Functional redundancy changes along a drought stress gradient for the shift of selection effect to complementarity effect in experimental plant communities

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1. Introduction

Global climatic changes are likely to trigger ecosystem disturbances leading to rapid loss of biodiversity and immense changes in species composition, which will change the functional attributes of communities (Butchart et al. 2010; Lloret and Granzow-de la Cerda 2013; Oke and Hager 2020). A large number of experimental studies have shown positive relationships between species richness and ecosystem functioning (Balvanera et al. 2006; Wang et al. 2011; Lefcheck et al. 2015; Li et al. 2018; Petruzzella et al. 2018; Xu et al. 2020). These positive relationships are typically explained by two types of mechanism: selection effect and complementarity effect (Huston 1997; Loreau and Hector 2001). Importantly, the degree to which the loss of a species impacts overall ecosystem functioning usually depends on whether there are other species within the community that perform similar ecosystem functions, a property commonly referred to as functional redundancy (Walker 1992; Naeem 1998). However, how the functional redundancy affects the relationships between species richness and ecosystem functioning is still unclear.

Functional redundancy of ecological communities is important for community stability and resilience to disturbance (Biggs et al. 2020). Moreover, functional similarities and differences among species should better capture species interactions than species number and thus should better predict ecosystem functioning (Cadotte et al. 2011; Mouquet et al. 2012; Srivastava et al. 2012; Cadotte 2013). However, in most of prior BEF studies, species richness was simply used to replace biodiversity. If each species has a unique role in ecosystem functioning, ecosystem functioning will increase with species richness. If the role of added species is already performed by other species, irrespective of increasing species richness, functional redundancy should lead to saturation in functioning (Loreau 1998; Naeem 2002). Although the functional redundancy is getting more attention, few studies have linked the redundancy differences across communities to ecological outcomes.

Through comparing species performances of mixed communities with those of monocultures, Loreau and Hector (2001) devised a statistical method for assessing the effects of biodiversity (the complementarity and selection effects). 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 and Hector 2001) and the selection 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 et al. 1997). Complementarity and selection effects are implicitly linked to species coexistence (via niche differences) and competitive exclusion (via fitness differences), respectively (Carroll et al. 2011; Loreau et al. 2012; Turnbull et al. 2013). According to the light-asymmetry hypothesis, light competition is size asymmetric in the sense that taller plants receive larger amounts of light than shorter plants, and this asymmetry in resource partitioning accelerates the rates of...
Competitive exclusion (De Malach and Kadmon 2017), leading to little contribution by shorter plants. We postulate that light competition is associated with the selection effect, which may lead to functional redundancy of short species owing to size-asymmetric competition. However, greater niche differences among species allow species to avoid competition (Cadotte et al. 2013; Kraft et al. 2014) and utilize different spatial and temporal resources (Reich 2014; Díaz et al. 2016), which may lead to most species contributing to ecosystem function (Fargione and Tilman 2005; Aarssen et al. 2006). We postulate that complementarity effects, which rely on niche differences, may allow every species to perform specific functions. Consequently, functional redundancy in communities may increase with selection effects but decrease with complementarity effects.

Although complementarity and selection effects are two components of biodiversity effects, their relative importance may change under different environmental conditions (Loreau 2000; Loreau and Hector 2001). According to the stress-gradient hypothesis, the importance of facilitation should increase with abiotic stress gradient, but that of competition should decrease with abiotic stress gradient (Bertness and Callaway 1994). Moreover, the selection effect may be important in environments where inter-specific competition is the dominant interaction (Fridley 2001), whereas the complementarity effect will be dominant in environments where facilitation is the dominant interaction (Chu et al. 2008). If functional redundancy indeed increases with the selection effect but decreases with the complementarity effect, we postulate that functional redundancy of communities may decrease with increasing abiotic stress gradient.

The occurrence of extreme climatic events, resulting from a high variability in temperature and precipitation (Kreyling et al. 2008; Jentsch et al. 2011), may change the abiotic stress intensity for individual species within communities. Nonetheless, there is a lack of studies evaluating the impact of extreme climatic events, such as drought, on functional attributes of communities. In this study, we carried out an artificial experiment involving plant communities with different diversity and exposed all of these communities to a drought stress gradient (no, moderate and intensive drought stress). Specifically, we tested the following hypotheses. (1) Increase in the selection effect will increase functional redundancy of communities, whereas increase in the complementarity effect will decrease functional redundancy of communities. (2) Functional redundancy of communities decreases along an increasing abiotic stress gradient. (3) With decreasing functional redundancy, ecosystem functioning becomes saturated at a higher richness level and a positive species richness-ecosystem functioning relationship gradually becomes evident.

2. Materials and methods

2.1. Experimental design

In March 2013, experimental plant communities were constructed in plastic containers (72 cm long × 64 cm wide × 42 cm deep) with five drainage holes at the bottom. Each container was first filled with a 27 cm layer of mixed and homogenized soil (total N: 0.763 ± 0.104 g kg⁻¹; total P: 0.216 ± 0.047 g kg⁻¹; pH: 6.436 ± 0.275; organic matter: 9.686 ± 0.667 g kg⁻¹; mean ± SE, n = 10) and then a 10 cm layer of a mixture of soil and a nutrient-rich potting compost (Table S1) at a volume ratio of 1:1 (total N: 4.612 ± 0.456 g kg⁻¹; mean ± SE, n = 10) and a then a 0.216 ± 0.047 g kg⁻¹; pH: 6.436 ± 0.275; organic matter: 9.686 ± 0.667 g kg⁻¹; mean ± SE, n = 10). The soil was collected from a mountainous area near Taizhou city in Zhejiang Province, China. The mixed soil-compost layer was added to facilitate seed germination and seedling establishment.

The species pool consisted of 16 native herbaceous species (Table S2). These 16 species were selected from the species that naturally grow in brush grassland communities of valley and hillside around Taizhou city in Zhejiang Province, China. Most species of brush grassland communities are annuals and perennials. Nine perennial species and seven annual species were selected to stimulate natural communities. Patrinia scabiosaeofolia Fisch. ex Trev., Achyranthes aspera L., Solanum nigrum L. and Artemisia migoana Kitam. are the most dominant species with the highest biomass. For species richness treatments, 46 communities were selected, consisting of one, two, four, eight or 16 species, i.e. 16 monocultures representing each individual species, 10 two-species mixtures, 10 four-species mixtures, nine eight-species mixtures and one 16-species mixture (Fig. S1 and Table S3). Each of the two-, four– or eight-species mixtures had a different species composition (Table S3). In the two-, four– and eight-species mixtures, species were randomly chosen from the species pool and no mixtures had exactly the same species composition.

In December 2013, a total of 800 seeds were sowed in each container and seed number of each species in a container was determined by dividing 800 by the number of species. One month after germination, 32 vigorous seedlings were retained and excess seedlings were removed which is similar to the density of natural shrub grass communities. Thus, at the start of the experiment, plant density was 32 seedlings per container, and each species was represented by the same number of seedlings (e.g. for four-species mixtures, there were eight seedlings for each of the four species in
the container). The 32 seedlings showed even spatial distribution in the container, and seedlings of the same species were not adjacent. In each container, undesired seedlings were removed, i.e. those not belonging to the species originally sown. All containers were randomly placed inside a plastic rain shelter at Taizhou University, Zhejiang Province, China, which was open at the bottom of the sides to allow air to be ventilated. The annual species produced seeds and generated in the next year. The communities in all containers were harvested in October 2016. For each container, above-ground parts of living plants were sorted by species, dried to constant mass at 80°C and weighed.

2.2. Drought manipulation

Three drought intensity treatments (no, moderate and intensive drought) were set up using automatic drip irrigation systems with control of irrigation time. To account for seasonal variation of evapotranspiration, 20 containers with different species compositions for each of the six treatment combinations of drought and invasion were randomly selected every other week and their volumetric soil water content was measured using a ProCheck analyzer (Decagon, Pullman, Washington, USA). Data collected using the ProCheck analyzer were adjusted based on the traditional way of measuring gravimetric soil water content (Fig. S2). Irrigation time was adjusted based on data from these measurements. For the no drought treatment, irrigation time was 20–35 min and gravimetric soil water content (15.5–19.8%) was maintained at a level similar to that of plant communities in the mountainous areas (Wugui mountain, E121.383°, N28.652°; Baiyun mountain, E121.419°, N28.667°; Beigu mountain, E121.112°, N28.856°) around Taizhou City, Zhejiang Province, China. For the intermediate and intensive drought treatments, irrigation time was 50% (gravimetric soil water content ranging from 12.4% to 15.4%) and 25% (gravimetric soil water content ranging from 10.0% to 12.6%) of that in the no drought treatment, respectively. Depending on weather conditions, plant communities in the containers were irrigated once a day between May and September, once every other day between March and April and between October and December, and once every week between January and February. Drought treatments started on March 12, 2015.

2.3. Light interception efficiency measurement

Photosynthetically active radiation (PAR) was measured using a PAR ceptometer (GLZ-C, Zhejiang Top Instrument Co., Ltd, China). The light interception efficiency in monocultures of each species was measured to reflect the light competition ability of each species. Three points were randomly selected within the central area (0.5 m × 0.5 m) of each species monoculture. Measurements were recorded between 11:00 and 14:00 when the sun irradiated the plot almost vertically (four times: May 2, 2015; September 15, 2015; July 14, 2016; October 4, 2016). The PAR above the community canopy and the PAR at ground level were measured at each of the three points. Light interception efficiency was calculated as follows: light interception efficiency = (PAR of canopy – PAR of ground)/PAR of canopy. The mean value of four measurements was used for data analysis.

2.4. Statistical analysis

2.4.1. Functional redundancy

To reflect the effect of functional redundancy on the BEF relationship, the Michaelis–Menten model for BEF relationship developed by Naeem (2002) was modified as follows:

\[ B = \frac{B_{\text{max}} \times X^a}{Fr + X^a} \]

The model was fitted using the trust-region reflective least squares algorithm in MATLAB. B is the biomass production of each plant community (pot), X is the relative species richness as a metric of diversity, varying between 0 (no species) and 1 (16 species). \( B_{\text{max}} \) represents the value for the pot with the most biomass under a certain drought stress condition (‘saturation biomass’). The a is a coefficient that represents interaction intensity among species (\( a \geq 1 \)). Fr is the minimum species richness for producing a ‘fair amount’ of biomass. A small value of Fr should express a high species equivalency (‘functional redundancy’).

Following the ’20/80’ rule of the Pareto principle (Woolhouse et al. 1997), species in each plant community were
Table 1. Results of general linear model for the effects of drought stress, species richness, the complementarity effect and the selection effect on the number of ‘redundant’ species of communities.

| Variable                  | df | MS    | F     | P       |
|---------------------------|----|-------|-------|---------|
| Drought stress (D)        | 2  | 17.917| 43.307| < 0.001 |
| Species richness (S)      | 3  | 411.863| 995.538| < 0.001 |
| D x S                     | 6  | 6.423 | 15.525| < 0.001 |
| Complementarity effect    | 1  | 0.052 | 0.126 | 0.723   |
| Selection effect          | 1  | 6.421 | 15.521| < 0.001 |
| Error                     | 88 | 0.414 |       |         |

ranked from the species with the highest biomass to the species with the least biomass. A few species having large amounts of biomass and performing most ecosystem functions (cumulative 80% of biomass production in this study) should be relatively important for ecosystem functioning. Many species producing little biomass (representing the last 20% of biomass production) should have little influence on ecosystem functioning and were considered as ‘redundant’ species. The number of redundant species for biomass production was calculated and represented functional redundancy of each community. ANOVA was used to test the effects of species richness of communities on the number of redundant species, and to test the effect of drought stress on the number of redundant species at each species richness level.

2.4.2. Complementarity and selection effects

The additive partitioning method (Loreau and Hector 2001) was used to quantify selection and complementarity effects. The complementarity effect for a specific number of species was N ∆YRM, where ∆Y was the average change in relative yield for all species in the mixture and M was the average monoculture yield. Higher complementarity effect indicates that more species have better performance than that of expected from monoculture biomass. The selection effect Ncov(∆Y,R,M) was calculated as the covariance between the monoculture yield of species (M) and their change in relative yield in the mixture (∆Y) multiplied by N of the mixture. Higher selection effect indicates that one or several species have greater and better performance while other species have less performance than that of expected from monoculture biomass.

ANOVA was used to test the effect of drought stress on complementarity and selection effects. These analyses allowed exploration of changes in complementarity and selection effects with drought stress gradients. To examine how the complementarity and selection effects affected functional redundancy, general linear models (GLM) were used to analyze data for the number of redundant species using SPSS 20.0 for Windows, with drought stress, species richness, complementarity effect and selection effect as explainable variables. Simple regression analysis was used to test relationships between the number of redundant species and the complementarity or selection effect under different drought stress conditions. These analyses allowed exploration of how changes in complementarity or selection effects affected functional redundancy of communities.

2.4.3. Species interactions

Changes in species interactions were examined using the deviation between the observed and expected biomass \( D_{\text{mixture-monoculture}} \).

\[
D_{\text{mixture-monoculture}} = \frac{O_i - E_i}{O_i}
\]

Where \( O_i \) is the observed biomass of species \( i \) in mixtures and \( E_i \) is the expected biomass, i.e. simply the monoculture biomass multiplied by the initial proportion of the species in mixture. If \( D_{\text{mixture-monoculture}} > 0 \), the species showed better performance than the expected yield; if \( D_{\text{mixture-monoculture}} < 0 \), the species showed worse performance than the expected yield. A single-sample t-test was used to test significant differences of \( D_{\text{mixture-monoculture}} \) of species from 0 under different drought stress conditions.

To explore the mechanism underlying changes in species interactions (expected to change from competition to facilitation in response to drought stress), simple regression analysis was used to test the relationships between species richness and soil water content at 0–5 cm depth and 40–45 cm depth under different drought stress conditions. These analyses allowed exploration of whether soil water was more fully used in highly diverse communities in response to drought stress.

2.4.4. Species competitive hierarchy

Patrinia scabiosafolia and A. migoana were not clonal species and had great competitive advantages in the control block, accounting for 81.03 ± 0.04% biomass in mixtures having P. scabiosafolia or/and A. migoana. These were considered dominant species. Achyrantes aspera L., Sesbania canabina (Retz.) Poir., Bidens pilosa L. and Justicia procumbens L. displayed a certain competitiveness and produced relatively large amounts of biomass (based on the Pareto principle, they did not belong to redundant species) in many mixtures of the control block; these were considered subdominant species. The other nine species (Medicago sativa L. disappeared from all mixtures and was not included in data analyses) usually made little contribution to biomass.
production and were considered as redundant species in mixtures of the control block.

To explore the effect of ability to compete for light on species competitive hierarchy, simple regression analysis was used to test relationships between light interception efficiency in monocultures of each species and their average biomass proportions in mixtures under different drought stress conditions. These analyses allowed exploration of how light-asymmetric competition affects functional redundancy of communities under different drought stress conditions.

To explore how drought resistance of each species affects their competitive ability, the drought resistance of each species was assessed by dividing the biomass in monocultures of each species by that in monocultures of the control block, as described previously by Suding et al. (2003). The change in biomass proportions for each species was assessed by subtracting mean biomass proportions in mixed communities of the control block from mean biomass proportions in mixed communities within drought blocks (moderate or intensive drought). Simple regression analysis was used to test relationships between drought tolerance of each species and their changes in biomass proportion under moderate and intensive drought stress conditions. These analyses allowed exploration of how the drought tolerance of species affects their contribution to biomass production of communities in response to drought stress.

3. Results

3.1. Functional redundancy

The value of Fr increased from 0.253 to 0.804 to 0.830 along the drought stress gradient, representing a gradual decrease in the functional redundancy of communities with increasing drought stress, and the species richness of biomass saturation increased with drought stress (Figure 1).

Consistent with the Pareto principle, only a few species contributed most of the biomass production in most communities. Communities with more species had more redundant species (Figure 2; control: $F = 618.92$, $df = 4$, $P < 0.001$; intermediate drought: $F = 452.99$, $df = 4$, $P < 0.001$; intensive drought: $F = 368.23$, $df = 4$, $P < 0.001$). However, with the increase in drought stress, the number of redundant species decreased significantly in communities with four, eight and 16 species (Figure 2; four species: $F = 7.75$, $df = 2$, $P = 0.002$; eight species: $F = 31.57$, $df = 2$, $P < 0.001$; 16 species: $F = 30.89$, $df = 2$, $P < 0.001$).

3.2. Complementarity and selection effects

Consistent with our expectation, complementarity effects increased with drought stress ($F = 20.95$, $df = 2$, $P < 0.001$), showing the same trend as Fr, while selection effects decreased with drought stress ($F = 8.85$, $df = 2$, $P < 0.001$), and this change had the opposite trend to that of Fr (Figure 3). Moreover, selection effect, a covariate factor with drought stress and species richness, positively affected the number of redundant species (Table 1, Figure 4). However, the complementarity effect showed no close link with the number of redundant species within communities (control: $r = 0.09$, $n = 34$, $P = 0.584$; intermediate drought: $r = 0.08$, $n = 34$, $P = 0.644$; intensive drought: $r = 0.27$, $n = 34$, $P = 0.12$).

3.3. Species interactions

We examined changes in species interactions using the deviation between observed and expected biomass ($D_{\text{mixture-monoculture}}$). In the control block, *P. scabiosaefolia* and *A. migoana* had a competitive advantage ($D_{\text{mixture-monoculture}} > 0$), while most other species had a competitive disadvantage ($D_{\text{mixture-monoculture}} < 0$) (Figure 5). These results indicated that competitive exclusion of other species by *Patrinia scabiosaefolia* and *Artemisia migoana* may be an important species interaction in the control block. However, with increasing drought stress, more and more species showed better performance than expected.
greater species richness had less soil water at 40 cm depth on species richness at different drought stress conditions: control, $r = -0.117$, $n = 50$, $P = 0.419$; moderate drought, $r = -0.686$, $n = 50$, $P < 0.001$; and intensive drought, $r = -0.729$, $n = 50$, $P < 0.001$.

Moreover, communities with greater species richness had less soil water at 40–45 cm depth in the moderate and intensive drought blocks (Figure 6). However, the species richness of communities had no significant effect on soil water at 40–45 cm depth in the control block.

### 3.4. Species competitive hierarchy

Biomass proportions of species in mixed communities depended positively on their light interception efficiency measured in monocultures in the control block (Figure 7A). However, light interception efficiency of species in monocultures had no close link with their biomass proportions in mixtures in the moderate and intensive drought blocks (Figure 7B–C). In the moderate and intensive drought blocks, however, the change in biomass proportions of species in mixed communities increased with their drought resistance (Figure 8), and even showed a significant relationship in the intensive drought block (Figure 8B).

### 4. Discussion

In this study, we measured biomass production as a general proxy for ecosystem functioning. The selection effect significantly increased functional redundancy (number of redundant species), while the complementarity effect had no significant effect. Functional redundancy of communities decreased with the increased drought intensity for the shift from the selection effect to the complementarity effect. The decrease of functional redundancy led to saturation of biomass production at a higher richness level, and the species richness-biomass relationship gradually tended toward a nearly linear, positive shape.

#### 4.1. Changes of functional redundancy with the selection and complementarity effects

Consistent with the first hypothesis, the number of redundant species increased with the selection effect. Functional dominance (the trait of dominant species) is assumed to mainly reflect the selection effect (Fu et al. 2014; Li et al. 2015; Mensah et al. 2016). Under the control treatment, *Patrinia scabiosaefolia* and *Artemisia migoana* had large competitive advantages (great height and light interception efficiency) and accounted for 81.03% biomass in mixtures containing the two species. Although competitive advantages were restrained under the moderate and intensive drought treatments, their proportions still take 51.49% and 42.61%. Consequently, functional dominance (such as light competition dominance in this study) of *Patrinia scabiosaefolia* and *Artemisia migoana* suppressed many other species which had little contributions to community biomass.

In contrast to our hypothesis, the complementarity effect had no close link with the complementarity effect. Functional diversity is assumed to mainly reflect the complementarity effect (Mouchet et al. 2010; Chanteloup and Bonis 2013; Mensah et al. 2016). Although we did not measure root traits of each species, over-utilization of soil water of mixtures (Fig. S3, had lower soil water content than that of all monocultures) should result from niche complementarity (Loreau and Hector 2001; Hector et al. 2002). Moreover, over-utilization of soil water only occurred under the moderate and intensive drought which indicates niche complementarity increased with increasing drought stress. We postulate that, compared with the competition effects of *Patrinia scabiosaefolia* and *Artemisia migoana*, functional complementarity for soil water utilization had a little effect on other species. Consequently, the number of redundant species showed no close link with the complementarity effect.

#### 4.2. Changes of functional redundancy with drought intensity

Consistent with the second hypothesis, functional redundancy decreased with increasing drought intensity, which should be ascribed to the decrease of selection effect and the increase of complementarity effect (Havens and Carlson 1998; Wang et al. 2013). Stress gradient hypothesis (Bertness and Callaway 1994) predict that competition will decrease with stress intensity (such as drought stress). In the control block, owing to the competition exclusion of *Patrinia scabiosaefolia* and *Artemisia migoana*, growth of many species was restrained, and they showed worse performance than expected (Figure 5). These species made little contribution to community biomass and were considered as redundant species. Expect of *Patrinia scabiosaefolia* and *Artemisia migoana*, many species had a higher relative yield than expected under the moderate and intensive drought treatments, which will lead to high complementarity effect (Figure 3; Fargione et al. 2007). We postulate that better performances of many species than expected (Figure 5) are most likely the reasons that decrease competition of dominant species. Expect of *Patrinia scabiosaefolia* and *Artemisia migoana*, many species had a higher relative yield than expected under the moderate and intensive drought treatments, which will lead to high complementarity effect (Figure 3; Fargione et al. 2007).
species or positive interactions (interspecific complementarity or facilitation). Consequently, decrease of functional redundancy with increasing drought stress should be ascribed to decrease of selection effect and increase of complementarity which is related to the change of interspecific interactions.

In this study, drought tolerance should be an important trait that affected their performance. *Patrinia scabiosaefolia* and *Artemisia migoana* had great biomass under no drought treatment, while had low drought tolerance (Figure 8). Improving stress tolerance at the expense of reducing growth is an important mechanism of adaptation to the stressful environment (Grime 1977; Munoz et al. 2016). Compared to the control treatment, biomass proportions of *Patrinia scabiosaefolia* and *Artemisia migoana* decreased under moderate and intensive drought treatments, which may be related to low drought tolerance and the adaptation to drought stress. Some redundant species under no drought treatment had high drought tolerance (Figure 8) and their biomass proportions increased. Consequently, decrease of functional redundancy with increasing drought stress may be related to low drought tolerance of dominant species and high drought tolerance of redundant species.

**4.3. Changes of species richness-biomass relationship with functional redundancy**

Consistent with the third hypothesis, with the decrease of functional redundancy, a positive species richness-biomass relationship gradually becomes evident. The positive species richness-biomass relationships in prior studies are usually related to the increased utilization of resources (Li et al. 2019; Mason et al. 2020). Under no drought treatment, light competition determined biomass performances of species (Figure 7). Competition for aboveground resources, such as light, has been shown to be size asymmetric (Weiner et al. 1990; Wichmann 2001). Larger plants have an overproportional advantage over smaller plants just from their size (Connolly and Wayne 1996; Freckleton and Watkinson 2001). Taller and larger plants, such as *Patrinia scabiosaefolia* and *Artemisia migoana*, use most of the light resources, and left little light resource for other smaller plant. Consequently, light resource utilization was determined by only some taller species, and did not consistently increase with the species richness. Under moderate and intensive drought treatments, light resource utilization was not a decisive factor and soil water utilization was also important for biomass
performance of species. Unlike light competition, soil water competition is multi-dimensional and thus symmetric, which are associated with root traits (e.g. root biomass, length, number and structure; Ferchaud et al. 2015; Bouda and Saisers 2017; Tylianakis et al. 2018; Albornoz et al. 2021). Soil water competition among species is relatively balanced so that not only superior species but also inferior species will play a specific role in the use of resources (Bartelheimer et al. 2008; del Rio et al. 2014), which make resources utilization consistently increased with species richness. Consequently, functional traits of species for resource utilization may be better than species richness to predict ecosystem functioning (Cadotte et al. 2011; Mouquet et al. 2012; Srivastava et al. 2012; Cadotte 2013). We postulate that, with the increasing of drought intensity, weakened light utilization and enhanced soil water utilization lead to decrease of functional redundancy and lead to positive species richness-biomass relationship.

5. Conclusions

In this study, functional redundancy of communities decreased with the increased drought intensity for the decrease of selection effect and the increase of complementarity effect. The decrease of functional redundancy led to saturation of biomass production at a higher richness level, and the species richness-biomass relationship gradually tended toward a nearly linear, positive shape. Our results indicated that species may be redundant for one ecosystem functioning (such as biomass production) but may be important for another ecosystem functioning (such as drought resistance), and biodiversity effects should be evaluated for predicted changes in climate (such as drought) and redundant species should be carefully defined. Moreover, the transient dynamics of BEF relationships revealed in this study indicated that climate change and its impact on species interactions and functional redundancy of communities should be considered carefully for the future study of the BEF relationship.

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Disclosure statement

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Availability of data and material

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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