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# Evenness alters the positive effect of species richness on community drought resistance via changing complementarity

Xiao-Yan Wang [a,1], Yuan Ge [b,1], Song Gao [a], Tong Chen [a], Jiang Wang [a,*], Fei-Hai Yu [a,c,*]

[a] School of Life Sciences, Taizhou University, Taizhou, China
[b] State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing, China
[c] Institute of Wetland Ecology and Clone Ecology, Taizhou University, Taizhou, China

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ABSTRACT

Biodiversity loss may decrease the resistance of ecosystems to disturbance. While many studies have tested the effects of species richness on the ability of communities to resist disturbance, few have considered the role of species evenness. We examined whether species evenness affects the relationship between species richness and the drought resistance of plant communities. We constructed experimental plant communities with four levels of species richness (1, 2-, 4- and 8-species) and three levels of species evenness (high, medium and low) and subjected them to two drought treatments (with vs. without drought). Species evenness significantly increased the drought resistance of the communities and also complementarity effects. Moreover, a positive relationship between species richness and the drought resistance of plant communities was found at high and medium evenness but not at low evenness. This result corresponded well with the fact that complementarity effects increased with species richness at high and medium evenness but not at low evenness. However, neither species evenness nor species richness significantly affected selection effects for the drought resistance of the communities. We conclude that species evenness can alter the relationships between species richness and the resistance to disturbance (e.g., drought) in plant communities by enhanced complementarity among species. Thus, in addition to species richness, evenness should also be considered an important indicator of the community resistance to future global changes, such as increased drought intensity and frequency.

## 1. Introduction

The acceleration of biodiversity loss is considered a global crisis and has received much attention in recent decades (Sala et al., 2000; Worm et al., 2006; Cardinale et al., 2012; Semper-Pascual et al., 2019; Dinerstein et al., 2020). A large body of studies have experimentally assessed the effects of biodiversity on various ecosystem functions such as productivity, nutrient cycling, litter decomposition and water purification (Yachi and Loreau, 1999; Hooper et al., 2005; Maestre et al., 2012b; Bardgett and van der Putten, 2014; Tilman et al., 2014; Peters et al., 2019; Zhang et al., 2019). Also, many studies have examined the effects of biodiversity on the resistance of ecosystems to natural and experimental disturbance (Tilman et al., 2006; Loreau et al., 2013; Isbell et al., 2015; Kunert and Cárdenas, 2015; Rodriguez-Ramirez et al., 2017; De Boeck et al., 2018; Ouyang et al., 2021; Wang et al., 2021). While a positive effect of species diversity on ecosystem functions (Tilman et al., 2001; Fitter et al., 2005) and their resistance to disturbance (Kennedy et al., 2002; Kunert and Cárdenas, 2015; Petruzzella et al., 2018; Ouyang et al., 2021) has been frequently reported, a neutral or even negative effect has also been shown (Zhang and Zhang, 2006; Wang et al., 2007; Creed et al., 2009; van Ruijven and Berendse, 2010; Lübbe et al., 2016; Kreyling et al., 2017; Pennekamp et al., 2018).

However, most of the studies testing effects of species diversity on the resistance of ecosystems to disturbance have considered species richness (e.g. Maestre et al., 2012a; Kunert and Cárdenas, 2015; Pennekamp et al., 2018). Species diversity includes not only species richness (and its associated functional diversity), but also species evenness, i.e. the relative abundance of each species within a community, as measured by the relative number of individuals or the relative cover or biomass of each species (Wilsey and Potvin, 2000; Polley et al., 2003; Maestre et al., 2012a; Lembrechts et al., 2018; Maureaud et al., 2019). Studies assessing the effect of species richness have commonly assigned an equal

* Corresponding authors at: School of Life Sciences, Taizhou University, Taizhou 318000, China (J. Wang & F.H. Yu).
*E-mail addresses:* wangjiang@tzc.edu.cn (J. Wang), feihaiyu@126.com (F.-H. Yu).
[1] These authors contribute equally.

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abundance for each component species in a community and thus have initially the highest level of species evenness (Wilsey and Potvin, 2000; Polley et al., 2003; Mattingly et al., 2007; Maureaud et al., 2019). However, plant communities in the real world are commonly composed of species of different abundances and frequently dominated by a few species (Grime, 1998; Wilsey et al., 2005). Moreover, the relative abundances of species can account for substantially more of the variance in plant community diversity than species richness (Stirling and Wilsey, 2001; Wilsey et al., 2005; Maureaud et al., 2019). Thus, for a complete understanding of the species diversity effect on the disturbance resistance of ecosystems, species evenness should be considered simultaneously. However, up to now, much less attention has been paid to the effect of species evenness on the ability of ecosystems to resist disturbance (Wilsey and Potvin, 2000; Ribas et al., 2015; Kreyling et al., 2017; Lembrechts et al., 2018).

Although ecosystem functioning (e.g., productivity) and stability (e.g., disturbance resistance) have internal connection for the close link with species interactions and population dynamics, their biotic mechanisms were always studied separately (Valencia et al., 2020; Wang et al., 2021). Complementarity and selection effects are mainly used to explain the positive effect of biodiversity on ecosystem functioning (Loreau and Hector, 2001), while the promoting effect of biodiversity on ecosystem stability was mainly ascribed to portfolio effects and having high disturbance-resistant species (Thibaut et al., 2013; Wilsey et al., 2014; Isbell et al., 2015). Niche differentiation among species may lead to the occurrence of complementarity (Hernandez and Picon-Cochard, 2016; Michalet et al., 2021), which may increase portfolio effects (Wang et al., 2021). In contrast, highly productive species may lead to the occurrence of selection (Fox, 2005; Montès et al., 2008), which may weaken portfolio effects (Wang et al., 2021). Additionally, how selection effects influence ecosystem stability depends on whether the highly productive species are disturbance-resistant or disturbance-prone species (de Mazancourt et al., 2013; Wang et al., 2021). Increasing species evenness may increase complementarity effects and decrease selection effects (Wilsey and Potvin, 2000; Polley et al., 2003; Wang et al., 2015), and is predicted to strengthen portfolio effects (Doak et al., 1998; Lhomme and Winkel, 2002) and thus ecosystem stability. So far, however, it is still unclear how evenness influences the effect of species richness on ecosystem stability such as disturbance resistance.

Drought is commonly considered a type of disturbance for plant communities and its occurrence is closely associated with global climate change (Reynolds et al., 2007; Maestre et al., 2012b; Gómez-Gener et al., 2020). Studies have shown that water use efficiency of plant communities increased with increasing species richness, suggesting that increasing species richness can promote the community resistance to drought (Naeem and Li, 1997; De Boeck et al., 2008; Vogel et al., 2012; Rodriguez-Ramirez et al., 2017). In response to drought, the complementarity effect is considered more important because complementarity between root systems allows for a higher ability of communities to take up soil water (De Boeck et al., 2006; Verheyen et al., 2008; Craven et al., 2016; Hernandez and Picon-Cochard, 2016). Thus, increasing species richness may promote the resistance of plant communities to drought by increasing complementarity among species and increasing species evenness may strengthen such an effect of species richness.

To assess the effects of species richness and evenness on the resistance of communities to drought, we constructed plant communities consisting of two, four and eight species with three levels of evenness (high, medium and low) and also communities of monocultures, and subjected them to two drought treatments (with vs. without drought). Specifically, we tested two hypotheses: (1) the positive effect of species richness on the resistance of communities to drought becomes stronger with increasing species evenness; (2) species evenness increases the community resistance to drought mainly by increasing complementarity among species.

## 2. Materials and methods

### 2.1. Species pool

The species pool used to construct experimental communities consisted of eight native herbaceous species, i.e. *Achyranthes bidentata* (Amaranthaceae), *Bidens pilosa* (Compositae), *Bidens tripartita* (Compositae), *Persicaria lapathifolia* (Polygonaceae), *Commelina communis* (Commelinaceae), *Cichorium intybus* (Compositae), *Antenoron filiforme* (Polygonaceae) and *Polygonum chinense* (Polygonaceae). Some of these species co-occur and have different evenness in the mountain herbaceous plant communities around Taizhou, Zhejiang Province, China, a subtropic region. *Achyranthes bidentata, C. intybus, A. filiforme* and *P. chinense* are perennials, and *B. pilosa, B. tripartita, P. lapathifolia* and *C. communis* are annuals.

### 2.2. Experimental design

We constructed experimental plant communities with four levels of species richness (1, 2-, 4- and 8-species) and three levels of evenness (high, medium and low) in containers (40 cm long × 30 cm wide × 40 cm high, Table A1), and subjected them to two levels of drought (with vs. without). For the 1-species treatment, we planted monoculture of each of the eight species in two containers, making 16 containers (communities). Of the two containers (communities) of each species, one was randomly selected and subjected to the drought treatment and the other was used as the control (without drought). For the 2-species treatment, five different 2-species mixtures were randomly selected from the species pool, and were replicated six times, making 30 containers (communities). The six sets of each of the five 2-species mixtures were randomly assigned to the six combinations of the two drought treatments and the three evenness treatments. Each treatment had five 2-species mixtures as replicates. The relative abundance of the two species was 1:1 at high evenness, 5:3 at medium evenness and 7:1 at low evenness. Similarly, for the 4-species treatment, five different 4-species mixtures were randomly selected from the species pool, and were replicated six times, making 30 containers. The six sets of the five 4-species mixtures were randomly assigned to the six combinations of the two drought levels and the three evenness levels. The relative abundance of the four species was 1:1:1:1 at high evenness, 3:3:1:1 at medium evenness and 12:2:1:1 at low evenness. Each treatment had five 4-species mixtures as replicates. For the 8-species treatment, 30 communities were established in 30 containers. They were randomly assigned to the six combinations of the drought and evenness treatments, with five replicates each. The relative abundance of the eight species was 1:1:1:1:1:1:1:1 at high evenness, 3:3:3:3:1:1:1:1 at medium evenness and 9:1:1:1:1:1:1:1 at low evenness. Each treatment had five 8-species mixtures as replicates. There were a total of 106 containers (experimental communities). Because of the limitation in space and regarding the number of similar-sized seedlings (see the description below), we did not include true replicates for the monoculture of each species.

On 3 January 2014, seeds of the eight species were sown in containers (32 cm long × 24 cm wide × 19 cm high) filled with commercial potting soil. On 21 March 2014, seedlings were transplanted to the experimental containers filled with loamy soil (organic matter: 1.49 ± 0.13 g $kg^{-1}$; total P: 0.10 ± 0.02 g $kg^{-1}$; total N: 0.71 ± 0.19 g $kg^{-1}$) collected from the mountain areas near Taizhou, Zhejiang Province, China. Each container was planted with 16 seedlings of the same species (for 1-species treatment) or different species (for the 2-, 4- and 8-species treatments). The 16 seedlings were planted into 4 rows × 4 columns, with 4 seedlings in each row or column. Seedlings of the same species were not adjacent if possible. One week after transplantation, seedling survival was checked and dead ones were replaced immediately.

All the containers were placed under two rainout shelters in the campus of Taizhou University (121°24′E, 28°39′N) in Taizhou, Zhejiang Province, China. The rainout shelters were open at the sides for

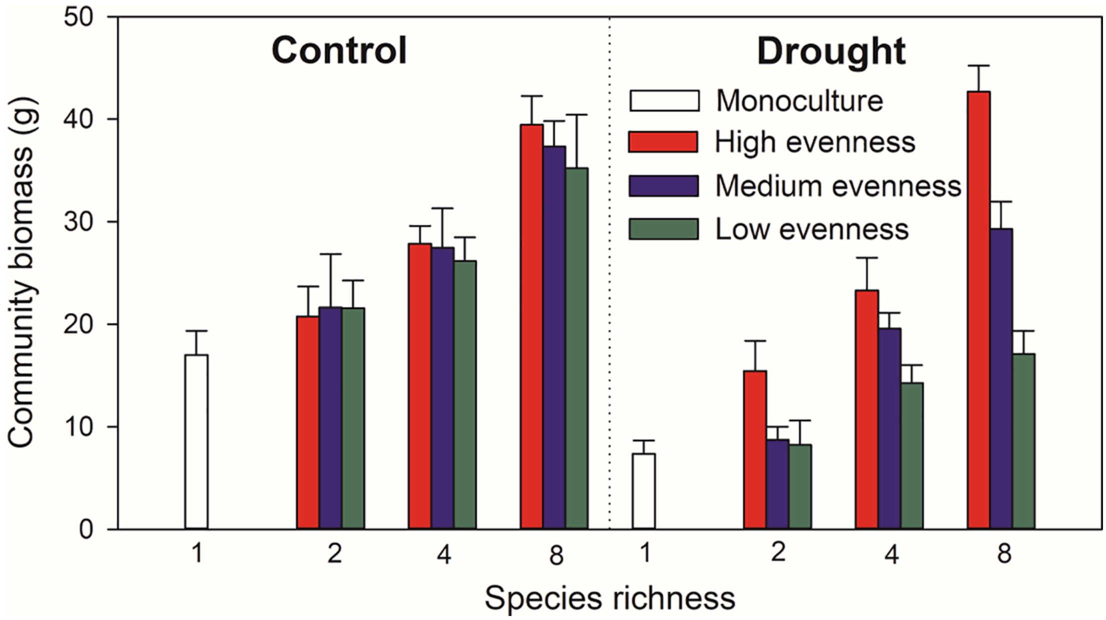


**Fig. 1.** Effects of drought, species richness and evenness on community biomass. *Mean* + *SE* are given.

ventilation. The drought treatment was started on 6 April 2014. Soil water content in each container was monitored every three days by a ProCheck analyzer (Decagon, Pullman, Washington, USA). By controlling frequency of watering, soil water content was controlled to about 8% for the drought treatment (each container was supplied with 1.5 L water once every three days before May 28 and once every two days after May 28) and about 20% for the control treatment (each container was supplied with 1.5 L water once every day before May 28 and twice every day after May 28). Undesired species were removed weekly.

The experiment was started in early April because the growth season starts quite early (March-April) in this subtropic region (Zhang and Yan, 2014). It was ended in September (see below) because at that time communities in all containers were very dense and the limitation of the container size became obvious. During the experiment, the daily mean temperature was 23.6 °C (ranging from 16.3 to 27.4 °C) and the relative humidity was 75.8% (ranging from 58 to 89%) in this region (according to weather forecast of China Weather Network). Since the temperature and thus evapotranspiration became much higher after May, water was supplied more frequently after May 28.

### 2.3. Harvest and measurements

Soil samples were collected on 24 June, 18 July and 21 August 2014. In each container, three soil cores (3 cm in diameter) were randomly collected, and soil water content (30–35 cm deep) was measured. Values of the three soil samples in each container were averaged. Plants communities were harvested on 8–10 September 2014. In each container, aboveground living plants were sorted to species, oven-dried at 60 °C for 48 h and then weighed.

### 2.4. Statistical analyses

The resistance of a plant community to drought was calculated as the ratio of aboveground biomass of the community in the drought treatment to that of the community with exact the same initial species composition in the control treatment (Tilman, 1996; Pfisterer and Schmid, 2002; Wang et al., 2007). Correspondingly, the resistance of a species to drought in a community was calculated as the ratio of aboveground biomass of the species in the community in the drought treatment to that of the species in the community with exact the same initial species composition in the control treatment.

Complementarity and selection effects were quantified with the data of the drought resistance using the additive partitioning method of Loreau and Hector (2001). The complementarity effect of a mixture was calculated as $N\overline{\Delta RY}\overline{M}$, where $N$ is number of species in the mixture, $\overline{\Delta RY}$ is the mean value of the change in the relative drought resistance (i.e., drought resistance of a species in mixture/drought resistance of a species in monoculture) across all species in the mixture and $\overline{M}$ is the mean value of the drought resistance of the monocultures across all species. The selection effect was calculated as $N\mathrm{cov}(\Delta RY, M)$, where $N$ is number of species, $\mathrm{cov}(\Delta RY, M)$ is the covariance between the drought resistance of species in monocultures ($M$) and their change in the relative drought resistance in the mixture ($\Delta RY$).

If the complementary responses among species plays an important role in the community drought resistance, then biomass decreases in susceptible species and compensatory increases in other species would cause great change in community structure. The change of community structure was reflected by the dissimilarity index of Bray and Curtis (1957):

$$D_{control-drought} = \frac{1}{2}\sum_{i=1}^{s}\left|x^i_{control} - x^i_{drought}\right|$$

where $S$ is number of species, $x^i_{control}$ is relative aboveground biomass of species $i$ in a community in the control treatment and $x^i_{drought}$ is relative aboveground biomass of species $i$ in the community in the corresponding drought treatment, which had the same species composition as the community in the control treatment. If the dissimilarity index equals to 0, all species have the same relative abundance between the drought and the control treatment; if dissimilarity equal to 1, no species has the same relative abundance.

If the complementarity between species plays a major role in drought resistance, the drought resistance of mixtures will be higher than that of the most resistant species in the mixtures. Over-drought resistance index ($OI$) was calculated as follows (Hector, 2002): $OI = Y/\mathrm{MAX}(M_i)$, where $Y$ was the drought resistance of a mixture, $M_i$ was the drought resistance of species $i$ in the monoculture. If $\log(OI) > 0$, the mixture should have higher drought resistance than that of the highest resistant species.

Whether competition or facilitation among species occurs in mixtures was investigated by calculating biomass deviation of each species in each mixture following the method of Loreau and Hector (2001): $D_i =$

**Table 1**
ANOVA results of species richness, evenness and their interaction on community drought resistance, complementarity and selection effects for the community drought resistance, community dissimilarity and over-yielding index.

| | Richness (R) | | Evenness (E) | | R × E | |
|---|---|---|---|---|---|---|
| Variable | *F* | *P* | *F* | *P* | *F* | *P* |
| Drought resistance | 10.55 | < 0.001 | 20.83 | < 0.001 | 2.78 | 0.041 |
| Complementarity effect | 11.35 | < 0.001 | 26.43 | < 0.001 | 2.85 | 0.038 |
| Selection effect | 0.45 | 0.639 | 2.35 | 0.110 | 0.97 | 0.438 |
| Dissimilarity index | 22.18 | < 0.001 | 18.86 | < 0.001 | 3.05 | 0.029 |
| Over-yielding index (*OI*) | 0.30 | 0.741 | 13.35 | < 0.001 | 2.39 | 0.069 |

Degree of freedom is (2, 36) for the effects of species richness and evenness and (4, 36) for the effect of their interaction.

$(O_i - E_i)/E_i$, where $D_i$ is the biomass deviation of species *i* in a mixture, $O_i$ is observed biomass of species *i* in the mixture, and $E_i$ is expected biomass of species *i* in the mixture, i.e. biomass of the monoculture of species *i* multiplied by the initial proportion of species *i* in the mixture. If $D_i > 0$, species *i* in the mixture shows a better performance than expected; if $D_i < 0$, then species *i* in the mixture performs worse than expected. If many species have positive values, facilitation or complementarity among species is the most important interspecific interaction; If only a few species have positive values and other species have negative values, interspecific competition is the most important interspecific interaction. Note that using only one monoculture per species increases the chances of stochasticity affecting subsequent calculations.

We used ANOVA to test the effects of species richness and evenness on community drought resistance, complementarity and selection effects, community structure changes (dissimilarity) and over-drought resistance index (*OI*). Linear regressions were conducted to assess the relationships of species richness with community drought resistance, complementarity effects and selection effects, structure changes (dissimilarity), over-drought resistance index (*OI*) and between community drought resistance and structure changes at each evenness level. Differences in regression coefficients (slopes) between evenness levels were tested with ANCOVA. No data transformation was needed before analysis. All analyses were implemented in SPSS 19.0 for windows (IBM, Armonk, NY, USA).

## 3. Results

### 3.1. Impacts of drought, species richness and evenness on community biomass

Drought reduced community biomass of monocultures, 2-, 4 and 8-species mixtures by 56.7, 49.1, 30.2, and 21.6%, respectively (Fig. 1, Table A2). Community biomass generally increased with species richness, and such an effect did not depend on species evenness in the control treatment but became stronger with increasing species evenness in the drought treatment (Fig. 1, Table A2).

### 3.2. Relationships of drought resistance with species richness and complementarity effects

Species richness, evenness and their interaction significantly affected the resistance of the communities to drought (Table 1). The community drought resistance increased with species richness at both high evenness (Fig. 2A; $R^2 = 0.51$, $n = 15$, $F = 13.25$, $P = 0.003$) and medium evenness (Fig. 2A; $R^2 = 0.31$, $n = 15$, $F = 5.87$, $P = 0.031$), but not at low evenness (Fig. 2A; $R^2 = 0.08$, $n = 15$, $F = 1.09$, $P = 0.316$), suggesting that evenness altered the relationship between species richness and community drought resistance. Furthermore, the slope of the linear regression did not differ significantly between the high and the medium evenness treatment (ANCOVA richness × evenness effect: $F = 0.20$, $P = 0.656$), but the intercept of the linear regression was significantly higher in the high than in the medium evenness treatment (ANCOVA evenness effect: $F = 9.07$, $P = 0.006$), i.e., community drought resistance was significantly higher at high than at medium evenness (Fig. 2A). The community drought resistance increased with increasing complementarity effects calculated based on the community drought resistance at all three evenness levels (Fig. 2B; $R^2 = 0.91$, $n = 15$, $F = 217.69$, $P < 0.001$ for high evenness; $R^2 = 0.86$, $n = 15$, $F = 78.42$, $P < 0.001$ for medium evenness; $R^2 = 0.71$, $n = 15$, $F = 31.80$, $P < 0.001$ for low evenness).

### 3.3. Relationships of species richness with complementarity and selection effects

Neither species richness nor evenness significantly affected selection effects (Table 1). However, species richness, evenness and their interaction had significant effects on complementarity effects (Table 1). Complementarity effects increased with species richness at both high (Fig. 3; $R^2 = 0.50$, $n = 15$, $F = 13.14$, $P = 0.003$) and medium evenness

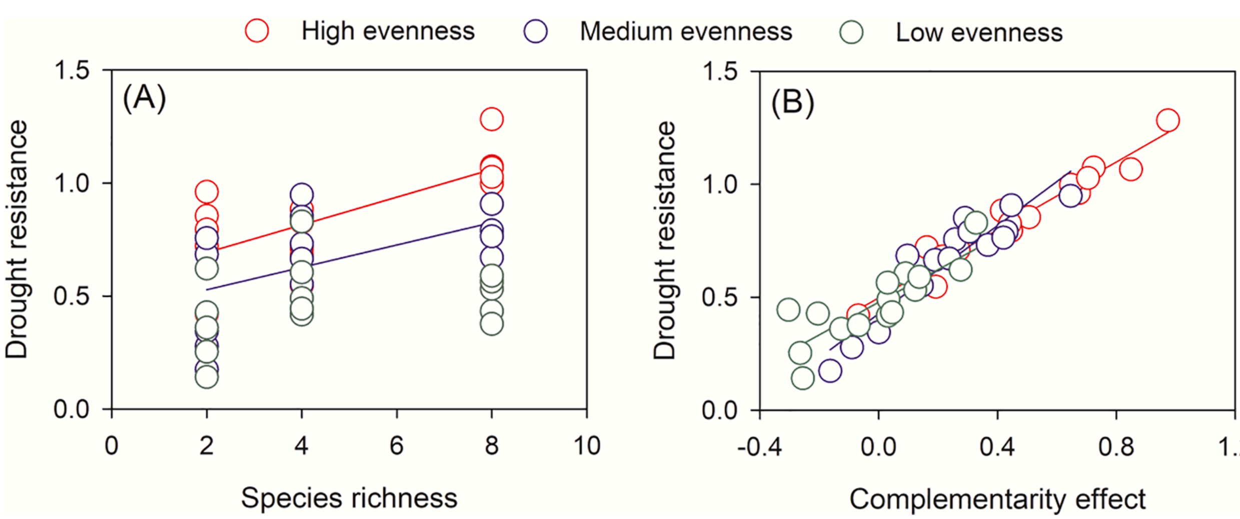


**Fig. 2.** Relationships of (A) species richness and (B) complementarity effects with the drought resistance of plant communities at each evenness level. The red, blue and green lines indicate the relationship at high, medium and low evenness, respectively.

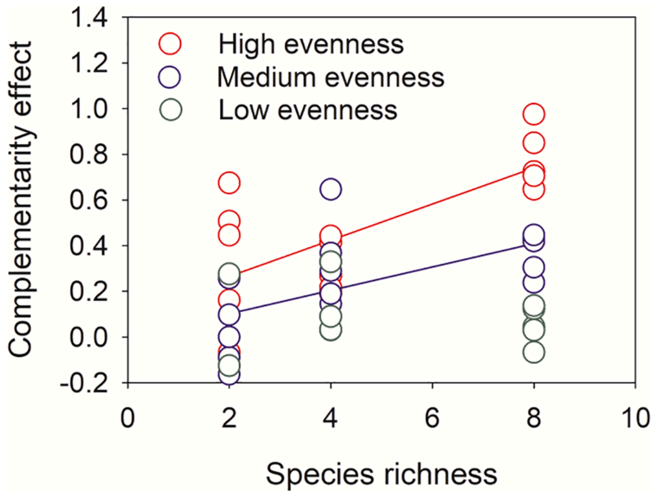


**Fig. 3.** Relationships of species richness with complementary effects for the community drought resistance at each evenness level. The red and blue lines indicate a significant relationship at high and medium evenness, respectively.

(Fig. 3; $R^2 = 0.37$, $n = 15$, $F = 7.61$, $P = 0.016$), but not at low evenness (Fig. 3; $R^2 = 0.04$, $n = 15$, $F = 0.53$, $P = 0.480$). The slope of the linear regression did not differ significantly between the high and the medium evenness treatment (ANCOVA richness × evenness effect: $F = 0.96$, $P = 0.336$), but the intercept of the linear regression was significantly higher in the high than in the medium evenness treatment (ANCOVA evenness effect: $F = 11.11$, $P = 0.003$), i.e. complementarity effects were significantly higher at high than at medium evenness (Fig. 3).

### 3.4. *Relationships of species richness with community structure changes*

The dissimilarity index between communities increased with species richness at both high evenness (Fig. 4A; $R^2 = 0.71$, $n = 15$, $F = 32.14$, $P < 0.001$) and medium evenness (Fig. 4A; $R^2 = 0.69$, $n = 15$, $F = 29.50$, $P < 0.001$), but there was no relationship between them at low evenness (Fig. 4A; $R^2 = 0.10$, $n = 15$, $F = 1.47$, $P = 0.247$). The slope of the linear regression did not differ significantly between the high and the medium evenness treatment (ANCOVA richness × evenness effect: $F = 0.02$, $P = 0.905$), but the intercept of the linear regression was significantly higher in the high than in the medium evenness treatment (ANCOVA evenness effect: $F = 8.56$, $P = 0.007$), i.e. the dissimilarity index was higher at high than at medium evenness (Fig. 4A).

The community drought resistance increased with the dissimilarity index at all three evenness levels (Fig. 4B; low evenness: $R^2 = 0.40$, $n = 15$, $F = 8.69$, $P = 0.011$; medium evenness: $R^2 = 0.66$, $n = 15$, $F = 24.73$, $P < 0.001$; high evenness: $R^2 = 0.79$, $n = 15$, $F = 49.49$, $P < 0.001$), but neither slopes (ANCOVA richness × evenness effect: $F = 0.11$, $P = 0.989$) nor the constants (ANCOVA evenness effect: $F = 3.00$, $P = 0.061$) of the regressions differed among three evenness levels.

### 3.5. *Interspecific interactions*

In the control treatment, only *Achyranthes bidentata* had a higher performance in mixtures than expected from its monoculture (biomass deviation > 0; Fig. 5A), indicating the prevalence of interspecific competition. In the drought treatment, however, most species performed better in mixtures than expected from their monocultures (biomass deviation > 0), and such an effect became more significant with increasing evenness (Fig. 5B), indicating the prevalence of positive interactions (complementarity or facilitation). Increasing species evenness significantly increased the log(*OI*) of the mixtures (Table 1): at low evenness, log(*OI*) was smaller than 0 for most mixtures, but at medium and high evenness, it increased significantly and even became positive (Fig. 6). These results suggest that the drought resistance of communities with high and medium evenness was higher than that of communities with low evenness due to increased positive interactions.

## 4. Discussion

We explored the effects of species evenness on the relationship between species richness and the resistance of communities to drought. As expected, drought strongly reduced community productivity. Interestingly, we found that the community drought resistance and complementarity effects were positively related, and they were also positively related to species richness at the two higher evenness levels but not at the low evenness level. These results, therefore, provide the first evidence that species evenness can alter the relationship between species richness and the community drought resistance via altering complementarity effects.

In a simulation study, Wang et al. (2021) found that complementarity effects can promote community stability via providing insurance or enabling portfolio effects, and that selection effects can contribute to ecosystem stability if they are due to the occurrence of highly resistant, productive species, but cannot if they are due to the presence of risk-

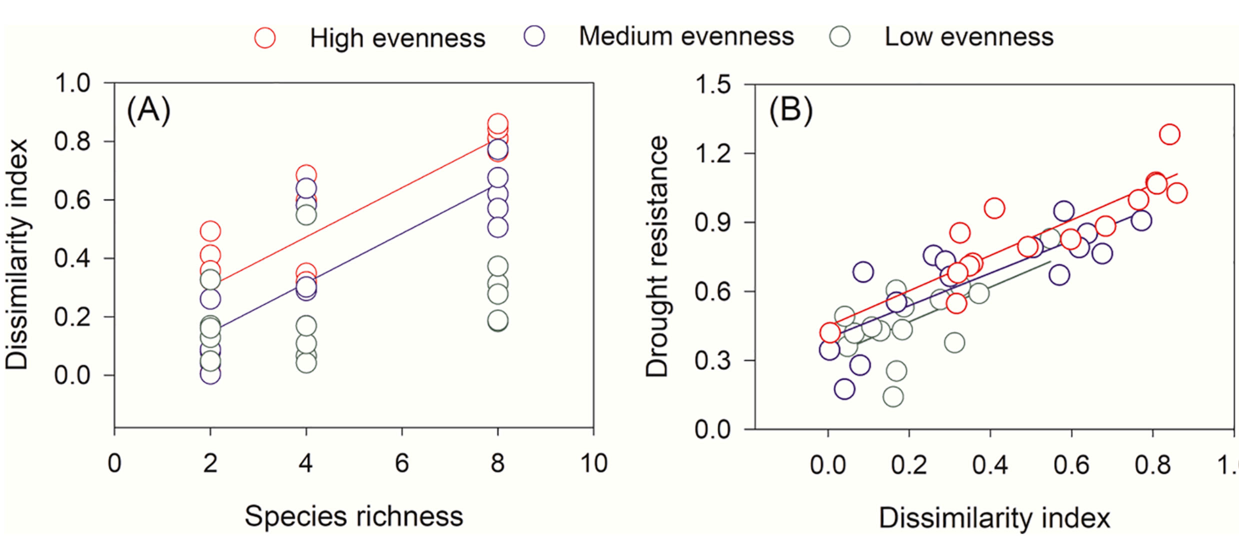


**Fig. 4.** Relationships of the dissimilarity index between communities with species richness (A) and the community drought resistance (B) at each evenness level. The red, blue and green lines indicate a significant relationship at high, medium and low evenness, respectively.

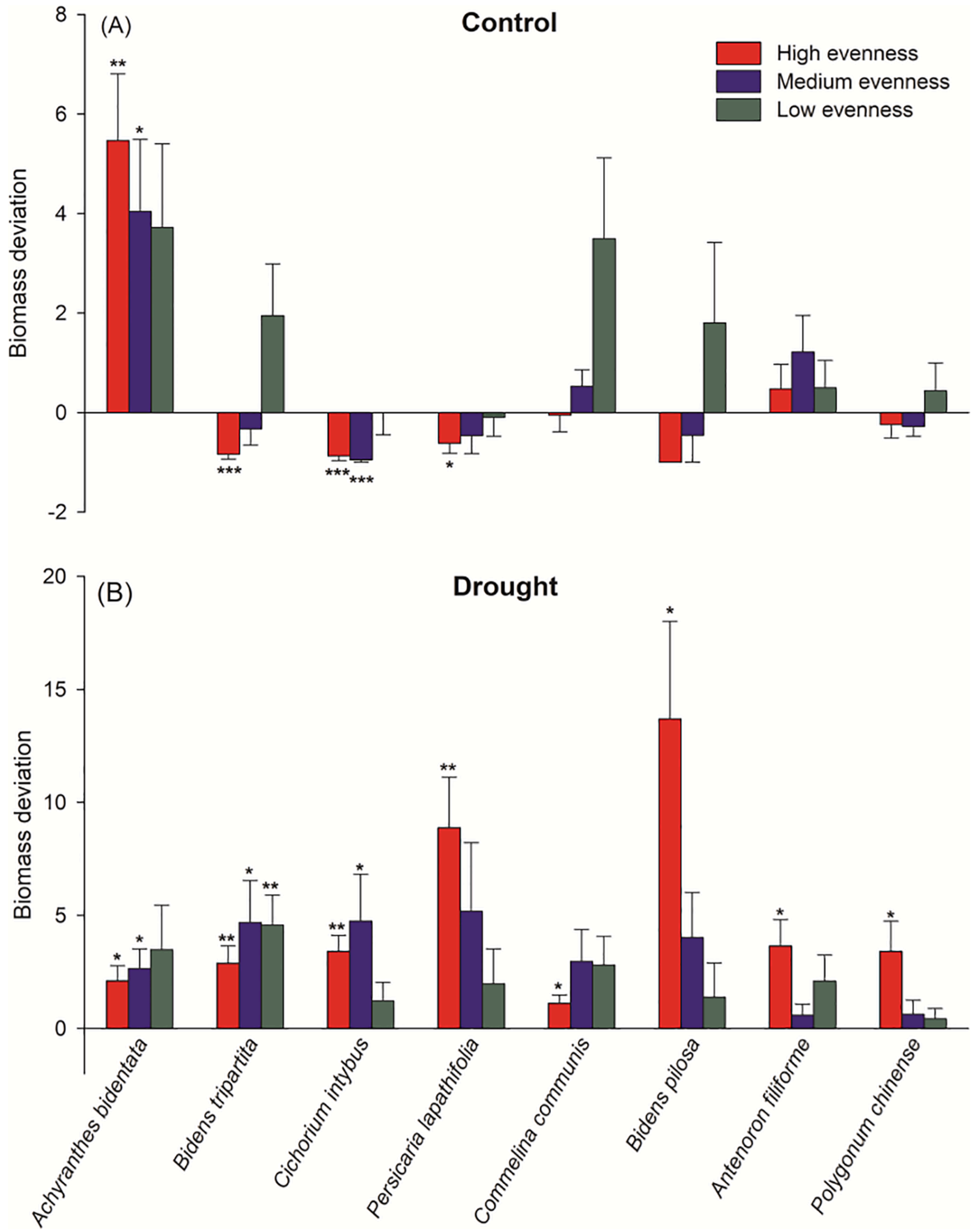


**Fig. 5.** Biomass deviation (ean + SE) of the eight species at each evenness level under the control (A) and the drought treatment (B). Symbols ($^{***}$ $P < 0.001$; $^{**}$ $P < 0.01$; * $P < 0.05$) indicate significant differences from zero (by one-sample t-tests).

prone, productive species. In our study, we found that the community drought resistance was positively related to complementarity effects (Fig. 2B), confirming that higher complementarity effects can result in higher ecosystem stability (Wang et al. 2021). This is likely because communities with more species and thus higher complementarity effects can provide higher insurance or stronger portfolio effects when the communities face perturbations (Yachi and Loreau, 1999; Thibaut et al., 2013; De Boeck et al., 2018).

Increasing species richness promoted the community drought resistance only at the two higher evenness levels but not at the low evenness level, indicating that evenness altered the richness effect on ecosystem stability. Increasing richness increased complementarity effects also only at the two higher evenness levels, suggesting that the influence of evenness on the richness effects was via its impact on complementarity effects. In the low-evenness communities, the difference in the relative abundance among species is great, so that complementarity effects among species played little role in the community drought resistance (Polley et al. 2003; Wang et al., 2015). Consequently, species richness had no impact on the drought resistance of the low-evenness communities.

Ecosystem stability reflects the outcomes of species interactions (Wang et al., 2021). In addition to differentiation in resource use, complementarity effects can also arise from positive species interactions (Hernandez and Picon-Cochard, 2016; Michalet et al., 2021). We observed that positive interactions among species also existed under the drought treatment (Fig. 5). Positive values of log(*OI*) indicate that the drought resistance of communities was higher than that of the highest resistant species in these communities, which may be ascribed to the increase in soil water utilization with species richness (Fig. A1, Verheyen et al., 2008; Hernandez and Picon-Cochard, 2016). However, the

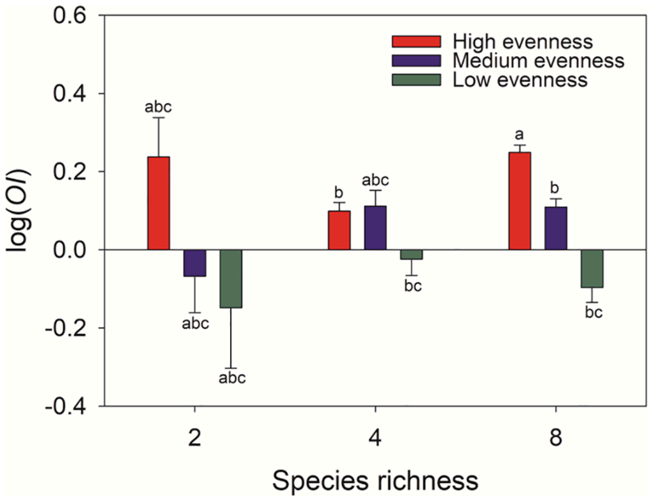


**Fig. 6.** Over-drought resistance index (*OI*) of communities (*Mean* + *SE*) with different levels of species richness and evenness. The different letters on the bars indicate significant differences ($P < 0.05$) between different evenness levels (by one-way ANOVA).

promotion effect of species richness on soil water utilization was restrained at the low evenness level (Fig. A1), which may be caused by restrained belowground interactions due to the presence of few roots for species with little abundance (Kahmen et al., 2005; Mariotte et al., 2013). Consequently, the higher-evenness mediated increase in the positive effect of species richness on the community drought resistance may be due to promotion of soil water utilization among species.

The positive effect of species richness on stability may also be ascribed to higher probability of having species with a higher resistance to perturbations (Wilsey et al., 2014; Isbell et al., 2015). In the control treatment, *A. bidentata* and *C. communis* had high biomass but low drought resistance (Fig. A2). Selection for such risk-prone species is predicted to impair the drought resistance of communities (Wang et al., 2021), but the mixtures with one of the two species had a higher resistance than those without them (Fig. A3). Although soil water content of mixtures decreased by the presence of one of the two species (Fig. A4), the reduction of soil water did not decrease the drought resistance of other six species, and even increased their drought resistance (Fig. A5). In the control treatment, the two species have great competitive advantage. However, the biomass of the two species is seriously limited due to drought. Although soil water content decreased in the mixtures, other six species may growth well for decrease of competitive pressure imposed by the two species. Consequently, how selection for the risk-prone species affects the community resistance may be also considered the responses of other species.

In this study, interspecific competition prevailed in the control treatment, while interspecific facilitation dominated in the drought treatment (Fig. 5). The shift from competition to facilitation with increasing drought led to the fact that complementarity effects played an important role in the drought resistance and increased with increasing species evenness (Polley et al., 2003; Kirwan et al., 2007; Isbell et al., 2009; Wang et al., 2015). However, if competition still prevails under drought, then selection effects may play a decisive role and is little affected by evenness (Polley et al., 2003; Emery and Gross, 2007). Therefore, future studies testing the effect of species evenness on the richness-stability relationship should consider the response of interspecific interactions to disturbance.

We conclude that species evenness can alter the relationships between species richness and the resistance of communities to disturbance (e.g. drought) by changing complementarity effects among species. Thus, in addition to species richness, evenness should also be considered an important indicator of the community resistance to future global changes, such as increased drought intensity and frequency (Gómez-Gener et al., 2020). We propose that, to facilitate vegetation recovery in frequently disturbed, degraded land, both species evenness and richness can be considered as efficient measures to increase the ability of communities to resist disturbance during restoration.

## CRediT authorship contribution statement

**Xiao-Yan Wang:** Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Funding acquisition. **Yuan Ge:** Conceptualization, Methodology, Investigation, Writing – original draft, Writing – review & editing, Funding acquisition. **Song Gao:** Methodology, Investigation, Writing – review & editing. **Tong Chen:** Methodology, Investigation, Writing – review & editing. **Jiang Wang:** Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Supervision, Funding acquisition. **Fei-Hai Yu:** Formal analysis, Writing – original draft, Writing – review & editing.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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*Data availability statement.*

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

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.108464.

## References

Bardgett, R.D., van der Putten, W.H., 2014. Belowground biodiversity and ecosystem functioning. Nature 515 (7528), 505–511. https://doi.org/10.1038/nature13855.

Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27 (4), 325–349. https://doi.org/10.2307/1942268.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486 (7401), 59–67. https://doi.org/10.1038/nature11148.

Craven, D., Isbell, F., Manning, P., Connolly, J., Bruelheide, H., Ebeling, A., Roscher, C., van Ruijven, J., Weigelt, A., Wilsey, B., Beierkuhnlein, C., de Luca, E., Griffin, J.N., Hautier, Y., Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Loreau, M., Meyer, S.T., Mori, A.S., Naeem, S., Palmborg, C., Polley, H.W., Reich, P.B., Schmid, B., Siebenkäs, A., Seabloom, E., Thakur, M.P., Tilman, D., Vogel, A., Eisenhauer, N., 2016. Plant diversity effects on grassland productivity are robust to both nutrient enrichment and drought. Philos. Trans. R. Soc. Lond., B, Biol. Sci. 371, 20150277. https://doi.org/10.1098/rstb.2015.0277.

Creed, R.P., Cherry, R.P., Pflaum, J.R., Wood, C.J., 2009. Dominant species can produce a negative relationship between species diversity and ecosystem function. Oikos 118 (5), 723–732. https://doi.org/10.1111/j.1600-0706.2008.17212.x.

De Boeck, H.J., Lemmens, C.M.H.M., Bossuyt, H., Malchair, S., Carnol, M., Merckx, R., Nijs, I., Ceulemans, R., 2006. How do climate warming and plant species richness affect water use in experimental grasslands? Plant Soil 288 (1-2), 249–261. https://doi.org/10.1007/s11104-006-9112-5.

De Boeck, H.J., Lemmens, C.M.H.M., Zavalloni, C., Gielen, B., Malchair, S., Carnol, M., Merckx, R., Van den Berge, J., Ceulemans, R., Nijs, I., 2008. Biomass production in experimental grasslands of different species richness during three years of climate warming. Biogeosciences 5, 585–594. https://doi.org/10.5194/bg-5-585-2008.

De Boeck, H.J., Bloor, J.M.G., Kreyling, J., Ransijn, J.C.G., Nijs, I., Jentsch, A., Zeiter, M., Wardle, D., 2018. Patterns and drivers of biodiversity–stability relationships under climate extremes. J. Ecol. 106 (3), 890–902. https://doi.org/10.1111/1365-2745.12897.

de Mazancourt, C., Isbell, F., Larocque, A., Berendse, F., De Luca, E., Grace, J.B., Haegeman, B., Wayne Polley, H., Roscher, C., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B.J., Loreau, M., Hooper, D., 2013. Predicting ecosystem stability from community composition and biodiversity. Ecol. Lett. 16 (5), 617–625. https://doi.org/10.1111/ele.12088.

Dinerstein, E., Joshi, A.R., Vynne, C., Lee, A.T.L., Pharand-Deschenes, F., Franca, M., Fernando, S., Birch, T., Burkart, K., Asner, G.P., Olson, D., 2020. A "Global Safety Net" to reverse biodiversity loss and stabilize Earth's climate. Sci. Adv. 6, eabb2824. https://doi.org/10.1126/sciadv.abb2824.

Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E., Thomson, D., 1998. The statistical inevitability of stability-diversity relationships in community ecology. Am. Nat. 151 (3), 264–276. https://doi.org/10.1086/286117.

Emery, S.M., Gross, K.L., 2007. Dominant species identity, not community evenness, regulates invasion in experimental grassland plant communities. Ecology 88 (4), 954–964. https://doi.org/10.1890/06-0568.

Fitter, A.H., Gilligan, C.A., Hollingworth, K., Kleczkowski, A., Twyman, R.M., Pitchford, J.W., 2005. Biodiversity and ecosystem function in soil. Funct. Ecol. 19 (3), 369–377. https://doi.org/10.1111/fec.2005.19.issue-310.1111/j.0269-8463.2005.00969.x.

Fox, J.W., 2005. Interpreting the 'selection effect' of biodiversity on ecosystem function. Ecol. Lett. 8, 846–856. https://doi.org/10.1111/j.1461-0248.2005.00795.x.

Gómez-Gener, L., Lupon, A., Laudon, H., Sponseller, R.A., 2020. Drought alters the biogeochemistry of boreal stream networks. Nat. Commun. 11, 1795. https://doi.org/10.1038/s41467-020-15496-2.

Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J. Ecol. 86 (6), 902–910. https://doi.org/10.1046/j.1365-2745.1998.00306.x.

Hector, A., 2002. Biodiversity and the functioning of grassland ecosystems: multi-site comparisons. In: Kinzig, A.P., Pacala, S., Tillman, D. (Eds.), The functional consequences of biodiversity. Princeton University Press, Princeton, N.J., pp. 71–95

Hernandez, P., Picon-Cochard, C., 2016. Presence of *Trifolium repens* promotes complementarity of water use and N facilitation in diverse grass mixtures. Front. Plant Sci. 7, 14. https://doi.org/10.3389/fpls.2016.00538.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr. 75 (1), 3–35. https://doi.org/10.1890/04-0922.

Isbell, F.I., Polley, H.W., Wilsey, B.J., 2009. Biodiversity, productivity and the temporal stability of productivity: patterns and processes. Ecol. Lett. 12, 443–451. https://doi.org/10.1111/j.1461-0248.2009.01299.x.

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T. M., Bonin, C., Bruelheide, H., de Luca, E., Ebeling, A., Griffin, J.N., Guo, Q., Hautier, Y., Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Manning, P., Meyer, S.T., Mori, A.S., Naeem, S., Niklaus, P.A., Polley, H.W., Reich, P.B., Roscher, C., Seabloom, E.W., Smith, M.D., Thakur, M.P., Tilman, D., Tracy, B.F., van der Putten, W.H., van Ruijven, J., Weigelt, A., Weisser, W.W., Wilsey, B., Eisenhauer, N., 2015. Biodiversity increases the resistance of ecosystem productivity to climate extremes. Nature 526 (7574), 574–577. https://doi.org/10.1038/nature15374.

Kahmen, A., Perner, J., Buchmann, N., 2005. Diversity-dependent productivity in semi-natural grasslands following climate perturbations. Funct. Ecol. 19 (4), 594–601. https://doi.org/10.1111/fec.2005.19.issue-410.1111/j.1365-2435.2005.01001.x.

Kennedy, T.A., Naeem, S., Howe, K.M., Knops, J.M.H., Tilman, D., Reich, P., 2002. Biodiversity as a barrier to ecological invasion. Nature 417 (6889), 636–638. https://doi.org/10.1038/nature00776.

Kirwan, L., Lüscher, A., Sebastià, M.T., Finn, J.A., Collins, R.P., Porqueddu, C., Helgadottir, A., Baadshaug, O.H., Brophy, C., Coran, C., Dalmannsdóttir, S., DELGADO, I., Elgersma, A., Fothergill, M., Frankow-Lindberg, B.E., Golinski, P., Grieu, P., Gustavsson, A.M., Höglind, M., Huguenin-elie, O., Iliadis, C., Jørgensen, M., Kadziuliene, Z., Karyotis, T., Lunnan, T., Malengier, M., Maltoni, S., Meyer, V., Nyfeler, D., Nykanen-Kurki, P., Parente, J., SMIT, H.J., Thumm, U., Connolly, J., 2007. Evenness drives consistent diversity effects in intensive grassland systems across 28 European sites. J. Ecol. 95 (3), 530–539. https://doi.org/10.1111/j.1365-2745.2007.01225.x.

Kreyling, J., Dengler, J., Walter, J., Velev, N., Ugurlu, E., Sopotlieva, D., Ransijn, J., Picon-Cochard, C., Nijs, I., Hernandez, P., Güler, B., von Gillhaussen, P., De Boeck, H.J., Bloor, J.M.G., Berwaers, S., Beierkuhnlein, C., Arfin Khan, M.A.S., Apostolova, I., Altan, Y., Zeiter, M., Wellstein, C., Sternberg, M., Stampfli, A., Campetella, G., Bartha, S., Bahn, M., Jentsch, A., Penuelas, J., 2017. Species richness effects on grassland recovery from drought depend on community productivity in a multisite experiment. Ecol. Lett. 20 (11), 1405–1413. https://doi.org/10.1111/ele.12848.

Kunert, N., Cárdenas, A.M., 2015. Are mixed tropical tree plantations more resistant to drought than monocultures? Forests 6, 2029–2046. https://doi.org/10.3390/f6062029.

Lembrechts, J.J., De Boeck, H.J., Liao, J., Milbau, A., Nijs, I., 2018. Effects of species evenness can be derived from species richness-ecosystem functioning relationships. Oikos 127 (3), 337–344. https://doi.org/10.1111/oik.04786.

Lhomme, J.-P., Winkel, T., 2002. Diversity–stability relationships in community ecology: re-examination of the portfolio effect. Theor. Popul. Biol. 62 (3), 271–279. https://doi.org/10.1006/tpbi.2002.1612.

Loreau, M., de Mazancourt, C., Duffy, E., 2013. Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. Ecol. Lett. 16, 106–115. https://doi.org/10.1111/ele.2013.16.issue-s110.1111/ele.12073.

Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412 (6842), 72–76. https://doi.org/10.1038/35083573.

Lübbe, T., Schuldt, B., Coners, H., Leuschner, C., 2016. Species diversity and identity effects on the water consumption of tree sapling assemblages under ample and limited water supply. Oikos 125 (1), 86–97. https://doi.org/10.1111/oik.02367.

Maestre, F.T., Castillo-Monroy, A.P., Bowker, M.A., Ochoa-Hueso, R., 2012a. Species richness effects on ecosystem multifunctionality depend on evenness, composition and spatial pattern. J. Ecol. 100, 317–330. https://doi.org/10.1111/j.1365-2745.2011.01918.x.

Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., García-Gómez, M., Bowker, M.A., Soliveres, S., Escolar, C., García-Palacios, P., Berdugo, M., Valencia, E., Gozalo, B., Gallardo, A., Aguilera, L., Arredondo, T., Blones, J., Boeken, B., Bran, D., Conceição, A.A., Cabrera, O., Chaieb, M., Derak, M., Eldridge, D.J., Espinosa, C.I., Florentino, A., Gaitán, J., Gatica, M.G., Ghiloufi, W., Gómez-González, S., Gutiérrez, J.R., Hernández, R.M., Huang, X., Huber-Sannwald, E., Jankju, M., Miriti, M., Monerris, J., Mau, R.L., Morici, E., Naseri, K., Ospina, A., Polo, V., Prina, A., Pucheta, E., Ramírez-Collantes, D.A., Romão, R., Tighe, M., Torres-Díaz, C., Val, J., Veiga, J.P., Wang, D., Zaady, E., 2012b. Plant species richness and ecosystem multifunctionality in global drylands. Science 335 (6065), 214–218. https://doi.org/10.1126/science:1215442.

Mariotte, P., Vandenberghe, C., Kardol, P., Hagedorn, F., Buttler, A., Schwinning, S., 2013. Subordinate plant species enhance community resistance against drought in semi-natural grasslands. J. Ecol. 101 (3), 763–773. https://doi.org/10.1111/jec.2013.101.issue-310.1111/1365-2745.12064.

Mattingly, W.B., Hewlate, R., Reynolds, H.L., 2007. Species evenness and invasion resistance of experimental grassland communities. Oikos 116, 1164–1170. https://doi.org/10.1111/j.0030-1299.2007.15406.x.

Maureaud, A., Hodapp, D., van Denderen, P.D., Hillebrand, H., Gislason, H., Spaanheden Dencker, T., Beukhof, E., Lindegren, M., 2019. Biodiversity-ecosystem functioning relationships in fish communities: biomass is related to evenness and the environment, not to species richness. Proc. R Soc. B 286 (1906), 20191189. https://doi.org/10.1098/rspb.2019.1189.

Michalet, R., Delerue, F., Liancourt, P., Pugnaire, F.I., Callaway, R., 2021. Are complementarity effects of species richness on productivity the strongest in species-rich communities? J. Ecol. 109 (5), 2038–2046. https://doi.org/10.1111/jec.v109.510.1111/1365-2745.13658.

Montès, N., Maestre, F.T., Ballini, C., Baldy, V., Gauquelin, T., Planquette, M., Greff, S., Dupouyet, S., Perret, J.-B., 2008. On the relative importance of the effects of selection and complementarity as drivers of diversity–productivity relationships in Mediterranean shrublands. Oikos 117 (9), 1345–1350. https://doi.org/10.1111/j.0030-1299.2008.16910.x.

Naeem, S., Li, S., 1997. Biodiversity enhances ecosystem reliability. Nature 390 (6659), 507–509. https://doi.org/10.1038/37348.

Ouyang, S., Xiang, W., Gou, M., Chen, L., Lei, P., Xiao, W., Deng, X., Zeng, L., Li, J., Zhang, T., Peng, C., Forrester, D.I., Meyer, C., 2021. Stability in subtropical forests: The role of tree species diversity, stand structure, environmental and socio-economic conditions. Glob. Ecol. Biogeogr. 30 (2), 500–513. https://doi.org/10.1111/geb.v30.210.1111/geb.13235.

Pennekamp, F., Pontarp, M., Tabi, A., Altermatt, F., Alther, R., Choffat, Y., Fronhofer, E. A., Ganesanandamoorthy, P., Garnier, A., Griffiths, J.I., Greene, S., Horgan, K., Massie, T.M., Mächler, E., Palamara, G.M., Seymour, M., Petchey, O.L., 2018. Biodiversity increases and decreases ecosystem stability. Nature 563 (7729), 109–112. https://doi.org/10.1038/s41586-018-0627-8.

Peters, M.K., Hemp, A., Appelhans, T., Becker, J.N., Behler, C., Classen, A., Detsch, F., Ensslin, A., Ferger, S.W., Frederiksen, S.B., Gebert, F., Gerschlauer, F., Gütlein, A., Helbig-Bonitz, M., Hemp, C., Kindeketa, W.J., Kühnel, A., Mayr, A.V., Mwangomo, E., Ngereza, C., Njovu, H.K., Otte, I., Pabst, H., Renner, M., Röder, J., Rutten, G., Schellenberger Costa, D., Sierra-Cornejo, N., Vollstädt, M.G.R., Dulle, H. I., Eardley, C.D., Howell, K.M., Keller, A., Peters, R.S., Ssymank, A., Kakengi, V., Zhang, J., Bogner, C., Böhning-Gaese, K., Brandl, R., Hertel, D., Huwe, B., Kiese, R., Kleyer, M., Kuzyakov, Y., Nauss, T., Schleuning, M., Tschapka, M., Fischer, M., Steffan-Dewenter, I., 2019. Climate-land-use interactions shape tropical mountain biodiversity and ecosystem functions. Nature 568 (7750), 88–92. https://doi.org/10.1038/s41586-019-1048-z.

Petruzzella, A., Manschot, J., van Leeuwen, C.H.A., Grutters, B.M.C., Bakker, E.S., 2018. Mechanisms of invasion resistance of aquatic plant communities. Front. Plant Sci. 9, 134. https://doi.org/10.3389/fpls.2018.00134.

Pfisterer, A.B., Schmid, B., 2002. Diversity-dependent production can decrease the stability of ecosystem functioning. Nature 416 (6876), 84–86. https://doi.org/10.1038/416084a.

Polley, H.W., Wilsey, B.J., Derner, J.D., 2003. Do species evenness and plant density influence the magnitude of selection and complementarity effects in annual plant species mixtures? Ecol. Lett. 6 (3), 248–256. https://doi.org/10.1046/j.1461-0248.2003.00422.x.

Reynolds, J.F., Smith, D.M.S., Lambin, E.F., Turner, B.L., Mortimore, M., Batterbury, S.P. J., Downing, T.E., Dowlatabadi, H., Fernández, R.J., Herrick, J.E., Huber-Sannwald, E., Jiang, H., Leemans, R., Lynam, T., Maestre, F.T., Ayarza, M., Walker, B., 2007. Global desertification: building a science for dryland development. Science 316 (5826), 847–851. https://doi.org/10.1126/science:1131634.

Ribas, A., Llurba, R., Gouriveau, F., Altimir, N., Connolly, J., Sebastià, M.T., 2015. Plant identity and evenness affect yield and trace gas exchanges in forage mixtures. Plant Soil 391 (1-2), 93–108. https://doi.org/10.1007/s11104-015-2407-7.

Rodriguez-Ramirez, N., Santonja, M., Baldy, V., Ballini, C., Montès, N., Michalet, R., 2017. Shrub species richness decreases negative impacts of drought in a Mediterranean ecosystem. J. Veg. Sci. 28 (5), 985–996. https://doi.org/10.1111/jvs.12558.

Sala, O.E., Stuart Chapin, F., III, Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H.A., Oesterheld, Martín, Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science 287 (5459), 1770–1774. https://doi.org/10.1126/science:287.5459.1770.

Semper-Pascual, A., Decarre, J., Baumann, M., Busso, J.M., Camino, M., Gómez-Valencia, B., Kuemmerle, T., 2019. Biodiversity loss in deforestation frontiers: Linking occupancy modelling and physiological stress indicators to understand local extinctions. Biol. Conserv. 236, 281–288. https://doi.org/10.1016/j.biocon.2019.05.050.

Stirling, G., Wilsey, B., 2001. Empirical relationships between species richness, evenness and proportional diversity. Am. Nat. 158 (3), 286–299. https://doi.org/10.1086/321317.

Thibaut, L.M., Connolly, S.R., He, F., 2013. Understanding diversity–stability relationships: towards a unified model of portfolio effects. Ecol. Lett. 16 (2), 140–150. https://doi.org/10.1111/ele.2012.16.issue-210.1111/ele.12019.

Tilman, D., 1996. Biodiversity: population versus ecosystem stability. Ecology 77, 350–363. https://doi.org/10.2307/2265614.

Tilman, D., Isbell, F., Cowles, J.M., 2014. Biodiversity and ecosystem functioning. In: Futuyma, D.J. (Ed.), Annu Rev Ecol Evol Syst. Palo Alto, Annual Reviews, pp. 471–493.

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T., Lehman, C., 2001. Diversity and productivity in a long-term grassland experiment. Science 294 (5543), 843–845. https://doi.org/10.1126/science:1060391.

Tilman, D., Reich, P.B., Knops, J.M.H., 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441 (7093), 629–632. https://doi.org/10.1038/nature04742.

Valencia, E., de Bello, F., Galland, T., Adler, P.B., Lepš, J., E-Vojtkó, A., van Klink, R., Carmona, C.P., Danihelka, J., Dengler, J., Eldridge, D.J., Estiarte, M., García-González, R., Garnier, E., Gómez-García, D., Harrison, S.P., Herben, T., Ibáñez, R., Jentsch, A., Juergens, N., Kertész, M., Klumpp, K., Louault, F., Marrs, R.H., Ogaya, R., Ónodi, G., Pakeman, R.J., Pardo, I., Pärtel, M., Peco, B., Peñuelas, J., Pywell, R.F., Rueda, M., Schmidt, W., Schmiedel, U., Schuetz, M., Skálová, H., Šmilauer, P., Šmilauerová, M., Smit, C., Song, MingHua, Stock, M., Val, J., Vandvik, V., Ward, D., Wesche, K., Wiser, S.K., Woodcock, B.A., Young, T.P., Yu, F.-H., Zobel, M., Götzenberger, L., 2020. Synchrony matters more than species richness in plant community stability at a global scale. Proc. Natl. Acad. Sci. U.S.A. 117 (39), 24345–24351. https://doi.org/10.1073/pnas.1920405117.

van Ruijven, J., Berendse, F., 2010. Diversity enhances community recovery, but not resistance, after drought. J. Ecol. 98, 81–86. https://doi.org/10.1111/j.1365-2745.2009.01603.x.

Verheyen, K., Bulteel, H., Palmborg, C., Olivié, B., Nijs, I., Raes, D., Muys, B., 2008. Can complementarity in water use help to explain diversity–productivity relationships in experimental grassland plots? Oecologia 156 (2), 351–361. https://doi.org/10.1007/s00442-008-0998-x.

Vogel, A., Scherer-Lorenzen, M., Weigelt, A., Moen, J., 2012. Grassland resistance and resilience after drought depends on management intensity and species richness. PLoS One 7 (5), e36992. https://doi.org/10.1371/journal.pone.0036992.

Wang, J., Wang, X.Y., Zhang, C.B., Liu, W.L., 2015. Initial community evenness increases the light resource use complementarity and sampling effects on species richness. Basic Appl. Ecol. 16 (4), 300–307. https://doi.org/10.1016/j.baae.2015.03.002.

Wang, S., Isbell, F., Deng, W., Hong, P., Dee, L.E., Thompson, P., Loreau, M., 2021. How complementarity and selection affect the relationship between ecosystem functioning and stability. Ecology 102 (6). https://doi.org/10.1002/ecy.v102.610.1002/ecy.3347.

Wang, Y., Yu, S., Wang, J., 2007. Biomass-dependent susceptibility to drought in experimental grassland communities. Ecol. Lett. 10 (5), 401–410. https://doi.org/10.1111/j.1461-0248.2007.01031.x.

Wilsey, B.J., Chalcraft, D.R., Bowles, C.M., Willig, M.R., 2005. Relationships among indices suggests that richness is an incomplete surrogate for grassland biodiversity. Ecology 86, 1178–1184. https://doi.org/10.1890/04-0394.

Wilsey, B.J., Potvin, C., 2000. Biodiversity and ecosystem functioning: importance of species evenness in an old field. Ecology 81, 887–892. https://doi.org/10.1890/0012-9658(2000)081[0887:BAEFIO]2.0.CO;2.

Wilsey, B.J., Daneshgar, P.P., Hofmockel, K., Polley, H.W., Cleland, E., 2014. Invaded grassland communities have altered stability-maintenance mechanisms but equal stability compared to native communities. Ecol. Lett. 17 (1), 92–100. https://doi.org/10.1111/ele.2013.17.issue-110.1111/ele.12213.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B. C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., Watson, R., 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314 (5800), 787–790. https://doi.org/10.1126/science:1132294.

Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. Proc. Natl. Acad. Sci. U.S.A. 96 (4), 1463–1468. https://doi.org/10.1073/pnas.96.4.1463.

Zhang, Q., Liu, Y.-P., Luo, F.-L., Dong, B.-C., Yu, F.-H., 2019. Does species richness affect the growth and water quality of submerged macrophyte assemblages? Aquat. Bot. 153, 51–57. https://doi.org/10.1016/j.aquabot.2018.11.006.

Zhang, X., Yan, X., 2014. Temporal change of climate zones in China in the context of climate warming. Theor. Appl. Climatol. 115 (1-2), 167–175. https://doi.org/10.1007/s00704-013-0887-z.

Zhang, Q.-G., Zhang, D.-Y., 2006. Species richness destabilizes ecosystem functioning in experimental aquatic microcosms. Oikos 112, 218–226. https://doi.org/10.1111/j.0030-1299.2006.14220.x.