COMMUNITY ECOLOGY - ORIGINAL RESEARCH

From selection to complementarity: the shift along the abiotic stress gradient in a controlled biodiversity experiment

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Abstract The effects of principal mechanisms (selection and complementarity) of biodiversity on ecosystem functionality have been well studied. However, it remains unknown how environmental conditions affect the relative strength of these two mechanisms. To answer this question, a controlled pot experiment was conducted in which species diversity was manipulated in low (natural soil) and high stress (mine tailing) plots, respectively. Our results demonstrate that the principal mechanism underlying the increasing biomass shifts from the selection to complementarity with increasing abiotic stress. The shift occurs because species interactions varied with increasing abiotic stress. Competition prevails in low stress plots, while facilitation dominates in high stress plots. In low stress plots, the monoculture biomass of a specific species is a good indicator of the competitive ability of that species in the mixture, and the dominant species significantly affects the plot biomass. In high stress plots, the tolerance indexes of all individual species increase with the manipulated species richness, providing clear evidence for the increasing role of facilitation.

Introduction

Laboratory and field experiments have shown that plant diversity positively affects productivity (Wardle 1999; Schwartz et al. 2000; Špaèková and Lepš 2001; Hector 2002; Hector et al. 2002; Pfisterer et al. 2004; Hooper et al. 2005; Spehn et al. 2005; Fargione et al. 2007). This can be explained by two major hypotheses: the selection effect (the greater probability of including a species or combinations of species with the trait of higher than average biomass in a randomly assembled high diversity community) and the complementarity effect (resource partitioning or facilitative interaction) (Huston 1997; Loreau and Hector 2001; Huston and McBride 2002). The selection and complementarity effects are not inherently exclusive, and both effects can operate simultaneously to affect productivity (Špaèková and Lepš 2001). Consequently, which principal mechanism causes the positive effects of biodiversity on productivity has been actively debated (Huston et al. 2000; Kaiser 2000; Naeem 2000; Wardle et al. 2000; Fargione et al. 2007).

The debate highlights the need to separate and quantify the selection and complementarity effects. Loreau (1998) showed that over-yielding (i.e. higher productivity of a mixture when compared with the monoculture productivity of the most productive species) cannot be accounted for by the selection effect. Hence, over-yielding can be considered as evidence of additional mechanisms beyond the

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selection effect. Loreau and Hector (2001) devised a statistical method to differentiate the selection and complementarity effects through comparing the mixture yield with the expected yield based on monocultures of component species. This statistical technique and the comparison of species performances of mixtures with monocultures have become important tools in assessing the effects of biodiversity change (Hector et al. 2002). However, previous results indicated that the relationship between species production in monocultures and that in the mixtures was more complex (Hooper and Vitousek 1998; Dukes 2001; Engelhardt and Ritchie 2001; Hector et al. 2002). The complex relationships may be attributed to the change in species interactions as a result of a trade-off between resource allocation to growth and to competition, a result of different competitive abilities to different resources of a specific species, or the consequence of the variation in a given environment in which resources are being competed for (Tilman 1988). To explain the change in selection and complementarity effects, a mechanistic understanding of species interactions is needed.

The stress gradient hypothesis predicts that the relative importance of facilitation and competition varies inversely across the abiotic stress gradient, with the facilitation being the dominant species interaction under high stress conditions (Bertness and Callaway 1994). However, a critical reappraisal of the hypothesis is needed because some experimental studies refuted its predictions (Liancourt et al. 2005; Maestre et al. 2005). These contradictory results may be related to the tolerance levels of species to certain abiotic stress. If stress-tolerant species are the experimental targets, the abiotic stress will not be particularly harsh for these species. As a result, competition may be expected. Consequently, species' interactions may vary from competition to facilitation as a function of the tolerance of a species to particular abiotic conditions (Bertness et al. 1992; Hacker and Bertness 1999). Although the selection and complementarity effects are potentially relevant, they have different implications and are applied to different environmental conditions (Loreau 2000; Loreau and Hector 2001). The selection effect may be particularly important in environments where inter-specific competition is promoted, and hence one or a few species have strong individual control over productivity (Fridley 2001). The complementarity effect will be dominant in environments where the facilitation is the dominant interaction (Chu et al. 2008). However, relatively few studies have empirically examined how these interactions affect the functioning of whole ecosystems (Mulder et al. 2001; Kikvidze et al. 2005). Therefore, the importance of facilitation and competition for maintaining ecosystem functioning is largely unknown (Callaway 2007).

Mine tailings are mechanically, physically, chemically and biologically deficient for plant species (Vega et al. 2006; Wang et al. 2011), and are characterized by instability and limited cohesion, a low content of nutrients and organic matter, and high levels of heavy metals (He et al. 2005; Wang et al. 2011). To assess the relative importance of selection and complementarity effects across gradients of abiotic stress, we performed a controlled pot experiment in which species diversity was manipulated in low (natural soil) and high (mine tailing) stress environments, respectively. Specifically, we aimed to determine: (1) whether the relative importance of selection and complementarity effects varied with increasing abiotic stress; (2) whether the shift in the strength of both the selection and complementarity effects was due to the change in species interaction.

Materials and methods

A plant species survey was conducted at Huangyan Pb/Zn mine tailing (28°34′23″N, 120°53′44″E) on 14 April 2008 (Online Resource 1). Eight species (*Bidens pilosa* Linn., *Phytolacca americana* Linn., *Commelina communis* Linn., *Mirabilis jalapa* Linn., *Chenopodium ambrosioides* Linn., *Solanum nigrum* Linn., *Brassica campestris* Linn. and *Xanthium sibiricum* Patrin ex Widder) were randomly selected for this experiment. *P. americana* is a perennial grass, and the other seven species are annual grasses. Seeds of the eight grass species were collected from the plants growing on the mine tailings or the surrounding area. The seeds of these species were sown in trays on 5–7 April 2009, and seedlings were transplanted 2 months after germination. Tailing soils was randomly collected from the bare mine tailings and then all the tailing soils were fully mixed (tailing properties: organic matter 330 ± 71.2 mg kg^{-1}, total P 50.3 ± 10.6 mg kg^{-1}, total N 120.7 ± 41.4 mg kg^{-1}, Cu 31.29 ± 3.81 mg kg^{-1}, Cd 8.92 ± 2.32 mg kg^{-1}, Pb 924.57 ± 61.23 mg kg^{-1}, Zn $1,312.45 \pm 52.44$ mg kg^{-1}). Natural soils was randomly collected from the Beigu Mountain in Linhai, Zhejiang, China and then all the natural soils were fully mixed (soil properties: organic matter $1,642.8 \pm 171.9$ mg kg^{-1}, total P 123.6 ± 21.7 mg kg^{-1}, total N 734.3 ± 162.8 mg kg^{-1}). Another plant species survey was conducted at the Beigu, Yunfeng and Baiyunshan mountains on 28 October 2011. The eight species used in this study also occur in these mountain areas.

Seedlings of the eight species were transplanted into plastic containers (plots) placed outdoors ($80 \times 80 \times 60$ cm^3) on 2–4 June 2009. Thirty-two plant seedlings were transplanted into each plot. We constructed 23 different communities to create four species richness levels (Table 1): eight monocultures, five mixtures of two species, five mixtures of four species and one mixture of eight

Table 1 The species combinations used at four different diversity levels

BP *Bidens pilosa* Linn., PA *Phytolacca americana* Linn., CC *Commelina communis* Linn., MJ *Mirabilis jalapa* Linn., CA *Chenopodium ambrosioides* Linn., SN *Solanum nigrum* Linn., BC *Brassica campestris* Linn., XS *Xanthium sibiricum* Patrin ex Widder

Diversity level			
1	2	4	8
BP	BP + XS	BP + CC + CA + SN	BP + PA + CC + MJ + CA + SN + BC + XS
PA	PA + MJ	PA + MJ + CA + BC	
CC	CC + CA	XS + PA + SN + MJ	
MJ	BP + PA	PA + BP + CC + BC	
CA	SN + BC	BP + CC + MJ + CA	
SN			
BC			
XS			

species with five replicates. The species in the mixtures were planted at equal densities. Plots filled with natural soil were considered as the low stress treatment, and plots filled with tailing soil were considered as the high stress treatment. The alternative technique of a random selection of species from a total pool was not used because, with a limited series of communities, equal representation of the species at each species richness level was not guaranteed. Instead, combinations were chosen to guarantee every species could be selected at least once at each of four diversity levels. Plots were weeded weekly. In addition to natural rainfall, water was added by artificially spraying during dry periods.

Plots were harvested about 12 months after the plot construction on 10 May 2010. All the aboveground and belowground biomass (living plants) were sorted to species, dried and weighed separately. In each plot, the species with the greatest biomass was identified as the dominant species of the plot.

Before the biomass harvesting, a water treatment experiment was conducted. The water content of each plot was determined 5 days after it received the same amount of water through artificial spraying (no water was added during the final 5 days before harvesting). Five soil cores to a depth of 0–20 cm were randomly collected in each plot. Five replicated samples from each plot were combined into one sample. Water content of the soil was calculated by comparing the weight of undried and dried soil [(weight of undried soil − weight of dried soil)/weight of dried soil]. Part of each sample was air-dried at room temperature, and then was homogenized and sieved (<2 mm) to remove plant root and small stones to determine total N. Briefly, 1.0 g of K_2SO_4 catalyst mixture and 5 ml of concentrated H_2SO_4 were added to 0.5 g of air-dried ground tailings in 10-ml digestion tubes. After heating, followed by the addition of 20 ml of distilled water and filtration, the contents of the tubes were transferred to 50-ml volumetric flasks. Total N in the filtrates was determined using the Berthelot reaction method (Page et al. 1982).

The tolerance responses to stress of selected species were assessed by comparing the species biomass in low stress plots to that in high stress plots, as described previously by Suding et al. (2003). The biomass ratio was expressed as tolerance index (TI):

$$TI = \frac{\text{Average biomass of species in certain diversity treatment of high stress plots}}{\text{Average biomass of species in the same diversity treatment of low stress plots}}$$

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

The deviation (D) of the biomass of a species in a mixture from the biomass could be expected based on its monoculture biomass (Špačková and Lepš 2001).

$$D_{\text{mixture−monoculture}} = \frac{O_i − E_i}{E_i}$$

where O_i is the observed biomass of species i in the mixture and E_i is the expected biomass, i.e. simply the monoculture biomass multiplied by the initial proportion of the species in the mixture. If $D_{\text{mixture-monoculture}} > 0$, the species expressed a better performance than the expected yield; if $D_{\text{mixture-monoculture}} < 0$, the species expressed a worse performance than the expected yield.

For each plot mixture, we calculated the over-yielding index (OI) as follows (Hector et al. 2002):

$$OI = Y/\mathrm{MAX}(M_i)$$

where Y was the biomass of a mixture; M_i was the biomass of ith species grown in the monoculture; OI was the ratio of the biomass of a mixture to the biomass of the most productive species in the mixture. For statistical analyses, log(OI) was used: if the biomass of each mixture reached the biomass of its most productive species in the monoculture, then the expectation of Log(OI) was zero.

ANOVA was used to test the effects of species richness and the identity of dominant species in mixtures in a sequential fitting order based on general linear model approaches through SPSS software (based on type I sum of squares; SPSS 11.5; SPSS, Chicago, Ill.). In the present study, simple regression analysis was used to examine the dependence of biomass on the selection or the complementarity effect, and also to examine the dependence of the OI and the TI on species richness.

Results

We explored the dependence of plot biomass on the selection and complementarity effects in low and high stress plots by using linear regression analysis (Fig. 1). The reverse biomass–complementarity effect relationships occur between low and high stress plots. The biomass negatively correlates with the complementarity effect in low stress plots but has a positive correlation in high stress plots. In contrast, the biomass positively correlates with the selection effect in low stress plots but negatively correlates in high stress plots. The results indicate that the main mechanism affecting biomass production shifts from the selection to the complementarity effect in response to increasing environmental stress.

Whether dominant species or species richness determine the plot biomass was also explored. In low stress plots, the biomass of mixtures are affected by the identity of dominant species (Table 2; $P < 0.01$) and positively correlate with the monoculture biomass of dominant species ($r = 0.919$, $P < 0.0001$, $n = 15$). However, species richness does not affect the biomass of mixtures ($P = 0.069$). In high stress plots, the biomass of mixtures positively correlates with species richness ($r = 0.909$, $P < 0.0001$, $n = 15$) but has no relationship with dominant species ($P = 0.082$). These results indicate that the main factor affecting the biomass of mixtures shifts from dominant species to species richness in response to increasing environmental stress. Moreover, both the selection and complementarity effects are significantly affected by the
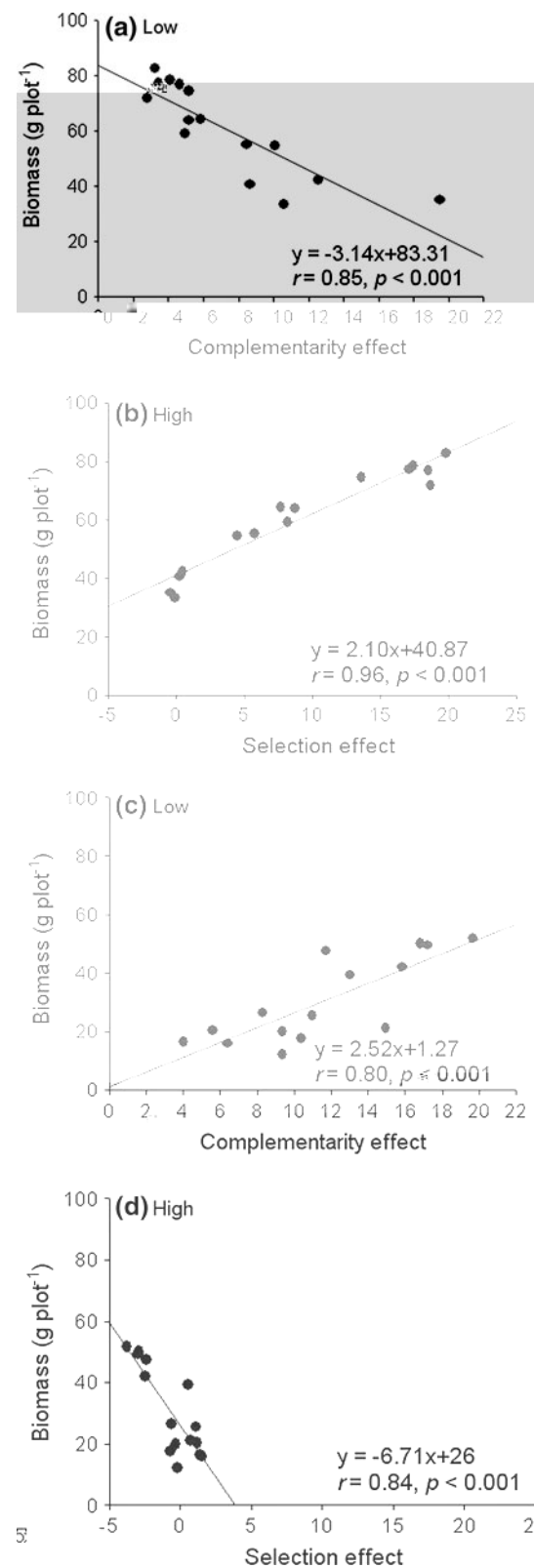

Fig. 1 Relationship between biomass and complementarity or selection effect in **a**, **c** low and **b**, **d** high stress plots. Results for linear regression ($n = 15$) are shown

Table 2 Results of ANOVA for diversity effects on plot biomass, selection effect and complementarity effect in low and high stress plots based on type I sum of squares: *arrows* indicate significant increase (↗) or decrease (↘) of the particular parameter with increased species richness or the monoculture biomass of dominant species

Source of variation	df	Plot biomass		Selection effect		Complementarity effect	
		F	P	F	P	F	P
Low stress plots							
Richness	2	5.622	0.069	4.945	0.184	4.276	0.165
Dominant species	4	34.971	**<0.01**↗	41.461	**<0.01**↗	70.097	**<0.01**↘
Richness × dominant species	4	0.656	0.653	0.686	0.638	3.627	0.120
High stress plots							
Richness	2	1,689.556	**<0.05**↗	61.795	**<0.05**↘	60.109	**<0.05**↗
Dominant species	6	86.291	0.082	1.428	0.565	1.693	0.529
Richness × dominant species	5	25.602	0.149	0.750	0.700	1.036	0.629

Significant *P*-values (*P* < 0.05) in *bold*

identity of dominant species in low stress plots ($P < 0.01$), while they are significantly affected by species richness in high stress plots ($P < 0.05$).

The covariance between the monoculture biomass of species and their relative yields in the mixtures exhibit different relationships between low and high stress plots (Fig. 2). In low stress plots, the biomass proportions of species in the mixtures and their monoculture biomass have a positive relationship. Moreover, the selection effect positively correlates with the monoculture biomass of dominant species (Table 2; $r = 0.928$, $P < 0.0001$, $n = 15$). However, in high stress plots, the monoculture biomass of species is not a good indicator of competitive ability in the mixtures. The species with a low or intermediate monoculture biomass frequently have high proportions in the mixtures, and the selection effect and the monoculture biomass of dominant species have no significant correlations (Table 2; Fig. 2).

The change in species interaction was also examined by the deviation between the observed and expected biomass ($D_{\text{mixture-monoculture}}$) in this study. In low stress plots, the dominant species show a competitive advantage ($D_{\text{mixture-monoculture}} > 0$) but most of the non-dominant species show a competitive disadvantage ($D_{\text{mixture-monoculture}} < 0$) (Fig. 3). This proves that a dominant competitive interaction exists in low stress plots. However, in high stress plots, both the dominant species and most of non-dominant species have better performances than expected ($D_{\text{mixture-monoculture}} > 0$). Most of mixtures have more biomass than the monoculture biomass of the most productive species in the mixtures (Fig. 4; Log(OI) > 0). Moreover, Log(OI) positively correlate with species richness ($r = 0.830$, $P < 0.0001$, $n = 15$). Only positive interaction (facilitation) can explain mixture plots having more biomass than the monoculture biomass of the most productive species in the mixtures.
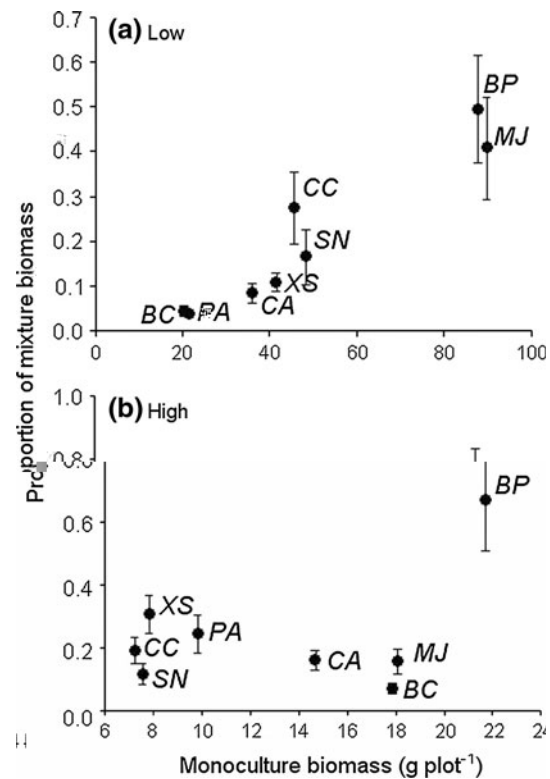

Fig. 2 Biomass proportions of species in mixtures as a function of monoculture biomass; values are mean ± SE ($n = 10$ for *PA* and *BP*; $n = 9$ for *MJ*, *CA* and *SN*; $n = 8$ for *CC* and *BC*; $n = 7$ for *XS*) in **a** low and **b** high stress treatments. Abbreviations for species names are listed in Table 1

The facilitation can be crucial in high stress environments by improving environmental conditions. In high stress plots, the nitrogen and water retention capability of mine tailings increase with species richness, as total N and water content positively correlate with species richness (Table 3; total N, $r = 0.847$, $P < 0.0001$, $n = 15$; water
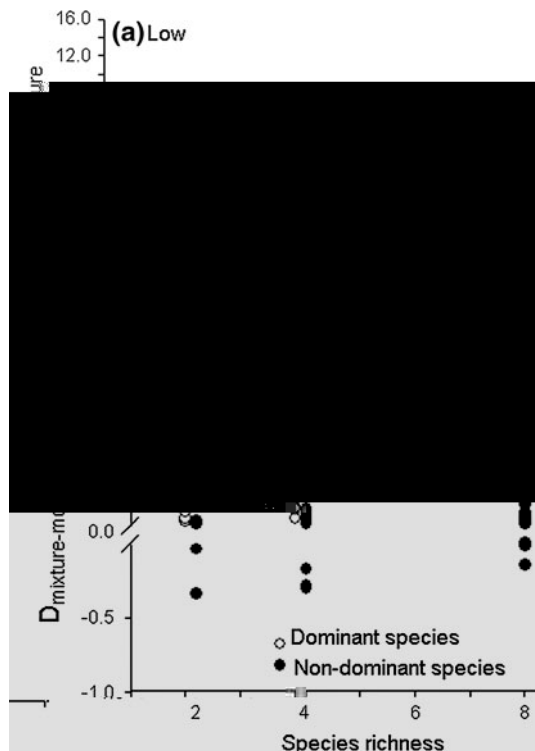
Fig. 3 Deviation ($D_{mixture-monoculture}$) of observed biomass of dominant or non-dominant species from their expected biomass in **a** low and **b** high stress mixture plots. Expected biomass was monoculture biomass multiplied by the initial proportion of the species in the mixture
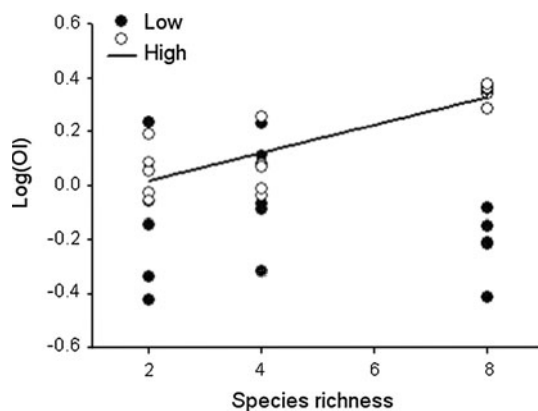

Fig. 4 Dependence of log[over-yielding index(OI)] on the number of species in low and high stress mixture plots. Only the regression for high stress plots is significant ($r = 0.83$, $n = 15$, $P < 0.0001$)

content, $r = 0.862$, $P < 0.0001$, $n = 15$). The facilitations between species may mitigate the impact of environmental stress as TI values of all eight species increase with species richness (Fig. 5).

Discussion

In our controlled pot experiment, we find a positive dependence of biomass on the selection effect in low stress plots, while, in high stress plots, the biomass positively depends on the complementarity effect. The relationship between the monoculture biomass of species and their relative yields in the mixtures exhibits different patterns. In low stress plots, there is a positive covariance between them. For example, the most productive species in monocultures also dominated in mixtures. Conversely, in high stress plots, most of the unproductive species in monocultures perform better than expected in mixtures ($D_{mixture-monoculture} > 0$), and most of the mixtures have more biomass than the monocultures of their most productive species [log(OI) > 0]. However, these better performances are not found in low stress plots. These differences occur because species interactions varied with abiotic stress: the competition prevails in low stress plots, while the facilitation dominates in high stress plots.

The relationship between the mixture and monoculture yield has become a critical issue in interpreting biodiversity experiments (Špaèková and Lepš 2001; Hector et al. 2002). In our study, the relationship between the mixture and monoculture yield shifts with species interactions that varied with abiotic stress. In low stress plots, the competition is the principal species interaction and the dominant species determines plot biomass. A positive selection effect occurred as species had a positive covariance between the relative yield and the monoculture yield (Fargione et al. 2007). Furthermore, the monoculture biomass of species is a good indicator of competitive dominance in the mixtures. When the species that are abundant in monoculture dominate the mixtures, strong dominance leads to a high selection effect and plot biomass; when the species that are not abundant in monoculture dominate the mixtures, weak dominance leads to a low selection effect and plot biomass. Therefore, the plot biomass has a positive dependence on the selection effect. In high stress plots, the principal species interaction shifts to facilitation. Both dominant species and non-dominant species perform better than their expected performances ($D_{mixture-monoculture} > 0$). A positive complementarity effect occurs as species, on average, have higher relative yield than the expected value (Fargione et al. 2007). The increase in the TI and the OI indicate that the function of facilitation is strengthened with the increase of plot species richness. The higher the species richness, the more positive the deviations of the average relative yield from the expected value and the greater the plot biomass. Consequently, the plot biomass positively links with the complementarity effect. Based on our results, we suggest that the positive covariance between the relative yields of species in the mixtures and their monoculture

Table 3 Results of ANOVA for diversity effects on total N and water content in low and high stress plots based on type I sum of squares: *arrows* indicate significant increase (:) of the particular parameter with increased species richness or the monoculture biomass of dominant species

Source of variation	df	Total N		Water content	
		F	P	F	P
Low stress plots					
Richness	2	1.367	0.353	2.644	0.185
Dominant species	4	2.880	0.172	3.966	0.103
Richness × dominant species	4	1.448	0.364	1.114	0.459
High stress plots					
Richness	2	93.771	**<0.05**:	152.496	**<0.05**:
Dominant species	6	6.944	0.283	8.912	0.251
Richness × dominant species	5	12.739	0.209	11.071	0.224

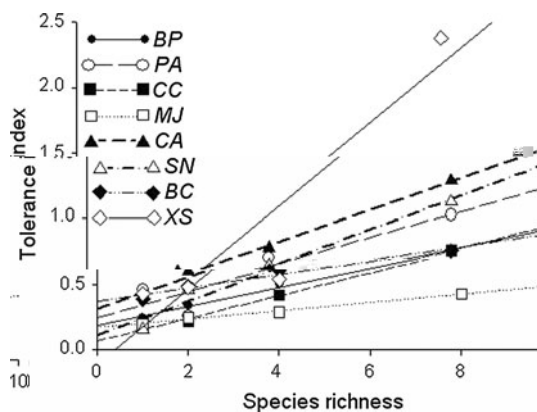Significant *P* values ($P < 0.05$) in *bold*

Fig. 5 Dependence of the tolerance index on the number of species in a monoculture or mixture for eight species plots used in experiments. *Regression lines* are shown for all the eight species, although not all are significant (see text for details). Species abbreviations are listed in Table 1

yields should disappear when species interactions shift from competition to facilitation.

Our results are consistent with the stress gradient hypothesis, i.e. that competition and facilitation vary inversely across gradients of abiotic stress. Facilitation is the dominant interaction under highly stressful conditions (Bertness and Callaway 1994), while competition dominates in low stress environments (Bertness and Callaway 1994; Brooker and Callaghan 1998; Callaway et al. 2002; Chu et al. 2008). However, species interactions may vary from competition to facilitation as a function of the tolerance of a species to particular abiotic conditions (Bertness et al. 1992; Hacker and Bertness 1999; Corcket et al. 2003; Lortie et al. 2004). In this study, the monoculture biomasses of eight species were greatly restrained and decreased greatly (the range of the decrease ratios of eight species is 54.2–83.8 %) in high stress plots, which indicate that the abiotic stress of mine tailings was close to their maximum. At the Huangyan Pb/Zn mine tailings site, bare

mine tailings soils have more heavy metals and less nutrients than those soils that have been phytoremediated for many years (Wang et al. 2011). The eight species used in this study have grown on phytoremediated and surrounding areas for many years. The environment of bare mine tailing soil should be very harsh for these species that have adapted to the soils of phytoremediated and surrounding areas. Consequently, facilitation is the main species interaction in high stress plots. However, we speculate that if highly stress-tolerant species are experimental targets where bare mine tailing soil is not very harsh for them, then competition may be expected in high stress plots (Liancourt et al. 2005). Pennings et al. (2003) found that competition remains the main interaction of salt-tolerant species under the great stress of soil salinity. Therefore, the two cases observed in this study may be the end points of a continuum from "optimum environment" to "extreme environment" for the eight plant species. Consequently, the shift between the selection and complementarity effects depends on experimental abiotic stress relative to the optimum conditions of the target species.

In our study, the diversity–biomass relationships exhibit different patterns between low and high stress plots. In low stress plots, the selection effect results in no significant relationship between the plot biomass and species richness. The plot biomass positively correlates with the selection effect. As a result, the plot biomass is determined by the characteristic of the dominant species and has no close link with species richness. For example, some species that are abundant in monocultures dominate some of the low diversity plots, which leads to low diversity plots with a high selection effect and high biomass, while other species that are not abundant in monocultures dominate some of the high diversity plots, which leads to high diversity plots with a low selection effect and low biomass.

In contrast, in high stress plots, the plot biomass and species richness have a significantly positive relationship.

The complementarity effect is the main mechanism which leads to a positive relationship between the plot biomass and species richness. Higher diversity plots have more facilitation that leads to a high complementarity effect and high plot biomass. Consequently, a positive relationship occurs in high stress plots. The facilitation may have been driven by the water retention of the plant communities, as we found that soil moisture increases with species richness. Moreover, the nutrient pool is significantly improved with the increase of species richness. The improvement may be the result of exudates released by the roots and microbial metabolites (Marschner and Romheld 1983; Leyval and Berthelin 1993), as the underground biomass of plots increases with species richness (data not shown). Many previous biodiversity experiments in natural environments did exhibit different diversity–biomass relationships (Loreau and Hector 2001; Fridley 2002; van Ruijven and Berendse 2003; Hooper and Dukes 2004; Spehn et al. 2005), while simple positive relationships generally occurred in harsh environments (Mulder et al. 2001; Callaway et al. 2002; Wang et al. 2011). Based on these biodiversity experiments and the results from this study, we speculate that the complex diversity–biomass relationships should shift to simple positive relationships when the principal mechanism shifts from the selection effect to the complementarity effect.

There are two important points to note from our results. First, we report results based on a 1-year experiment. But both the selection and complementarity effects are likely to change over time. In a 10-year biodiversity experiment, Fargione et al. (2007) found that the selection effect decreased and the complementarity effect increased over time. Second, the pot experiment limits environmental fluctuations and spatial heterogeneity, which are important for resource partitioning between species under natural conditions (Špaèková and Lepš 2001). As a result, niche differentiation, an important component of the complementarity effect, may be restrained in our pot experiment.

In conclusion, our study finds a shift in the mechanism of the biodiversity effect on productivity along an abiotic stress gradient. The shift occurs because species interaction varied with the magnitudes of abiotic stress. Competition prevails in low stress plots, which leads to the selection effect positively determining the plot biomass. Facilitation becomes the principal species interaction in high stress plots, and the biomass of plots positively depends on the complementarity effect. Although the pot experiment has its limitation for resource partitioning, it indicates that the shift in species interactions caused by the change in abiotic stress will determine the principal mechanism of the bio-diversity effect.

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