

## RESEARCH ARTICLE



# Precipitation reduction alters herbaceous community structure and composition in a savanna

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## Abstract

**Questions:** In the changing climate scenario, the decline in precipitation is expected to alter water availability for plants, which in turn affects plant community structure and composition. The responses of community composition and structure to declines in precipitation are well documented in other biomes but remain understudied in water-limited savannas.

**Location:** A savanna ecosystem in southwest China.

**Methods:** We used a four-year (2014–2017) precipitation manipulation experiment to examine changes in herbaceous community composition and structure across the species, functional group and community levels under precipitation reduction.

**Results:** Precipitation reduction significantly decreased the average height and percentage cover of the herbaceous community, while increasing species richness and the Pielou evenness index. Precipitation reduction significantly decreased average height, percentage cover and relative abundance of graminoids and perennials, but increased those of forbs and annuals. Precipitation reduction prompted a shift in the dominant species of the herbaceous community towards *Fimbristylis monostachya*.

**Conclusions:** The results show that precipitation reduction changed the composition and structure of the herbaceous community of this savanna. Furthermore, they provide strong evidence that changes in herbaceous community structure and composition in response to the intensity and duration of precipitation reduction in this savanna exhibited relatively low thresholds, which suggests that the herbaceous community's response to a decline in precipitation was essentially nonlinear. These findings imply that even relatively small declines in precipitation may stimulate shifts in plant community structure and composition and affect the function and stability of savanna ecosystems.

## KEYWORDS

community dynamics, drought stress, nonlinear response, plant functional groups, species diversity

## 1 | INTRODUCTION

Water is an essential resource for plant growth, survival and distribution worldwide (Scheffers et al., 2016). The availability of water will change in the coming decades because of shifting precipitation patterns worldwide (IPCC 2013). Any increase in precipitation variability will impact plant community dynamics through altered mortality, recruitment, and structure (Canham & Murphy, 2016; Felton & Smith, 2017). These effects could be buffered by various regulatory mechanisms at the species, population, and community levels (Elst et al., 2017; Niu et al., 2014). However, the direction of change in community dynamics across biomes in response to declines in precipitation is quite complex (Cleland et al., 2013; Felton & Smith, 2017; Smith, Wilcox, Power, Tissue, & Knapp, 2017). Previous studies have found large (Anderson, 2008; Copeland et al., 2016; Martínez-Vilalta & Lloret, 2016; Nogueira, Bugalho, Pereira, & Caldeira, 2017) or small (Tredennick, Kleinhesselink, Taylor, & Adler, 2018) effects of declines in precipitation on community dynamics, depending strongly on the vegetation type and the magnitude of precipitation change. Changes in community dynamics triggered by declines in precipitation are expected to affect ecosystem function and stability. Better understanding of the responses of community dynamics to decreasing precipitation is crucial, and will aid in predicting changes in ecosystem functions associated with future climate change.

The processes underlying shifts in composition of plant functional groups are often used to explain the responses of community dynamics to environmental stress and to evaluate the changes in ecosystem function (Fry et al., 2013; Hooper & Vitousek, 1997). However, different plant functional groups may exhibit dissimilar responses to changing precipitation patterns, based on their differing levels of sensitivity (Wilcox et al., 2017; Zhang et al., 2017). For example, if the dominant species or groups allocate their resources to maintaining superiority under declines in precipitation rather than defending against the disturbance, they may be more vulnerable (Gherardi & Sala, 2015; Smith & Knapp, 2003). This weakened dominance by previously dominant species under declines in precipitation may trigger a degradation of ecosystem function (Sasaki & Lauenroth, 2011). Conversely, subdominant or rare species may increase in abundance and thus mitigate the effects and stabilize ecosystem function (Kardol et al., 2010; Mariotte, Vandenbergh, Kardol, Hagedorn, & Buttler, 2013). However, intensified inter- and intra-specific competition and potential interactions with other factors (e.g., canopy and N limitation) under declines in precipitation may indirectly affect changes in the composition of plant functional groups (Gleason et al., 2017; Rysavy, Seifan, Sternberg, & Tielbörger, 2016; Yu, Saha, & D'Odorico, 2017), leading to large uncertainties in our understanding of shifts in community composition and structure in response to declines in precipitation. The responses of different plant functional groups in a specific community to declines in precipitation may be temporally nonlinear due to the cumulative effects and diverse levels of sensitivity (Chapman, Tunnicliffe, & Bates, 2018; Dudley et al., 2017). Thus,

a more complete understanding of the processes underlying shifts in composition of plant functional groups under declines in precipitation is needed and may help to explain the underlying mechanisms of species coexistence and community dynamics in response to declines in precipitation (Elst et al., 2017).

Savannas, which cover approximately 20% of the global land surface (Grace, San José, Meir, Miranda, & Montes, 2006), are particularly sensitive to changes in precipitation (Berry & Kulmatiski, 2017; Fensham, Fairfax, & Ward, 2009; Strickland, Liedloff, Cook, Dangelmayr, & Shipman, 2016). Most studies on community dynamics under declines in precipitation have been conducted in grasslands, shrublands, tundra and forests (Beier et al., 2012; Hoover, Wilcox, & Young, 2018), but few in savanna regions. As a vital component of savanna ecosystems, the understorey herbaceous species play a central role in determining the ecosystem stability and functions such as diversity maintenance and nutrient cycling (Ratnam, Tomlinson, Rasquinha, & Sankaran, 2016). Understorey herbaceous species are more sensitive to alterations in precipitation than overstorey woody plants (Stuart-Haëntjens et al., 2018). Declines in precipitation may therefore cause large changes in species composition and community structure in water-limited ecosystems, especially among herbaceous communities (Copeland et al., 2016; Prevéy & Seastedt, 2014). Although some studies have examined species composition under declines in precipitation in savanna ecosystems (Fay, Carlisle, Knapp, Blair, & Collins, 2003; O'Connor, 1994; Pandey & Singh, 1992; Weltzin & McPherson, 2000), these studies either did not treat the effects of precipitation on community dynamics as a main focus or only involved the overstorey woody species dynamics. The current evidence base is insufficient to understand the changes in herbaceous community dynamics in savannas with decreasing precipitation. Therefore, it has become critical to advance our understanding of the impact of declines in precipitation on the herbaceous community composition and structure to help explain changes in the global distribution of savannas and predict their responses to future declines in precipitation.

In order to disentangle the effects of declines in precipitation on plant community structure and composition of savannas, a precipitation manipulation experiment was conducted. Precipitation reduction significantly decreased the growth of woody species in this savanna ecosystem, but the community composition of the overstorey remained unchanged (Jin, Li, Liu, Liu, Zhang, Sha, et al., 2018a). We know little about the impact of precipitation reduction on the community dynamics of the understorey herbaceous layer, so a four-year study was performed to explore the response of the herbaceous community to declines in precipitation. The following research questions were addressed: (a) How do declines in precipitation affect community structure and composition of the herbaceous community in savannas; (b) do the different functional groups have similar responses to declines in precipitation? and (c) do different species (e.g., dominant species and subordinate species) respond differently to declines in precipitation?



## 2 | MATERIALS AND METHODS

### 2.1 | Study site

This experiment was conducted at the Yuanjiang Savanna Ecosystem Research Station (YSERS; 23°27' N, 102°10' E, 551 m a.s.l.) of the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, located in Yuanjiang county, Yunnan Province, China. The local climate is dry and hot, with a long-term mean annual temperature of 24.0°C, and mean annual precipitation of 786.6 mm (over the last 36 years), approximately 81.0% of which occurs during the rainy season (May to October). During the study period, mean annual temperature at the weather station of YSERS was 25.0, 25.1, 24.4 and 25.2°C in 2014, 2015, 2016 and 2017, respectively, and total annual precipitation from 2014 to 2017 was 662.1, 798.2, 754.9 and 839.3 mm, respectively (Appendix S1). The soil is shallow (~35 cm in depth) and consists of approximately 65% gravel. It is classified as a Ferralic Cambisol based on the classification system of the Food and Agriculture Organization of the United Nations (IUSS Working Group WRB, 2015). Yuanjiang savanna (canopy height ~6 m) is considered to be most typical and representative of China (Editorial Committee for Vegetation of Yunnan, 1987). The tree layer is dominated by *Lannea coromandelica* and *Polyalthia cerasoides*, the shrub layer by *Campylotropis delavayi*, and the herbaceous layer by *Heteropogon contortus*.

### 2.2 | Experimental design

We conducted a four-year (2014–2017) precipitation manipulation experiment in a reasonably uniform area of savanna vegetation. A randomized block design with three replicate blocks was adopted; each block contained four randomly distributed treatment plots: ambient control, 30% precipitation reduction, 50% precipitation reduction and 70% precipitation reduction, totaling 12 experimental plots. Precipitation reduction experimental plots were set up using rainout shelters, which were described in more detail in Jin, Li, Liu, Zhang, Sha, et al. (2018a). The rainout shelters were constructed with a steel frame (7 m in height) and covered with transparent 1.2-mm polyethylene sheets (permitting over 85% penetration of photosynthetically active radiation) to reduce the net input of precipitation to the soil. The polyethylene sheets were hung at an angle above the tree canopy to assist intercepted rain to drain away. Precipitation reduction experimental plots had perimeters of 10 m × 10 m and were separated by 1-m walkways. The various precipitation reduction treatments were established by adjusting the number of polyethylene sheets (1 × 3.5 m in size) and the distance between adjacent sheets to change the covered area of each plot. Intercepted rain was drained by PVC pipes (20 cm in diameter) installed in the lower edges of the roof. The outer edge of the whole precipitation manipulation experimental site was fenced for the entire study period to prevent the entry of vertebrate herbivores.

Soil moisture (v/v, %) and soil temperature at 10 cm depth in the central area of each experimental plot were continuously monitored using a frequency domain reflectometer (CS616, Campbell

Scientific, Logan, UT, USA) and recorded in a datalogger (CR800, Campbell Scientific) every 30 min, from 2014 to 2017. These data demonstrated that the rainout shelters effectively lowered soil moisture, and a detailed report on differences in soil moisture and temperature among the different treatments over the study period is given in Appendix S1.

### 2.3 | Biotic data

Three 1 m × 1 m herbaceous quadrats were randomly placed in the interior (9 m × 9 m) of each experimental plot to limit edge effects. Biotic data were collected once a year (2014–2017) in late October, when the most of grass species in this region could be reliably identified and reached their maximum growth (Jin, Li, Liu, Liu, Zhang, Song, et al., 2018). For all herbaceous species, we recorded the name, abundance (number of rooted individuals), height (cm; determined by mean value of natural height from three to five individuals) and percentage cover (%). In order to improve accuracy, a grid method with 16 cells was used to estimate the percentage cover of each species. Moreover, in consideration of the effects of the overstorey (trees and shrubs) on the dynamics of understorey plants (Halpern & Lutz, 2013), overstorey coverage was carefully estimated for each quadrant based on the method outlined by Strong (2011).

To examine different functional groups' responses to precipitation reduction, we assigned species to one of three functional groups defined by their different growth forms: graminoids, forbs, and legumes. We also divided all herbaceous plants into two functional groups (annuals and perennials) on the basis of their life forms (Appendix S2). The percentage cover of a species was summed as the percentage cover for each functional group. The average height of functional groups was calculated by the mean value of all species' height within the specific plant functional groups. The relative abundance of each species was expressed as the abundance divided by the total abundance of all species. Relative abundances of functional groups were computed by summing the relative abundances of all species of each functional group.

Changes in community biodiversity were assessed by species richness and the Pielou evenness index (referred to as "Pielou index" hereafter). Species richness in each plot was defined as the total number of species detected in the three quadrats. The Pielou index ( $J$ ) was calculated as  $J = (-\sum P_i \ln P_i) / \ln S$ , where  $P_i$  is the relative abundance of species  $i$  and  $S$  is species richness.

An importance value (IV) for each species for each 1 m × 1 m quadrant was calculated by summing its relative abundance ( $R_a$ ), relative cover ( $R_c$ ), and relative height ( $R_h$ ), and expressed as follows:  $IV = (R_a + R_c + R_h) / 3$ . We also classified each species as dominant ( $IV > 0.5$ ), subordinate ( $IV > 0.2$ ), or rare ( $IV < 0.2$ ) species based on the IV of species (Kardol et al., 2010; Mariotte et al., 2013). *Heteropogon contortus* was classified as the dominant species; four species (*Panicum psilopodium*, *Cajanus scarabaeoides*, *Fimbristylis monostachya* and *Evolvulus alsinoides*) were classified as subordinate species, and all other species were rare species. The IVs of species

for each quadrat were summed as the IVs of dominant, subordinate, and rare species.

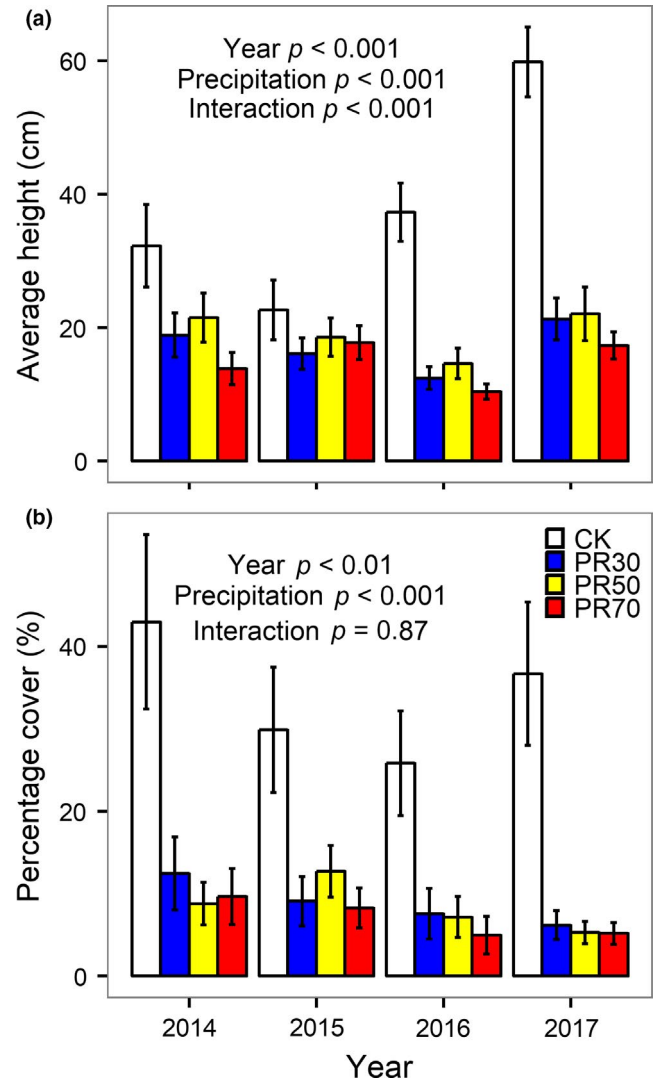
## 2.4 | Statistical analyses

Linear mixed-effects models with repeated measures were used to evaluate the effects of precipitation reduction on community diversity (species richness and Pielou index), functional group level (relative abundance), average height and percentage cover of community and different functional groups, and IV of the three groups (dominant, subordinate and rare species) and the three main species, in which the precipitation treatments, overstorey coverage, and year were fixed factors, and block was a random factor. These variables were log transformed to meet normality when necessary. When an effect of a treatment was found, the differences among the precipitation treatments were compared with a Tukey's HSD test at  $p < 0.05$ . All statistical analyses were performed using R version 3.1.3 (R Core Team, R Foundation for Statistical Computing, Vienna, Austria), with the "vegan" package (R Core Team) for calculating the diversity index, the "nlme" package (R Core Team) for linear mixed-effects models, and the "lsmeans" package (R Core Team) for Tukey's post-hoc test.

## 3 | RESULTS

### 3.1 | Average height and percentage cover on the community and functional group levels

On the community level, average height varied by the year, precipitation treatment, and their interaction ( $p < 0.001$ ), but was unaffected by overstorey coverage and its interaction with other factors ( $p > 0.05$ ; Figure 1a). Overall, precipitation reduction significantly decreased the average height of the community relative to the control ( $p < 0.05$ ), whereas the difference in height amongst the different intensities of precipitation reduction were not significant ( $p > 0.05$ ). Specifically, precipitation reduction significantly reduced the average height of the community in the last two years (2016 and 2017;  $p < 0.001$ ). Average height of different functional groups (graminoids, forbs, legumes, annuals and perennials) varied by year, precipitation treatment and their interaction ( $p < 0.05$ ), except the effects of year interacted with precipitation treatment on forbs ( $p > 0.05$ ) (Appendices S3 and S4). Average height of annuals was reduced by overstorey coverage ( $p < 0.01$ ). Precipitation reduction significantly decreased average height of graminoids, legumes, annuals and perennials ( $p < 0.01$ ; Appendices S3 and S4), but height of these functional groups remained stable ( $p > 0.05$ ) among the different intensities of precipitation reduction. Percentage cover varied by the year, precipitation treatment, and overstorey coverage in the community ( $p < 0.05$ , Figure 1b), for graminoids, and perennials ( $p < 0.05$ ; Appendices S3 and S5). Precipitation reduction significantly decreased percentage cover of the community, graminoids, and perennials ( $p < 0.05$ ) over the experimental period relative to the control (Figure 1b), but no differences in percentage

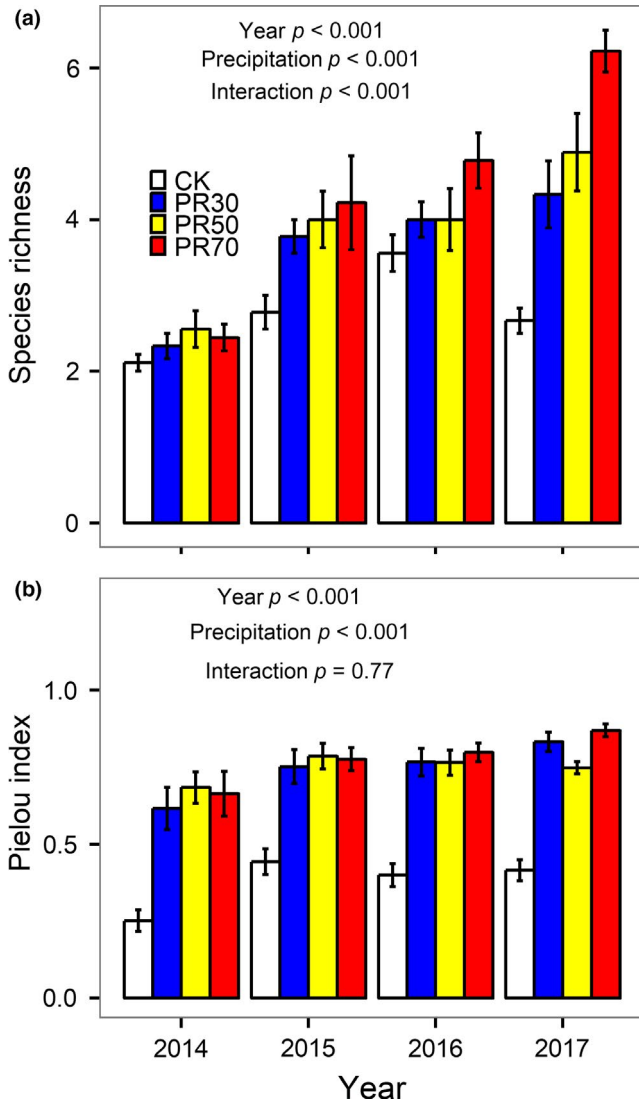


**FIGURE 1** Average height (cm) and percentage cover (%) of the herbaceous community changed with varied precipitation treatments (CK, control; PR30, 30% precipitation reduction; PR50, 50% precipitation reduction; PR70, 70% precipitation reduction) during the study period (2014–2017). Statistical results above the bars show the linear mixed-effects model. Bars represent means  $\pm$  SE

cover among the different intensities of precipitation reduction were observed.

### 3.2 | Community-level biodiversity

Overall, species richness and Pielou index varied significantly with year, precipitation treatment, and their interactions ( $p < 0.001$ ) but were unchanged by overstorey cover ( $p > 0.05$ ), with the exception of precipitation reduction and year interaction on Pielou index ( $p = 0.77$ , Figure 2). On average, these two indices were higher in precipitation reduction than in the control ( $p > 0.05$ ) across the experimental period, but no differences were observed among the different intensities of precipitation reduction ( $p > 0.05$ ).



**FIGURE 2** Community-level diversity changed with varied precipitation treatments (CK, control; PR30, 30% precipitation reduction; PR50, 50% precipitation reduction; PR70, 70% precipitation reduction) during the study period (2014–2017). Statistical results above the bars show the linear mixed-effects model. Bars represent means  $\pm$  SE

### 3.3 | Relative abundance on functional group levels

With an exception of the effect of year on legumes, relative abundance of the different growth forms (graminoids, forbs and legumes) changed significantly with year and precipitation treatment ( $p < 0.05$ ), but was unchanged by their interaction or by overstorey cover (Figure 3). Overall, precipitation reduction significantly increased the relative abundance of forbs and legumes relative to the control, but significantly decreased that of graminoids across the experimental period ( $p < 0.05$ , Figure 3).

Relative abundance of the life forms (annuals and perennials) varied significantly with precipitation treatment ( $p < 0.001$ ). Precipitation reduction significantly increased the relative abundance of annuals relative to the control but decreased that of perennials ( $p < 0.05$ ; Figure 4) across the experimental period.

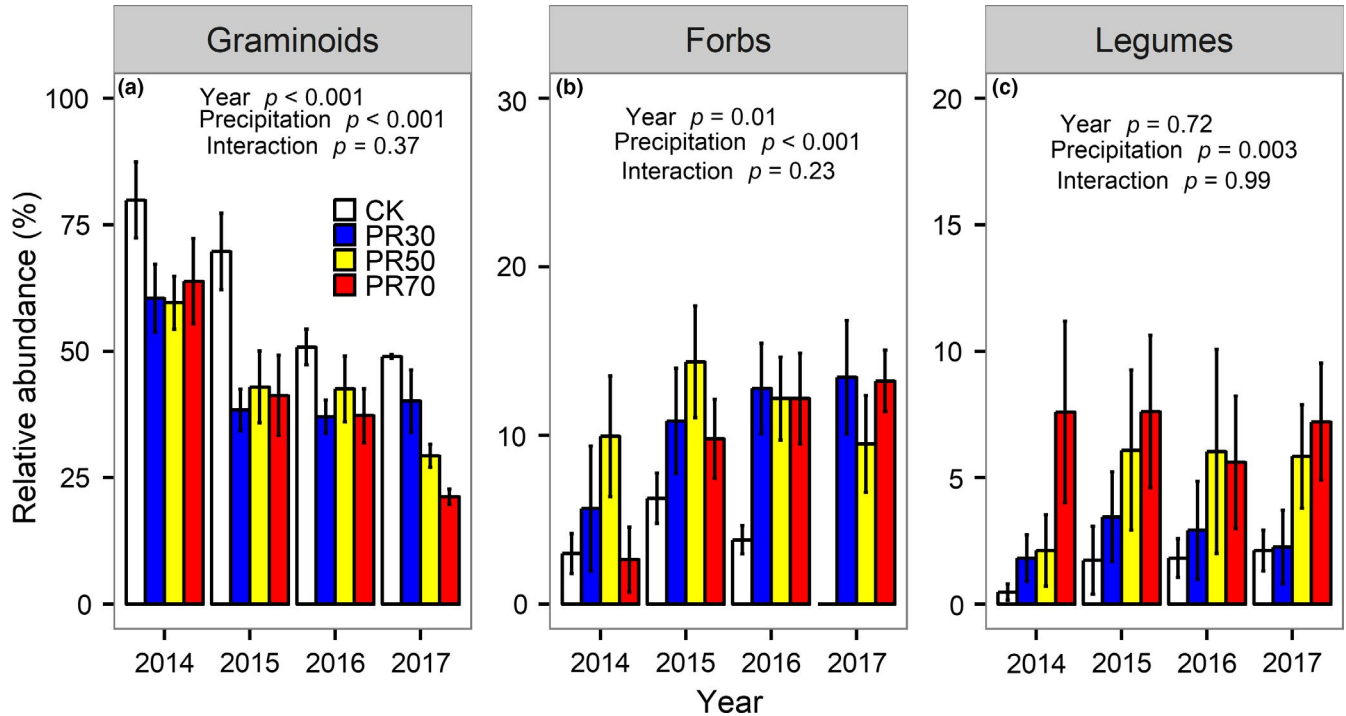
### 3.4 | IVs of specific plant groups and main species

IVs of dominant, subordinate, and rare species varied by year and precipitation treatment ( $p < 0.05$ ) (Figure 5). Precipitation reduction significantly decreased the IV of dominant species relative to the control (Figure 5a). In contrast, the IV of subordinate species remained stable ( $p = 0.045$ ; Figure 5b) under various precipitation treatments and precipitation reduction significantly increased the IV of rare species ( $p < 0.05$ ) over the experimental period relative to the control (Figure 5c). For some main species such as *Panicum psilopodium* and *Cajanus scarabaeoides*, the IV remained stable under precipitation reduction across the experimental period ( $p > 0.05$ ; Figure 5d,e). In contrast, precipitation reduction significantly increased the IV of *Fimbristylis monostachya* ( $p < 0.05$ ) across the experimental period (Figure 5f).

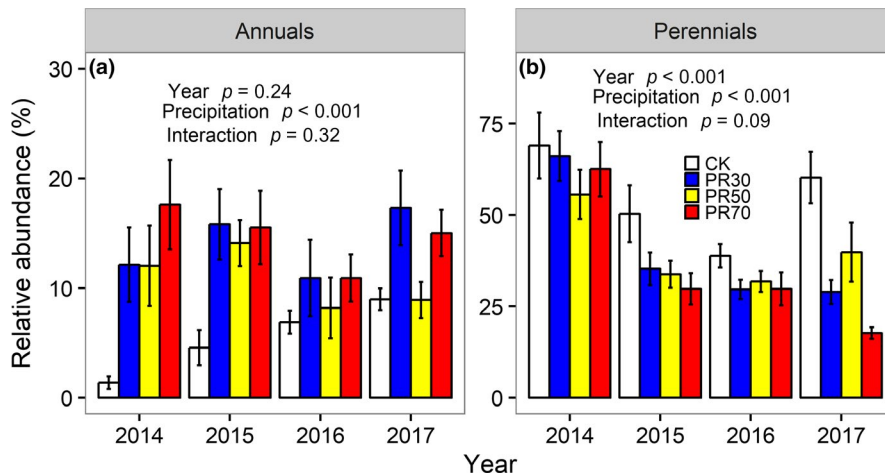
## 4 | DISCUSSION

### 4.1 | Effects of precipitation reduction on height and cover

On the whole, the results of the present study indicate that precipitation reduction significantly reduced the average height and percentage cover of the community, consistent with the findings derived from savannas (O'Connor, 1994) and other biomes (e.g., Mediterranean and grasslands) (Byrne, Adler, & Lauenroth, 2017; Camarero, Sangüesa-Barreda, & Vergarechea, 2016). Interestingly, our data also showed that average height and percentage cover markedly decreased from the control to 30% precipitation reduction, but little change was observed following further reductions in precipitation (Figure 1), which indicated the existence of very low thresholds for the changes in height and cover of the herbaceous community under varying levels of precipitation reduction. This finding can be primarily attributed to the sensitivity of plants to environmental stress (Hoover, Duniway, & Belnap, 2017). Generally, the height and cover of plants (especially those in arid and semi-arid regions) are much more sensitive than other traits under conditions of stress (Qin, Sun, & Wang, 2018). On the individual level, some important leaf traits associated with the height and cover of herbaceous plants (e.g., number of leaves, leaf area and leaf length) can shrink under drought conditions due to the morphological plasticity to reduce water loss (Rodiyati, Arisoesilaningih, Isagi, & Nakagoshi, 2005). Drought can affect the height and cover of the herbaceous community by impacting the plant growth and species recruitment (Canham & Murphy, 2016; Weltzin & McPherson, 2000). In particular, the growth rate (net primary productivity) of the herbaceous community in this savanna dramatically decreased under 30% precipitation reduction during the study period (Jin, Li, Liu, Liu, Zhang, Song, et al., 2018), causing the decrease in height and cover. Moreover, precipitation reduction apparently changed the abundance of different plant functional groups in the present study (Figures 3 and 4), disproportionately depressing the abundance of the most dominant groups (e.g., graminoids and perennials), indicating that declines in precipitation could affect the density and species recruitments of the herbaceous community and then lead to decreased community cover and height. In addition, the percentage cover of the herbaceous community



**FIGURE 3** Relative abundance (%) of different growth forms (graminoids, forbs and legumes) changed with varied precipitation treatments (CK, control; PR30, 30% precipitation reduction; PR50, 50% precipitation reduction; PR70, 70% precipitation reduction) during the study period (2014–2017). Statistical results above the bars show the linear mixed-effects model. Bars represent means  $\pm$  SE



**FIGURE 4** Relative abundance of different life forms (perennials and annuals) changed with varied precipitation treatments (CK, control; PR30, 30% precipitation reduction; PR50, 50% precipitation reduction; PR70, 70% precipitation reduction) during the study period (2014–2017). Statistical results above the bars show the linear mixed-effects model. Bars represent means  $\pm$  SE

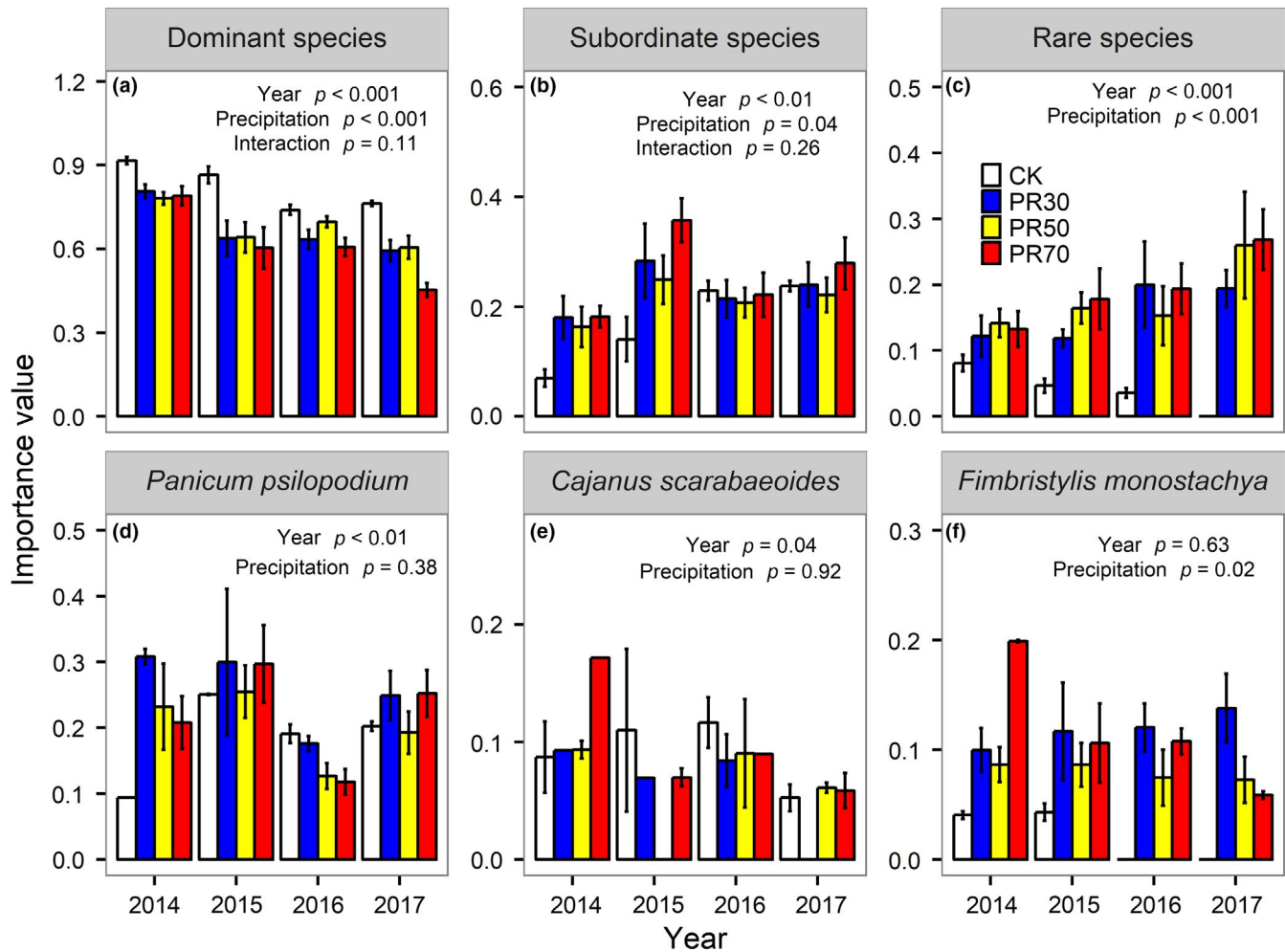
in the present study changed with overstorey cover. Growth of understorey plants may be affected by overstorey cover through controlling light availability (Ansley, Mirik, Heaton, & Wu, 2013), and this possibility cannot be overlooked. These results highlight that, in future, relatively small declines in precipitation may induce large decreases in height and cover of the herbaceous community in savanna regions.

#### 4.2 | Effects of precipitation reduction on community diversity

Species richness and Pielou index in this savanna showed an obvious increase under precipitation reduction during the four-year

experimental period, i.e., drought significantly elevated the species richness of the herbaceous community in this study, which is similar to the previous findings of O'Connor (1994) for a grass savanna. These findings suggest that future declines in precipitation in savanna regions may increase the species richness of the herbaceous community. In the present study, the dominant position of *Heteropogon contortus* in the herbaceous community was weakened (declined importance value [IV]; Figure 5) with prolonged drought. This would provide open niches that could facilitate germination and establishment of other drought-tolerant species (e.g., forbs), resulting in enhanced species richness.

Our results are in contrast, however, to the common finding that drought reduces the species richness in various grasslands



**FIGURE 5** Importance value of (a) dominant species, (b) subordinate species, (c) rare species and (d–f) some main species (*Panicum psilopodium*, *Cajanus scarabaeoides* and *Fimbristylis monostachya*) changed with varied precipitation treatments (CK, control; PR30, 30% precipitation reduction; PR50, 50% precipitation reduction; PR70, 70% precipitation reduction) during the study period (2014–2017). Statistical results above the bars show the linear mixed-effects model. Bars represent means  $\pm$  SE

(Copeland et al., 2016; Farzam & Ejtehadi, 2017; Liu, Estiarte, Ogaya, Yang, & Peñuelas, 2017). These differences may involve competitive mechanisms, with the competitive interaction between overstorey and grass increased under stress (Scholes & Archer, 1997; Weltzin & McPherson, 2000). Gleason et al. (2017) found that the effects of drought on species diversity were amplified by competition. Herbaceous plants in savannas may face more severe drought stress because of a reduction in soil moisture and exacerbated pressure on grass from the overstorey under drought (Rysavy et al., 2016; Yu et al., 2017). In addition, under a precipitation reduction of 30% the Pielou index showed a large increase relative to the control, but there were no obvious differences among the different intensities of precipitation reduction, suggesting the presence of a low threshold. Water is one of the predominantly limited factors in semi-arid and arid regions, and its availability affects the abundance of species through the regulation of species recruitment and mortality (Weltzin & McPherson, 2000). However, with intensified drought, species and their individuals tend to maintain

a dynamic stability in a limited space over the short term owing to increasing intraspecific competition and differences in the drought resistance of plants. These findings imply that even relatively small declines in precipitation in savanna regions may affect the community resistance and lead to changes in species distribution.

#### 4.3 | Effects of precipitation reduction on community composition

Precipitation reduction in this savanna ecosystem caused a clear shift in herbaceous community composition (Figure 5), which is consistent with the results from a restored tallgrass prairie (Smith, Schuster, & Dukes, 2016) and a desert grassland (Gherardi & Sala, 2015). The IV of dominant species in the present study significantly decreased with decreasing precipitation, whereas it increased for rare species and was unchanged for subordinate species. These results suggest that the responses of different components of the herbaceous community to drought stress were asynchronous (i.e.,

dissimilar response among the components over time). The community could adjust the relative importance of different components under drought stress as a potential buffering mechanism to maintain ecosystem stability (Wilcox et al., 2017). As observed in the present study, the status of rare species tended to increase under drought conditions, in parallel with a weakening in the dominant position of the dominant species. It may be that the resistance of dominant species declined because of persistent drought stress and a favoring of the other, more drought-resistant, species (Gherardi & Sala, 2015; Smith & Knapp, 2003). However, the IV of subordinate species remained unchanged under precipitation reduction in our study, which could be explained by the fact that subordinate species have a higher resistance against drought (Elst et al., 2017; Mariotte et al., 2013). Moreover, different species in the present study also exhibited asynchronous responses to a decline in precipitation; the status of *Fimbristylis monostachya* was increased under precipitation reduction, whereas those of two main species (*Panicum psilopodium* and *Cajanus scarabaeoides*) were unchanged, suggesting that *F. monostachya* could be more drought-resistant and that the successive declines in precipitation in this region in particular would be expected to facilitate the growth of *F. monostachya* and accelerate this species' dominance in the herbaceous community. The IV of the dominant species, *Heteropogon contortus*, was slightly decreased during the first stage of the drought, whereas it decreased significantly in the last two study years (2016 and 2017). These nonlinear responses to persisted drought could be attributed to the delayed or cumulative effects of drought (Dudney et al., 2017). Therefore, future declines in precipitation in savanna regions may cause a shift in community composition.

#### 4.4 | Response of functional groups to precipitation reduction

Drought resistance and resilience of a community are determined by plant functional group composition (Carlsson, Merten, Kayser, Isselstein, & Wrage-Mönning, 2017). Our results demonstrated threshold changes in height, percentage cover, and relative abundance of different plant functional groups with the different precipitation treatments, which suggests that the underlying changes in plant traits and the composition of plant functional groups in response to drought stress were nonlinear. For the growth forms, precipitation reduction significantly reduced average height, percentage cover, and the relative abundance of graminoids, and significantly elevated those of forbs and legumes. These findings suggest that forbs and legumes may be more resistant to drought due to different root traits (Chelli et al., 2016; Mulhouse, Hallett, & Collins, 2017; Tetetla-Rangel, Dupuy, Hernández-Stefanoni, & Hoekstra, 2017). The graminoids in this savanna ecosystem belong to the shallower- and fibrous-rooted species, whereas the forbs and legumes belong to tap-root species (Jin et al., 2017; Jin, Li, Liu, Liu, Zhang, Song, et al., 2018). The shallower and fibrous roots for graminoids may limit their ability to access deeper soil water following a reduction in surface soil water and increased overstorey and intraspecific competition (Collins & Bras, 2007). This would in turn lead to reductions in height, percentage cover,

and relative abundance of graminoids. Forbs and legumes, obviously owing to their taproots, can acquire water from much deeper soil layers than can graminoids, which facilitates their survival and growth in drought conditions (Collins & Bras, 2007; Lindh, Zhang, Falster, Franklin, & Brännström, 2014). Precipitation reduction significantly decreased the average height, percentage cover and relative abundance of perennials but significantly increased those of annuals, in accordance with studies in different grasslands reporting that water reduction favored annual plants (Cleland et al., 2013). This may be because annuals are suited to increased growth and reproduction under drought conditions because of their shorter life span and more rapid growth than those of perennials (Pake & Venable, 1995). On the whole, contrasting effects among the different functional groups were shown under precipitation reduction in this savanna, suggesting that different plant functional groups may have evolved different adaptation strategies related to morphological or physiological traits to cope with drought stress. These findings suggest that the herbaceous community in savannas may be able to adapt to future declines in precipitation by shifting the abundance of different plant functional groups and changing the species distributions.

## 5 | CONCLUSIONS

The present study showed that the composition and structure of the herbaceous community in this savanna nonlinearly varied with declines in precipitation over a four-year experimental period. In particular, precipitation reduction decreased the average height and percentage cover of the herbaceous community and elevated species richness and the Pielou index. Furthermore, most changes in plant traits and herbaceous community processes in response to declines in precipitation were asynchronous on the species and plant functional group levels. Our study provides strong evidence for the existence of a very low threshold for changes in herbaceous community structure and composition under varying precipitation treatments during the study period, which suggests that the herbaceous community responses to precipitation reduction were essentially nonlinear. These findings imply that ongoing climate change, especially precipitation reduction, may further affect the community dynamics of savannas, resulting in declines in ecosystem function and stability.

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## CONFLICTS OF INTEREST

None declared.



## DATA AVAILABILITY

The data sets generated during the current study are stored as separate data files at the Global Change Research group, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, China.

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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.** Precipitation, soil moisture and soil temperature during the study period

**Appendix S2.** List of species and their classification on plant functional groups in the herbaceous layer during the study period

**Appendix S3.** Results of linear mixed-effects models testing the effects of treatments with average height and percentage cover in community and functional group levels

**Appendix S4.** Average height of different functional groups changed with varied precipitation treatments during the study period

**Appendix S5.** Percentage cover of different functional groups changed with varied precipitation treatments during the study period.

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