RESEARCH ARTICLE

Effects of functional diversity and functional dominance on complementary light use depend on evenness

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Abstract

Questions: Does functional diversity play a more important role than species richness in complementary resource use? Is the effect of functional diversity on complementarity greater when species evenness is higher? Does functional dominance play an important role in resource use when species evenness is low?

Location: An arable field in Linhai City, Zhejiang Province, China.

Methods: We assembled experimental plant communities with different species richness (one, two, four, eight and 12 species) and evenness (low and high). In each community, we quantified light interception efficiency (*LIE*) and light complementarity index (*LC*) to reflect light use. We measured four functional traits related to light capture to quantify functional diversity and functional dominance. We then tested effects of observed species richness, functional diversity and functional dominance on *LIE*, *LC* and above-ground biomass in the low and high evenness communities.

Results: Functional diversity was positively related to *LIE*, *LC* and above-ground biomass in the high evenness communities, but not in the low evenness communities. In contrast, functional dominance was positively related to *LIE* and negatively related to *LC* in the low evenness communities, but not in the high evenness communities. Moreover, functional dominance had a larger promotion to above-ground biomass in the low evenness communities. Observed species richness and evenness had a significant interactive effect on *LIE* and *LC*. *LIE* of a species mixture of the low evenness communities was positively correlated with *LIE* of the monoculture consisting of the species with the highest initial abundance in the species mixture, while *LC* of a species mixture of the low evenness communities was negatively correlated with it.

Conclusions: Functional diversity and functional dominance play a crucial role in light complementary use of plant communities, and their effects on light complementarity are mediated by species evenness. Thus, interactions of functional traits and evenness may greatly affect ecosystem functioning.

KEYWORDS
above-ground biomass, community-weighted mean, experimental communities, functional diversity Q index, light complementarity, light interception efficiency

1 | INTRODUCTION

A large number of experimental studies have shown positive relationships between species diversity (especially richness) and ecosystem functioning (Balvanera et al., 2006; Cardinale et al., 2006; Venail et al., 2015; Wang et al., 2011). One of the underlying mechanisms is that complementary resource use among co-existing species potentially allows more diverse communities to exploit resources more thoroughly (Loreau & Hector, 2001; Tilman, Lehman, & Thompson, 1997). However, mixtures do not always outperform monocultures of their component species (Roscher et al., 2011; Trenbath, 1974), and absence of a positive relationship between species richness and ecosystem functioning has also been reported (Balvanera et al., 2006; Smith & Knapp, 2003; Zuo, Knops, & Zhao, 2012). Thus, to better understand the effect of species diversity on ecosystem functioning, we need to explore the mechanistic link between species diversity and resource complementarity.

Functional traits are a key to investigate how species interact and function (Petchey & Gaston, 2002), and complementary resource use should be largely determined by inter-specific trait differences in resource use (Petchey & Gaston, 2002, 2006). Consequently, trait-based functional diversity may be a more meaningful predictor of ecosystem functioning than species richness (McGill, Enquist, Weiher, & Westoby, 2006). In a recent study, Cadotte (2017) found that increasing functional diversity increased the complementarity effect of plant communities even after controlling for the effect of species richness, but such a complementarity effect was also largely influenced by a single functional trait. Although several studies have shown that complementary resource use increases with increasing functional diversity (Milcu et al., 2017; Roscher et al., 2012; Wagg et al., 2017), these studies have not disentangled the effects of species richness and functional diversity. Moreover, Grossman, Cavender-Bares, Hobbie, Reich, and Montgomery (2017) found that species richness still played a crucial role in promoting biomass production even after controlling the effect of functional diversity. Consequently, species richness and a single functional trait may intrinsically relate to functional diversity and affect the role of functional diversity.

Complementary resource use mainly results from resource partitioning and niche differentiation among species differing greatly in functional traits (Tilman et al., 2001). However, when species differ substantially in their abundances (i.e. when species evenness is low), ecosystem functioning may be determined mainly by the functional traits of dominant species, but not determined by those of low-abundant species (Garnier et al., 2004; Laughlin, 2011). Consequently, high functional complementarity is likely to be expressed in communities consisting of species with relatively equal abundances (i.e. in communities with high species evenness), but not expressed in communities with low species evenness (Jiang, Wan, & Li, 2009). Moreover, communities with higher species evenness should have a higher ability for complementarity in resource use and should be more productive (Kirwan et al., 2007; Wilsey & Potvin, 2000). So far, however, no study appears to have tested the interactive effect of species evenness and functional diversity on complementary resource use.

Complementarity and selection are two important mechanisms used to explain the role of species diversity in ecosystem functioning (Díaz & Cabido, 2001; Tilman et al., 1997). A variety of functional traits (functional diversity) among species are assumed to mainly reflect the complementarity effect, and the traits of dominant species (functional dominance) are assumed to mainly reflect the selection effect (Mensah, Veldtman, Assogbadjo, Kakaï, & Seifert, 2016). Effects of functional diversity and functional dominance on ecosystem functioning have received increasing attention recently (Baraloto et al., 2012; Clark, Flynn, Butterfield, & Reich, 2012; Ruiz-Jaen & Potvin, 2011; Song, Wang, Li, & Zhou, 2014). Mensah et al. (2016) found that functional diversity and functional dominance were not exclusive and simultaneously affected ecosystem functioning. Moreover, Grime (1998) proposed that functional dominance played a more important role in ecosystem functioning when species differed substantially in their abundances. Yet, it is still not well understood how species evenness affects the relative importance of functional diversity and functional dominance in ecosystem functioning.

In a field experiment, we constructed plant communities with different levels of species richness (one, two, four, eight and 12 species) and evenness (low and high). We measured plant functional traits relevant to light capture to quantify functional diversity (Rao, 1982) and functional dominance (Garnier et al., 2004). Specifically, we tested the hypotheses that (a) functional diversity plays a more important role in complementary resource use than species richness, (b) the effect of functional diversity on complementarity is greater when species evenness is higher, and (c) functional dominance plays an important role in resource use when species evenness is low.

2 | METHODS

2.1 | Study site

An arable field in Linhai City, Zhejiang Province, China (121°53′26.26″E, 28°09′51.13″N) was ploughed in April 2010 and harrowed three times before experimental plots were established in October 2010. Plots (1 m × 1 m × 1 m) were built with bricks. A water-osmosis plastic membrane was placed in the bottom of the plots, and then they were filled with fully mixed, mountain, yellow soil (organic matter: 1.44 ± 0.19 g/kg; total P: 0.13 ± 0.03 g/kg; total N: 0.62 ± 0.17 g/kg). The region has a subtropical climate with an annual rainfall of 1,800 mm, which occurs mostly during spring and summer. The annual mean temperature is 19.5°C. Photosynthetically active radiation (PAR, 11:00–14:00 hr) at the experimental site ranged from 1,300 to 1,800 μmol m^{-2} s^{-1}.

2.2 | Experimental design

Two blocks (30 m × 30 m) were established and separated by 5-m wide walkways (Supporting Information Appendix S1). One block

was used for the control, and the other for the invasion treatment in which the invaders were added after light measurement of this study. Within each block, 176 plots were established and separated by 1-m wide walkways. The experiment had five levels of species richness (one, two, four, eight and 12 species) and two levels of species evenness (low and high). We used a total of 16 common native species, all occurring in the mountains near Linhai City, to construct the experimental communities in the plots (Supporting Information Appendix S2). All species are biennial or perennial except for *Setaria viridis* and *Digitaria sanguinalis*, which are annuals. In each block, each of the 16 species was planted in monoculture in one plot (total 16 plots), and each of 20 mixtures containing different species combinations were established in two plots for each of the other four species richness levels (i.e. two, four, eight and 12 species, total 160 plots). The species assigned to each mixture were chosen by a random draw from the 16 species. For each species mixture in each block, we created a high evenness community (plot) by assigning equal relative abundance to all species, and created a low evenness community by randomly assigned relative abundance levels to component species (3:1 for two-species mixtures, 8:2:1:1 for four-species mixtures, 12:2:2:2:2:2:1:1 for eight-species mixtures, and 12:2:1:1:1:1:1:1:1:1:1:1 for 12-species mixtures). We used such a low evenness level as grassland communities in the mountains around Linhai City are usually dominated by a single species with a relative density of 47.2% to 78.4%. In the low evenness treatments, the corresponding evenness levels (calculated as E_a; Alatalo, 1981) were 0.795, 0.632, 0.589 and 0.478 for the two-, four-, eight- and 12-species mixtures, respectively; in the high evenness treatments, all evenness values were 1.

Seeds of the 16 species were collected in the mountains around Linhai City and sown in plastic containers (64 cm × 42 cm × 27 cm) in November 2010 to over winter. In May 2011, seedlings were transplanted into the plots. Each plot was planted with 48 seedlings, and the density was similar to the natural density (40–60 plants/m^2) of plant communities in the mountains around Linhai City. In each plot, seedlings of the same species were not placed next to each other, and the 48 seedlings were evenly distributed. Ten days after transplantation, we checked the status of each seedling and the dead ones were replaced. The plots were weeded monthly.

2.3 | Measurements and calculations

In October 2012, we measured four species traits relevant to light capture (plant height, area of a single leaf, leaf angle and cover of a single plant). For measurement, we randomly selected 20 plants and 50 leaves from the monoculture of each species. Leaf area was determined using WinFOLIA (Regent, CA) and leaf angle was measured as the angle between the plane of the leaf and the ground surface. Cover of a single plant was measured by laying 100 cell grids (2.5 cm × 2.5 cm cells in a 10 × 10 grid) over each plant and counting the number of grid cells occupied by the plant. All plants of the two

annuals (*S. viridis* and *D. sanguinalis*) died during the experiment so that their traits were not measured.

The PAR was measured using a PAR ceptometer (GLZ-C, Zhejiang Top Instrument, China). Three points were randomly selected in the central 0.5 m × 0.5 m area of each plot. Between 11:00–14:00 hr on cloudless days on 1–4 October 2012, PAR above canopy and at ground level were measured at each of the three points. Light interception efficiency (*LIE*) of a community in a plot was estimated as:

$$LIE = \frac{\text{PAR above community canopy} - \text{PAR at ground level}}{\text{PAR above community canopy}}$$

The mean value of *LIE* at the three points of a community was used as *LIE* of the community. Leaf area index (LAI) of the community was determined using an electronic fisheye sensor (LAI 2000; Li-COR, Lincoln, NB, US).

On 21–24 October 2012, we measured species richness in each mixture (communities with more than one species). Due to competition or stochastic deaths of individual plants, species richness observed ($SR_{observed}$) was different from species richness planted, and the maximum value of $SR_{observed}$ was 11. Evenness observed was estimated using the relative abundance of each species in the plot. The evenness index of Alatalo (1981) was calculated as follows:

$$E_a = \left(\left(\sum_{i=1}^{S} P_i^2\right)^{-1} - 1\right) \Bigg/ \left(\exp\left(-\sum_{i=1}^{S} P_i \ln P_i\right) - 1\right),$$

where P_i is the relative abundance of species i and S is $SR_{observed}$ in the plot.

We calculated the Euclidean distance between species using the data of the four functional traits of the 14 species (all plants of *S. viridis* and *D. sanguinalis* died so that no data were available for these two species; Walker, Kinzig, & Langridge, 1999). As the four traits differed greatly in units and scales (Supporting Information Appendix S1), we used the methods of Heemsbergen et al. (2004) for calculation. We first transformed the data of each of the 14 species into rank values (with the smallest value as 1, the second smallest as 2, the third smallest as 3, …, and the largest as 14) and then calculated the Euclidean distance using the ranks of the four functional traits of the 14 species:

$$d_{ij} = \left[\sum_{k=1}^{K} \left(A_{ki} - A_{kj}\right)^2\right]^{1/2},$$

where d_{ij} is the Euclidean distance between species i and j, A_{ki} and A_{kj} are the rank values of species i and j for trait k, and K is the number of traits measured (here $K = 4$). Based on the Euclidean distance, we calculated the functional diversity Q index (FD_Q; Rao, 1982):

$$FD_Q = \sum_{i-1}^{S-1} \sum_{j=i+1}^{S-1} d_{ij} p_i p_j,$$

where S is $SR_{observed}$ in a community and p_i and p_j are the relative abundance of species i and j in the community, respectively.

The community-weighted mean (CWM) value of a given functional trait was calculated as (Garnier et al., 2004):

$$CWM = \sum_i^s p_i x_i,$$

where p_i is the relative abundance of species i in a community, S is $SR_{observed}$ in the community, and x_i is the trait value for species i. x_i was calculated with the trait value of species i divided by the largest trait value among the 14 species (Supporting Information Appendix S1). The trait value ranges from 0 to 1.

We calculated the light complementarity index (LC) according to Yachi and Loreau (2007):

$$LC = e_{mix} - \left(\frac{1}{S}\right) \sum_{i=1}^s e_i,$$

where e_i is light interception efficiency of monoculture of species i, e_{mix} is light interception efficiency of mixtures, and S is $SR_{observed}$ of the community. e_i and e_{mix} were, respectively, calculated as:

$$e_i = \frac{\Delta E_i}{\Delta E_{i-max}}$$

$$e_{mix} = \frac{\Delta E_{mix}}{\Delta E_{mix-max}},$$

where ΔE is the light actually intercepted in the community and ΔE_{max} is the maximum light interception of the community. ΔE, E_{i-max}, $E_{mix-max}$ and g were calculated as:

$$\Delta E = L_0 - L_G$$

$$\Delta E_{i-max} = L_0 g(q_i, LAI_{mono-i})$$

$$\Delta E_{mix-max} = L_0 g(\bar{q}, LAI_{mix})$$

$$g(q, LAI) = 1 - (1-q)^k + q(1-q)^k (LAI - k),$$

where L_0 is PAR above the community canopy, L_G is PAR at ground level, q_i is the species-specific light interception rate per leaf (q_i is calculated using LIE divided by the total number of leaves of each monoculture of species i), k is the largest integer of LAI, LAI_{mono-i} is leaf area index of species i in the monoculture, LAI_{mix} is leaf area index in the mixture and $\bar{q}$ is the average value of q for all the species in the mixture.

2.4 | Statistical analysis

Three plots in the high evenness treatment and six plots in the low evenness treatment had no living plants. Monocultures were not included in the regression or correlation analyses as their functional diversity indices were undefined, resulting in a final sample size of 157 high evenness plots (communities) and 154 low evenness plots (communities). Above-ground biomass was harvested after 1 year of light measurement. Because invaders were added to the invasion block after the light measurement, the above-ground biomass in the invasion block was not included in data analysis.

The data of *LIE*, *LC* and above-ground biomass were analysed with GLM using R (v 2.12.2; R Foundation for Statistical Computing, Vienna, Austria). CWM of the four functional traits (plant height, area of a single leaf, leaf angle and cover of single plant) were closely positively correlated with each other (Supporting Information Appendix S3). Furthermore, plant height is an important trait relevant to light competition (Cadotte, 2017). Therefore, only CWM of plant height ($CWM_{plant\ height}$) was used. In GLM, we included block, evenness, $SR_{observed}$, FD_Q, $CWM_{plant\ height}$ and their interaction terms (block was not included in the GLM for above-ground biomass). We assessed the significance with log-likelihood ratio tests (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). In these tests, a model with the term of interest was compared to a model without the term of interest, and the calculated log-likelihood ratios were approximate to the distribution of χ^2. The significance of a two-way interaction effect of evenness with one of other terms, for instance, were obtained by comparing the model without the two-way interaction with the model with all two-way interactions but without three-way and four-way interactions. The significance of main effects of evenness, $SR_{observed}$, FD_Q and $CWM_{plant\ height}$ were obtained by comparing the models without each main effect with the model with all four main effects but without interactions. With these analyses, we could explore the effects of $SR_{observed}$, FD_Q and $CWM_{plant\ height}$ on light use and above-ground biomass, and thus test our first hypothesis. We could also explore whether evenness had an interaction effect with FD_Q or $CWM_{plant\ height}$.

Linear regressions were used to explore relationships of *LIE*, *LC* and above-ground biomass with $SR_{observed}$, FD_Q and $CMW_{plant\ height}$ in the high and low evenness communities separately. In these analyses, we could explore how the effects of FD_Q and $CMW_{plant\ height}$ changed with evenness, and thus test our second and third hypotheses. The relationships of CWM of area of a single leaf, leaf angle and cover of a single plant with *LIE* and *LC* in the high and low evenness communities were also explored (Supporting Information Appendices S4 and S5).

Although relative species abundance might have changed due to competition or stochastic deaths during the course of experiment, species with the largest initial abundance in the low evenness communities may still play an important role in ecosystem functioning (Polley, Wilsey, & Derner, 2003). In the low evenness communities, eight species were randomly designated as the species with the largest initial abundances. To test their effects, we used linear regressions to examine relationships of *LIE* and *LC* of the low evenness communities with *LIE* of the monocultures of the species with the largest initial abundances in the low evenness communities. The linear regressions were performed using SPSS 20.0 for Windows (SPSS, Chicago, IL, USA).

3 | RESULTS

Although species number and abundance changed over time, species evenness was still significantly higher in the high than in the low evenness communities at planting ($t = 20.3$, $n = 311$, $p < 0.0001$) and $SR_{observed}$ was highly positively related to species richness at planting ($r = 0.831$, $n = 311$, $p < 0.0001$). FD_Q was positively related

to $SR_{observed}$ in the high evenness communities ($r = 0.210$, $n = 157$, $p < 0.0001$), suggesting that FD_Q and $SR_{observed}$ are not independent from each other in the high evenness communities. However, FD_Q was not positively related to $SR_{observed}$ in the low evenness communities ($r = 0.036$, $n = 154$, $p = 0.681$). $CWM_{plant\ height}$ had no significant relationship with $SR_{observed}$ in the high ($r = 0.105$, $n = 157$, $p = 0.189$) or the low ($r = 0.104$, $n = 154$, $p = 0.233$) evenness communities.

The $SR_{observed}$ did not have any effect on LIE, LC and above-ground biomass (Tables 1 and 2). However, there were significant interactive effects of $SR_{observed}$ and evenness on LIE and LC (Table 1; for LIE, $\chi^2 = 4.591$, $p = 0.032$; for LC, $\chi^2 = 6.934$, $p < 0.001$), and there was a marginally interactive effect of $SR_{observed}$ and evenness on above-ground biomass (Table 2: for above-ground biomass, $\chi^2 = 3.843$, $p = 0.071$). $SR_{observed}$ was positively related to LIE and above-ground biomass (Figures 1a and 3a) in the high evenness communities, but not in the low evenness communities (Figures 1d and 3d).

The FD_Q significantly affected LIE and LC (Table 1). As indicated by a significant interaction between evenness and FD_Q (Table 1: for LIE, $\chi^2 = 14.780$, $p < 0.001$; for LC, $\chi^2 = 10.107$, $p < 0.001$; Table 2: for above-ground biomass, $\chi^2 = 4.260$, $p = 0.028$), the effects of FD_Q on LIE, LC and above-ground biomass depended on evenness of the communities. Consistent with our second hypothesis, FD_Q was positively related to LIE, LC and above-ground biomass (Figures 1b, 2b, and 3b) in the high evenness communities, but not in the low evenness communities (Figures 1e, 2e, and 3e).

The $CWM_{plant\ height}$ significantly affected LIE and above-ground biomass (Tables 1 and 2). As indicated by a significant interaction between evenness and $CWM_{plant\ height}$ (Table 1: for LIE, $\chi^2 = 9.267$, $p < 0.001$; for LC, $\chi^2 = 4.327$, $p = 0.039$; Table 2: for above-ground biomass, $\chi^2 = 4.469$, $p = 0.025$), the effect of $CWM_{plant\ height}$ on LIE, LC and above-ground biomass also depended on evenness of the communities. Consistent

with our third hypothesis, $CWM_{plant\ height}$ was positively correlated with LIE and negatively related to LC in the low evenness communities (Figures 1f and 2f), but not in the high evenness communities (Figures 1c and 2c). Although $CWM_{plant\ height}$ had a positive effect on above-ground biomass in the high evenness communities (Figure 3c), a larger promotion was found in the low evenness communities (Figure 3f).

Moreover, LIE of a mixture of the low evenness communities was positively correlated with LIE of the monoculture consisting of the species with the largest initial abundance in the mixture (Figure 4a), but LC of a mixture was negatively correlated with it (Figure 4b). As plant height of the species with the largest initial abundance was positively correlated with LIE in their monocultures (Supporting Information Appendix S6), the negative effect of $CWM_{plant\ height}$ on LC was likely related to the effect of the species with the highest initial abundance.

4 | DISCUSSION

We manipulated species richness and evenness of experimental plant communities, and quantified functional diversity and functional dominance. We found that functional diversity played an important role in complementary resource use in plant communities with relatively high species evenness, but functional dominance determined resource use in plant communities with low species evenness. Although species richness had little effect on resource use, the interaction of species richness and evenness had a significant effect on resource use.

4.1 | Relative importance of functional diversity and species richness on resource use

Consistent with several biodiversity ecosystem function studies (Chen et al., 2016; Naeem & Wright, 2003), a positive correlation between species richness and functional diversity was also found in this study.

TABLE 1 Results of linear models for the effects species evenness, richness, functional diversity (FD_Q) and functional dominance ($CWM_{plant\ height}$) on light interception efficiency (LIE) and light complementarity index (LC) of the plant communities

Effect	df	LIE χ^2	LIE p	LC χ^2	LC p
Block	1	0.002	0.989	0.008	0.967
Evenness (E)	1	0.206	0.650	0.971	0.324
Species richness (S)	1	0.005	0.946	3.145	0.076
FD_Q (F)	1	4.151	**0.024**	4.263	**0.002**
$CWM_{plant\ height}$ (C)	1	7.357	**0.007**	0.790	0.374
E × S	1	4.591	**0.032**	6.934	**<0.001**
E × F	1	14.780	**<0.001**	10.107	**<0.001**
E × C	1	9.267	**<0.001**	4.327	**0.039**
S × F	1	0.244	0.621	0.014	0.908
S × C	1	1.750	0.186	0.427	0.513
F × C	1	0.536	0.464	0.032	0.858

Bold values indicate having significant effect.

TABLE 2 Results of linear model for the effects species evenness, richness, functional diversity (FD_Q) and functional dominance ($CWM_{plant\ height}$) on above-ground biomass of the plant communities

Effect	df	Aboveground biomass χ^2	Aboveground biomass p
Evenness (E)	1	0.056	0.813
Species richness (S)	1	3.703	0.071
FD_Q (F)	1	0.483	0.487
$CWM_{plant\ height}$ (C)	1	12.883	**<0.001**
E × S	1	3.843	0.071
E × F	1	4.260	**0.028**
E × C	1	4.469	**0.025**
S × F	1	2.079	0.149
S × C	1	0.162	0.687
F × C	1	3.938	0.066

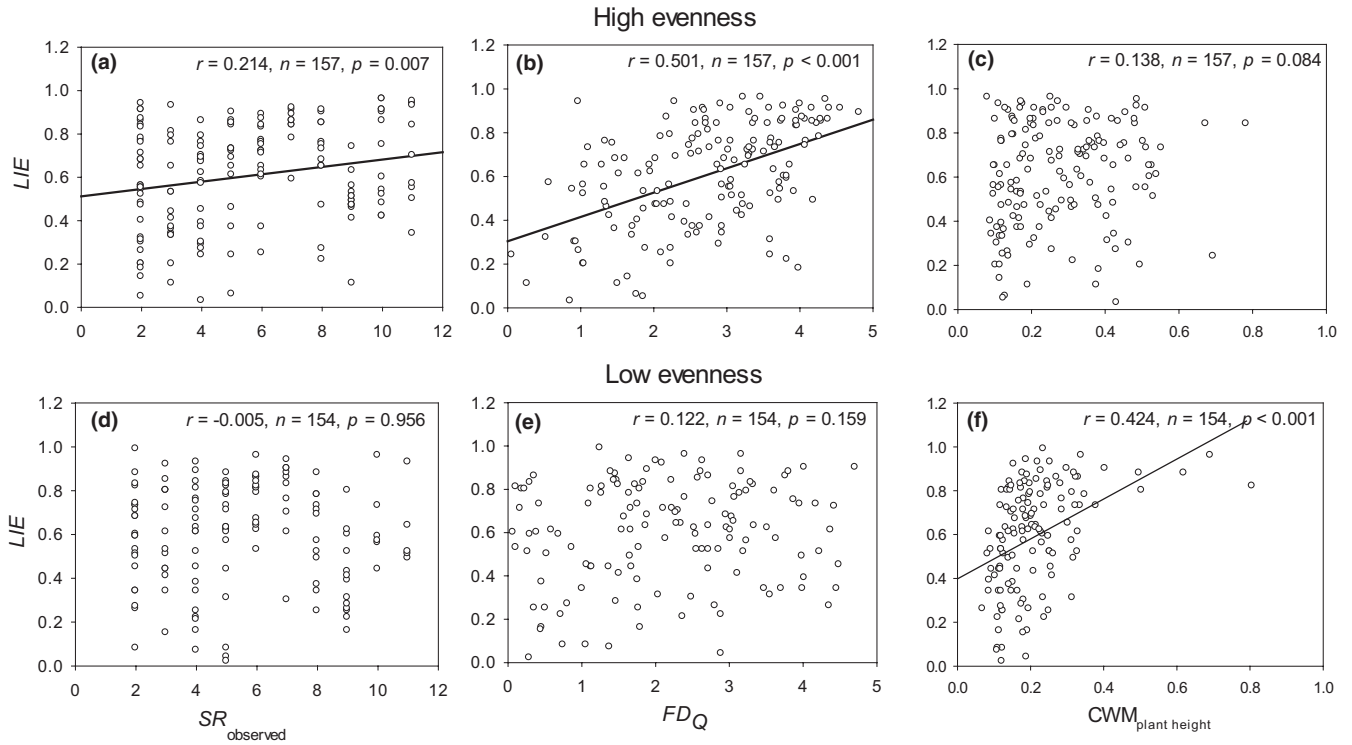Bold values indicate having significant effect.

FIGURE 1 Relationships of light interception efficiency (*LIE*) with (a, d) observed species richness ($SR_{observed}$), (b, e) functional diversity Q index (FD_Q) and (c, f) CWM value of plant height ($CWM_{plant\ height}$) in the high (a–c) and low (d–f) evenness communities
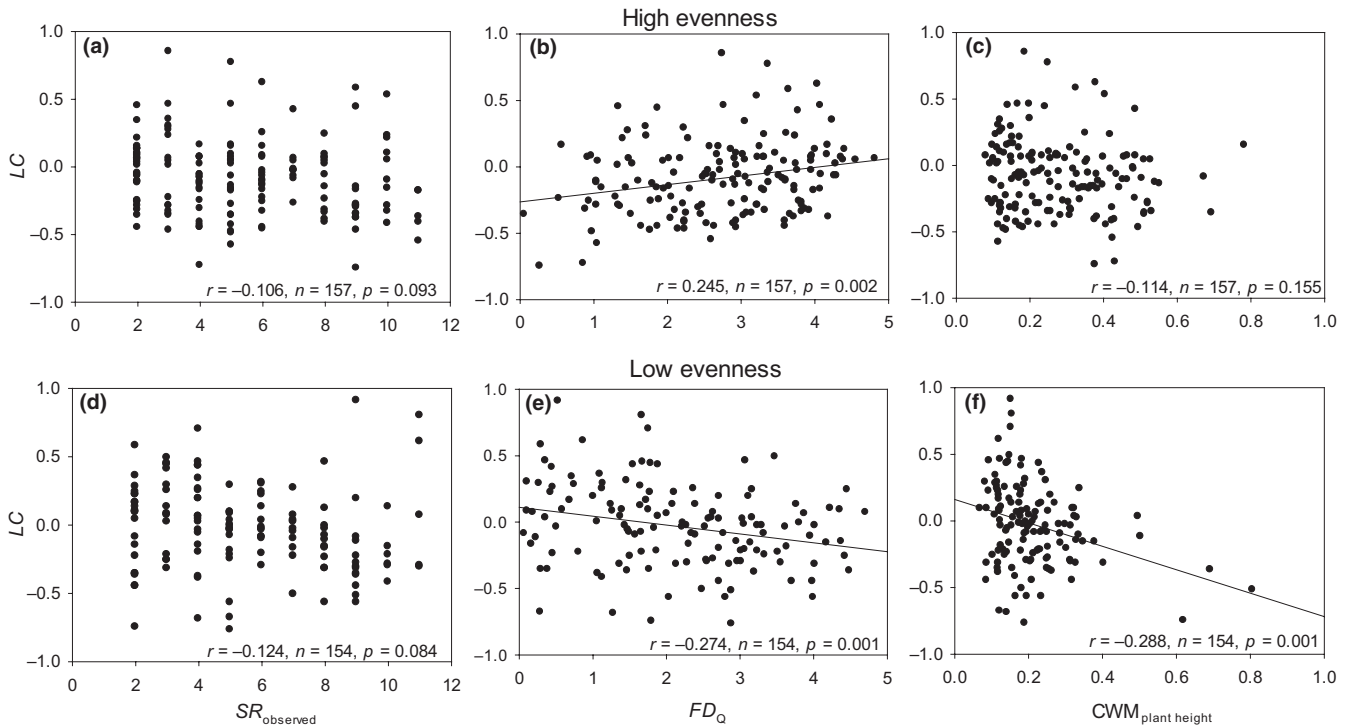

FIGURE 2 Relationships of light complementarity index (*LC*) with (a, d) observed species richness ($SR_{observed}$), (b, e) functional diversity Q index (FD_Q) and (c, f) CWM value of plant height ($CWM_{plant\ height}$) in the (a–c) high and (d–f) low evenness communities

Communities with higher species richness have a higher possibility of having species with some specific trait values, such as *A. bidentata*, *P. americana* and *M. cordata* in our study. Consequently, the trait difference between these species and others will be larger and leads to higher functional diversity. We also found that both species richness and functional diversity promoted light inception efficiency (*LIE*)

in the high evenness communities. However, species richness and functional diversity are confounded in this study and many biodiversity experiments (Flynn, Mirotchnick, Jain, Palmer, & Naeem, 2011). We separate their effects by analysing the effect of one factor at the fixed level of another factor (Supporting Information Appendix S7). Functional diversity still had promoted *LIE* after removing the effect of species richness, while species richness had no significant effect on *LIE* after removing the effect of functional diversity. From the results of this study, we conclude that functional diversity may play a more important role in resource use. However, Grossman et al. (2017) found that species richness rather than functional diversity played a crucial role in promoting biomass production. In this study, species richness and evenness had a significant interactive effect on *LIE*. Moreover, the promotion of functional diversity to *LIE* disappeared in the low evenness communities. Various dimensions of biodiversity may intrinsically relate to each other and interactively affect each other (Cadotte, Carscadden, & Mirotchnick, 2011). Consequently, we emphasize the importance of evenness for understanding how species richness and functional diversity affect ecosystem functioning.

Increases in productivity with species richness may stem from functional complementarity and partition of available resources among multiple species (Cardinale et al., 2007; Loreau, 2000; Loreau & Hector, 2001; Morin, Fahse, Scherer-Lorenzen, & Bugmann, 2011). In the high evenness communities, species richness can serve as a surrogate for functional diversity. For this reason, the positive relationship between species richness and above-ground biomass may be explained in terms of correlated diversity along a functional axis (Cadotte et al., 2011). However, in the low evenness communities,

species richness has no positive link with functional diversity, and has no promotion to above-ground biomass. From the results of this study, we speculate that different effects of species richness on biomass production in prior studies may be due to different co-variation patterns of species richness, functional diversity and evenness.

4.2 | Relative importance of functional diversity and functional dominance on resource use

Understanding relative importance of functional diversity and functional dominance in mediating the diversity effect on ecosystem functioning is urgently needed (Mensah et al., 2016). We showed that relative importance of functional diversity and functional dominance was mediated by species evenness. The positive correlation between functional diversity and *LIE* observed in the high evenness communities disappeared in the low evenness communities. Moreover, functional diversity increased *LC* in the high evenness communities, but not in the low evenness communities. These results support our second hypothesis and suggest that the complementarity effect of functional diversity on light use depends on species evenness of plant communities. In contrast, functional dominance as indicated by CWM$_{plant\ height}$ had no significant effect on *LIE* in the high evenness communities and a positive effect in the low evenness communities. These results support our third hypothesis and suggest that functional dominance plays an important role in light use when species evenness is low. Communities of low evenness are commonly dominated by one or a few plant species (Mulder et al., 2004; Orwin & Bardgett,
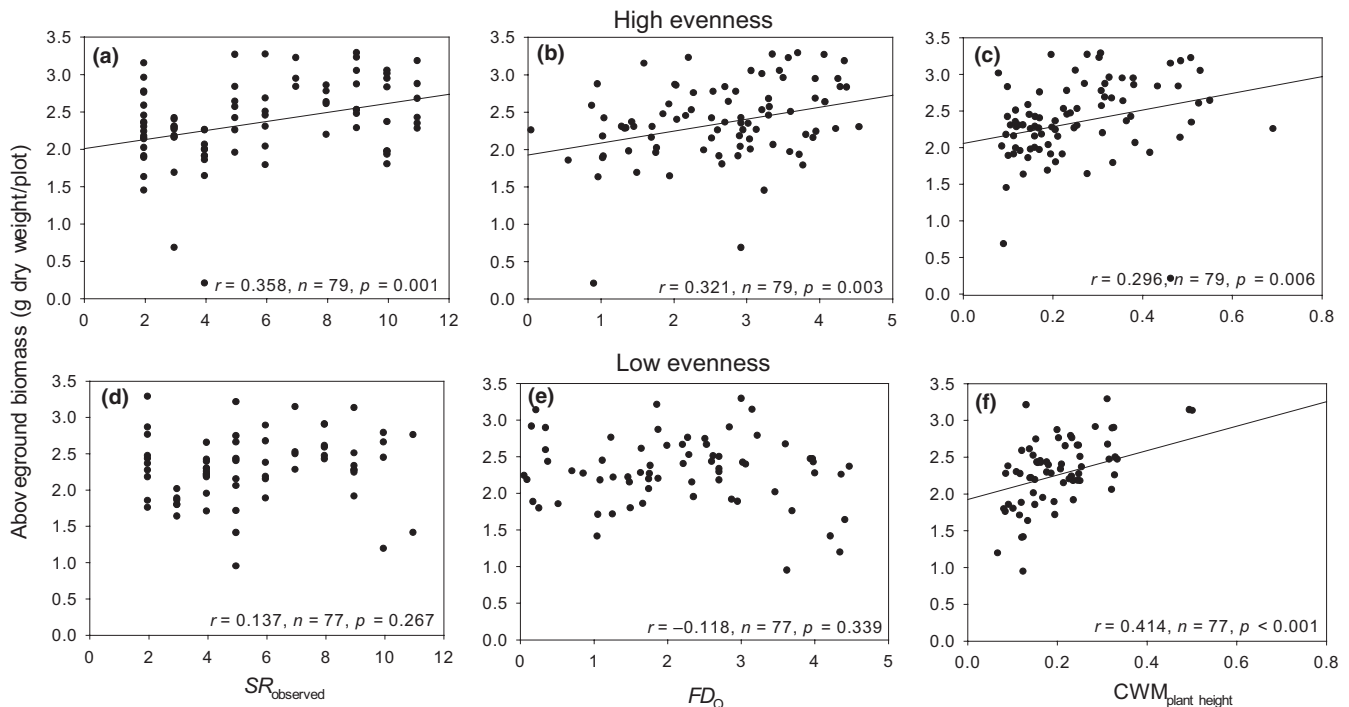

FIGURE 3 Relationships of above-ground biomass with (a, d) observed species richness (*SR*$_{observed}$), (b, e) functional diversity Q index (*FD*$_Q$) and (c, f) CWM value of plant height (CWM$_{plant\ height}$) in the (a–c) high and (d–f) low evenness communities
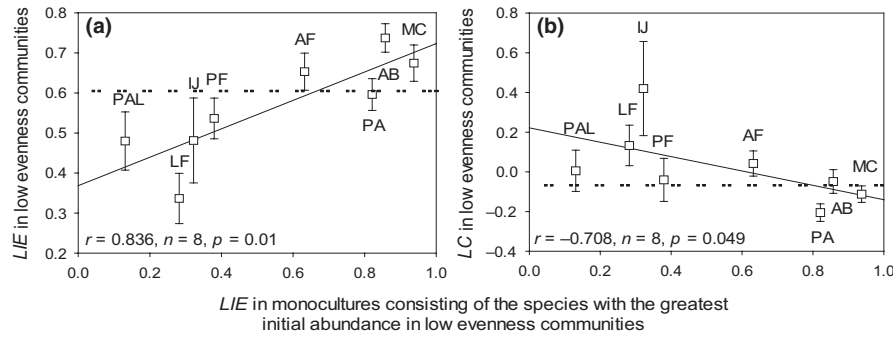
FIGURE 4 Relationships of light interception efficiency (*LIE*, (a) and light complementarity index (*LC*, (b) of a low evenness community (mixture) with *LIE* of the monoculture consisting of the species with the largest initial abundance in the low evenness community. The dashed lines show the mean values in the high evenness communities. Species codes: PAL—*Plantago asiatica*, LF—*Lysimachia fortunei*, IJ—*Inula japonica*, PF—*Pterocypsela formosana*, AF—*Antenoron filiforme*, PA—*Phytolacca americana*, AB—*Achyranthes bidentata*, and MC—*Macleaya cordata*

2014). These dominant species contribute to most of the community biomass and thus are likely to play a key role in resource use and ecosystem functioning (Sasaki & Lauenroth, 2011; Smith & Knapp, 2003). In this study, taller plant species (*A. bidentata*, *P. americana* and *M. cordata*) had a higher ability for light competition and thus intercepted most of the light. Consequently, the presence of these dominant species led to positive relationships between CWM$_{plant\ height}$ and *LIE* in the low evenness communities. As functional diversity and functional dominance are not exclusive and simultaneously influence ecosystem functioning (Mensah et al., 2016), we postulate that increasing species evenness increases the role of functional diversity but decreases that of functional dominance.

4.3 | Roles of species with the greatest initial abundance in resource use

We found that *LIE* of the low evenness communities was positively correlated with *LIE* of the monocultures consisting of the species with the largest initial abundances and *LC* of the low evenness communities was negatively correlated with it. Differences in functional traits among species reflect differences in competitive abilities of the species to capture resources, and thus such inter-specific trait differences stand for trait competitive hierarchy among species (Kunstler et al., 2012, 2016; Mayfield & Levine, 2010). Consequently, trait competitive hierarchy of the most abundant species may greatly affect resource complementary use (Legner, Fleck, & Leuschner, 2013; Lorentzen, Roscher, Schumacher, Schulze, & Schmid, 2008). In this study, the low evenness communities were artificially constructed with species of different initial abundances. When taller and larger plant species have larger initial abundances (such as *A. bidentata*, *P. americana* and *M. cordata*), they can preempt light over shorter and smaller plants (Falster & Westoby, 2003; Freckleton & Watkinson, 2001; Roscher, Schumacher, Schmid, & Schulze, 2015; Weiner & Damgaard, 2006). As a result, light complementary use is lower in such low evenness communities compared to that in the high

evenness communities due to a limited contribution from the shorter and smaller species for their little initial abundance and competitive disadvantage (Anten & Hirose, 1999). In contrast, when shorter and smaller species have larger initial abundances (such as *P. asiatica* and *L. fortunei*), light complementary use is higher in such low evenness communities than in the high evenness communities due to a disproportionate contribution from the taller and larger species to light use. This explains why *LC* of the low evenness communities was negatively correlated with *LIE* of the monocultures of the species with the largest initial abundance. Based on these results, we speculate further that resource complementarity may be negatively correlated with trait competitive hierarchy of dominant species when communities have low species evenness.

5 | CONCLUSIONS

Functional diversity has a positive link with species richness and plays a crucial role in complementary resource use of high evenness communities, but such an impact disappears in communities of low evenness. Functional dominance plays an important role in resource use of low species evenness communities. Therefore, the effect of functional diversity on resource use may positively depend on evenness, while the effect of functional dominance may negatively depend on evenness. Different co-variation patterns of species richness, functional diversity and evenness may lead to different effects of species diversity on biomass production.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1 Experimental treatments with five levels of species richness (1, 2, 4, 8 and 12 species) and two levels of evenness (high and low)

Appendix S2 The characteristics of 16 species used in the experiment. Family, life form and four functional traits (mean ± *SE*) related to light interception were given

Appendix S3 Correlations among CWM value of the four traits (plant height, area of a single leaf, leaf angle and cover of single plant)

Appendix S4 Relationships of light interception efficiency (*LIE*) with CWM value of area of a single leaf ($CWM_{area\ of\ a\ single\ leaf}$), (b, e) leaf angle ($CWM_{leaf\ angle}$) and cover of a single plant ($CWM_{cover\ of\ a\ single\ plant}$) in the high and low evenness communities

Appendix S5 Relationships of light complementarity index (*LC*) with CWM value of area of a single leaf ($CWM_{area\ of\ a\ single\ leaf}$), leaf angle ($CWM_{leaf\ angle}$) and cover of a single plant ($CWM_{cover\ of\ a\ single\ plant}$) in the high and low evenness communities

Appendix S6 The relationship between plant height of the species with the largest initial abundance and light interception efficiency of their monocultures

Appendix S7 Coefficient of correlation of light interception efficiency with the functional diversity Q index (FD_Q) at each level of observed species richness ($SR_{observed}$) and with $SR_{observed}$ at each level of FD_Q