled experiments. However, in natural communities, the initial abundance of the communities is almost never evenly distributed between species (Ugland & Gray, 1982; Wilson et al., 1996; Weiher & Keddy, 1999). The SR effect on LIE depends on the initial abundance of the superior. This means that different relationships between SR and biomass (positive, negative, hump-shaped, U-shaped and no relationship) are more likely found in natural communities (Schläpfer & Schmid, 1999; Mittelbach et al., 2001; Smith & Knapp, 2003; Balvanera et al., 2006; Zuo et al., 2012). Consequently, the interactive effects of evenness and species richness on light interception in this study may be important mechanisms that could help to reconcile the seemingly mixed results from previous studies.

## Authors' contributions

J.W. designed the experiment. J.W., C.B.Z. and W.L.L. performed the experiments. J.W. and X.Y.W. analyzed the data. J.W. wrote the original manuscript. X.Y.W. provided editorial advice.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2015.03.002>.

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