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

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Abstract

Alth ugh evenness has been r ved t affect the effect f s ecies richness n ec system r cesses, the tentially affected mechanism has still rarely been studied directly. In this study, different s ecies richness levels (1, 2, 4, 8 and 12) were mani ulated in l w- and high-evenness l ts, and light interce ti n efficiency (LIE) f the l ts was measured t determine light res urce use. The results sh wed that there was a sitive relati nshi between s ecies richness (SR) and LIE in the high-evenness l ts during tw years f this ex eriment. H wever, the sitive relati nshi disa eared in the l w-evenness l ts. Only in the high-evenness l ts, the values f transgressive veryielding (D_{max}) were sitively c rrelated with the c m lementarity effect, which increased with SR. M re ver, m st f 12-s ecies mixtures had sitive D_{max} ($D_{max} > 0$) which further c nfirmed the c m lementarity effect n LIE. The resence f *Phytolacca americana* r *Macleaya cordata* significantly increased LIE in the high-evenness l ts but did n t increase LIE in the l w-evenness l ts. M re ver, the d minance f su eri r (*P. americana* r *M. cordata*) was sitively c rrelated with the selecti n effect. Our results suggest that high initial evenness will increase the c m lementarity and sam ling effects f SR n light interce ti n and may be an im rtant mechanism that can influence the effect f SR n ec system r cesses, such as bi mass r ducti n.

Zusammenfassung

Wenn auch gezeigt w rden ist, dass die Evenness den Effekt des Artenreichtums auf Ök system r zesse beeinflusst, s sind die tentiell betr ffenen Mechanismen selten direkt untersucht w rden. In dieser Untersuchung richteten wir bei unterschiedlichem Artenreichtum (1, 2, 4, 8 und 12) Beete mit geringer und h her Evenness ein und ma en die Lichtaufnahmeeffizienz (LIE) der Beete um die Lichtnutzung zu bestimmen. Es gab eine sitive Beziehung zwischen Artenreichtum und LIE in den Beeten mit h her Evenness in diesem zweijährigen Ex eriment. Indessen verschwand die sitive Beziehung auf den Beeten mit geringer Evenness. Nur auf den Beeten mit h her Evenness war das "transgressive veryielding (D_{max})" sitiv mit dem K m lementaritätseffekt k rreliert, der mit dem Artenreichtum zunahm. Die meisten der 12-Arten-Mischungen hatten ein sitives D_{max}, was zusätzlich den K m lementaritätseffekt auf die LIE bestätigt. Die Anwesenheit v n *Phytolacca americana* der *Macleaya cordata* steigerte die LIE signifikant in den Beeten mit h her Evenness, aber nicht in den Beeten mit geringer Evenness. Die D minanz überlegener K nkurrenten (*P. americana* der *M. cordata*) war sitiv mit dem Selekti nseffekt

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membrane was laced at the b tt m f the l ts and then they were filled with fully mixed m untain yell w s il (rganic matter: $1.44 \pm 0.19\,\mathrm{g\,kg^{-1}}$, t tal P: $0.13 \pm 0.03\,\mathrm{g\,kg^{-1}}$, t tal N: $0.62 \pm 0.17\,\mathrm{g\,kg^{-1}}$). During the study eri d, the ex erimental field was surr unded by rice fields. The regi n has a semitr ical climate with an annual rainfall f 1800 mm, which ccurs m stly during s ring and summer. The annual average tem erature is 19.5 °C. The h t synthetically active radiati n (PAR, 11:00–14:00) ranges fr m 1300 t 1800 μm l $\mathrm{m^{-2}\,s^{-1}}$ at the ex erimental site.

Tw treatments were assigned t each ex erimental l t. The treatments had five s ecies richness levels (1, 2, 4, 8 and 12) and tw evenness levels (high and l w). All 16 s ecies in ur s ecies l were lanted in m n culture with ut re licati n. The s ecies l c ntained *Antenoron filiforme* (Thunb.) R b. et Vaut., *Setaria viridis* (Linn.) Beauv., *Plantago asiatica* Linn., *Lysimachia fortunei* Maxim., *Inula japonica* Thunb., *Pterocypsela formosana* (Maxim.) Shih., *Achyranthes bidentata* Blume., *Phytolacca americana* Linn., *Digitaria sanguinalis* (Linn.) Sc ., *Macleaya cordata* (Willd.) R. Br., *Polygonum perfoliatum* Linn., *Acalypha australis* Linn., *Talinum paniculatum* (Jacq.) Gaertn., *Reynoutria japonica* H utt., *Mirabilis jalapa* Linn. and *Tubocapsicum anomalum* (Franch. et Sav.) Makin . Exce t f *S. viridis and D. sanguinalis*, all ther s ecies are biennial r erennial, and all 16 s ecies are c mm n native s ecies in the m untain area ar und Linhai city. The reas n f r selecting many biennial r erennial s ecies was that the relative abundance f the s ecies c uld be mani ulated m re accurately during the study eri d. Twenty mixtures, c ntaining different lant c m siti ns, were established at f ur levels f s ecies richness. The s ecies assigned t each mixture were ch sen by a se arate rand m draw f the a r riate number f s ecies fr m the s ecies l. F r each rand m draw, we assigned equal relative abundance am ng s ecies t create high evenness treatment. As the grassland c mmunities in the m untain area ar und Linhai city are usually d minated by a single s ecies, and the d minance (calculated using the number f lants) ranged fr m 47.2% t 78.4%, we mainly mani ulated the d minance (3:1 in 2-s ecies, 8:2:1:1 in 4-s ecies, 12:2:2:2:2:2:1:1 in 8-s ecies and 12:2:1:1:1:1:1:1:1:1:1:1 in 12-s ecies mixtures) t create l w-evenness treatment. The c rres nding evenness values (calculated as E1/D; Smith & Wils n, 1996) are 0.80, 0.51, 0.43 and 0.30 f r the 2-s ecies, 4-s ecies, 8-s ecies and 12-s ecies mixtures, res ectively.

Seeds f the 16 s ecies were c llected fr m the lants gr wing n the m untain area ar und Linhai city. The seeds were s wn in lastic c ntainers (64 cm × 42 cm × 27 cm) in N vember 2010. In May 2011, the y ung seedlings were trans lanted int the l ts ab ut ne m nth after germinati n. Each l t c nsisted f 48 seedlings. The lant density was similar t natural densities (40–60 lants $\mathrm{m^{-2}}$) f lant c mmunities in the m untain area ar und Linhai city. In each l t, the number f seedlings trans lanted f r each s ecies f ll wed the ex erimental treatment designs. Seedlings f the same s ecies were n t trans lanted adjacently and the 48 seedlings were evenly distributed in each l t. Ten days after trans lantati n, the dead seedlings were rem ved and re laced with new seedlings f the same s ecies in rder t maintain the riginal s ecies abundance distributi n.

Data collection

The h t synthetically active radiati n was measured using a PAR ce t meter (GLZ-C, Zhejiang T Instrument C ., Ltd, China).

richness effects, regardless f any further shifts in c mmunity structure.

Data analysis

D_{max} assesses the degree t which transgressive veryielding ccurs:

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

where OT is the bserved LIE f a given mixture and $\max(M_i)$ is the maximum m n culture LIE f the s ecies f und in that mixture. $D_{max} > 0$ indicates the transgressive veryielding (L reau, 1998). D_{max} is an a r riate measure if ne is interested in whether c m lementarity is ccurring because the sam ling effect al ne cann t give a significantly sitive D_{max} (Hust n et al., 2000; Tilman et al., 2001).

We used the bi mass data and the additive artiti ning meth d (L reau & Hect r, 2001) t quantify the selecti n and c m lementarity effects. The c m lementarity effect f r a s ecific number f s ecies N is $N\overline{\Delta \text{RY}}\overline{M}$, where $\overline{\Delta \text{RY}}$ is the average change in relative yield f r all s ecies the mixture and $\overline{M}$ is the average m n culture yield. The selecti n effect Nc v $(\Delta\text{RY}, M)$ was calculated as the c variance between m n culture yield f s ecies M and their change in relative yield in the mixture ΔRY multi lied by N f the mixture.

The data f bi mass were l g-transf rmed and the data f c m lementarity and selecti n effects (abs lute value) were sqrt-transf rmed and then the data sign was reinstated (i.e. ±). Data analyses were executed by R 2.12.0 s ftware. The data f LIE was analyzed with general linear m dels (Schmid et al., 2002). F r LIE (see Table 1), we fitted the f ll wing terms in sequential rder: (1) year, (2) evenness, (3) s ecies richness, (4) s ecies c m siti n (the mixtures with different s ecies c m siti n) within s ecies richness, (5) interacti ns the revi us terms and (6) the resence f each s ecies within s ecies richness. The de endence f LIE and D_{max} n SR, the de endence f D_{max} n the c m lementarity effect and the de endence f the d minance f *P. americana* r *M. cordata* n SR were analyzed using sim le regressi n. The difference f LIE am ng l ts with different s ecies c m-siti ns (l ts with ut *P. americana* and *M. cordata*, with the resence f *P. americana*, with the resence f *M. cordata* and with the resence f *P. americana* and *M. cordata*) were analyzed using the general linear m del (ANOVA). The d minance difference between the high- and l w- evenness mixtures was analyzed using the aired-sam le T test.

Results

The difference in s ecies c m siti n am ng l ts ex lains the m st variance f light interce ti n efficiency (LIE, Table 1). S ecies richness and evenness

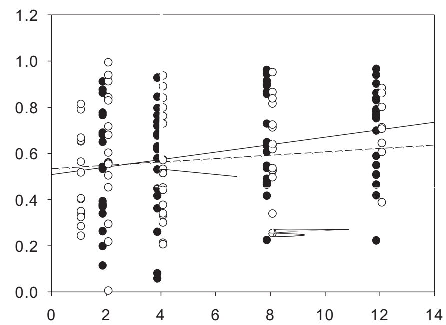
Table 1. Analyses f variance f r light interce ti n efficiency er l t. Each line re resents a term fitted by the multi le regressi n, all wing mixing f multilevel fact rs and c ntinu us variables in sequence.

Line	S urce f variati n	*df*	Light interce ti n efficiency (%SS)
1	Year	1	0.01
2	Evenness	1	1.09*
3	Richness (SR)	1	4.12***
4	S ecies c m siti n within SR	52	23.94***
5	Year × evenness	1	0.35
6	Year × SR	1	0.18
7	Year × c m siti n	52	16.15***
8	Evenness × SR	1	2.67**
9	Evenness × s ecies c m siti n within SR	51	13.29***
10	*M. cordata* resence within SR	1	1.72*
11	*P. americana* resence within SR	1	3.42***
12	Residuals	136	25.86

Listed are numbers (line) and names (s urce f variati n) f terms, degrees f freed m (d.f.), and % sum f squares (% SS) indicating increases in multi le R^2 (ex lained variance) due t the additi n f this term t the m del. Significant terms are indicated by asterisks (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). All ther s ecies were n t significant, ex laining 7.15% f the t tal variance, and were n t included in the table. N te that the full m del ex lains m re than 74% f the t tal variance (% SS residual <26).

had a significant interactive effect n LIE (see evenness × s.r. interacti n in Table 1): s ecies richness had a significantly sitive effect in the high-evenness l ts (Fig. 1; 2012: LIE = 0.325SR + 0.494, $F = 8.766$, $P = 0.004$; 2013: LIE = 0.613SR + 0.446, $F = 44.484$, $P < 0.001$) but had n significant effect in the l w-evenness l ts (2012: LIE = 0.139SR + 0.533, $F = 1.685$, $P = 0.198$; 2013: LIE = 0.075SR + 0.524, $F = 0.492$, $P = 0.485$). M re ver, LIE f high-evenness l ts was higher than that f l w-evenness l ts (Table 1; $t = 2.178$, $df = 318$, $P = 0.030$). The effect f evenness r SR n LIE did n t significantly change ver the years (n nsignificant interacti n between E and year, and between SR and year in Table 1).

D_{max} f the high-evenness l ts significantly increased as SR r se and was greater than zer in m st f the 12-s ecies mixtures (Fig. 2; 2012: $D_{max} = 0.445\text{SR} - 0.313$, $F = 18.306$, $P < 0.001$; 2013: $D_{max} = 0.239\text{SR} - 0.184$, $F = 4.498$, $P = 0.037$). H wever, in the l w-evenness l ts, D_{max} had n significant relati nshi with SR. In the high-evenness l ts, D_{max} had a sitive relati nshi with the c m lementarity effect (Fig. 3; 2012: $r = 0.325$, $n = 78$, $P = 0.004$; 2013: $r = 0.318$, $n = 78$, $P = 0.005$), which als increased with SR (C m lementarity effect = 0.374SR − 6.028, $F = 12.014$, $P = 0.001$). H wever, the c m lementarity effect had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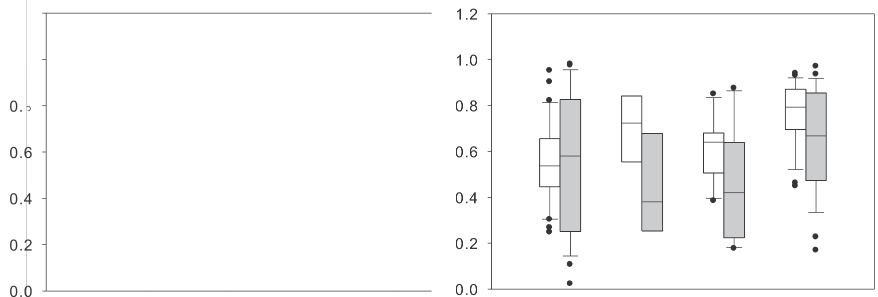
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in the high-evenness plots. However, in some of 2-species and 4-species low-evenness mixtures, high initial abundance of *A. filiforme* increased light interception. In 8-species and 12-species low-evenness mixtures, *A. filiforme* still contributed 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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