

# Effect of Changing Precipitation Timing on Phylogenetic and Functional Community Structure in A Semi-Arid Steppe

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## Research Article

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# Abstract

Changes in the amount and timing of precipitation may affect plant species coexistence. However, little is known about how these changes in precipitation structure plant communities. Here, we conducted a six-year field precipitation manipulation experiment in the semi-arid steppe of Inner Mongolia, China to assess the importance of species loss and colonization to community assembly by incorporating phylogenetic information on functional relatedness. Our results demonstrated that the decline in plant species richness under decreasing precipitation in the late and entire growing season could be attributed to a decrease in species colonization and an increase in species loss, respectively. The increase in species richness under increasing precipitation in the late growing season was mainly caused by increases in colonizing species. Species with lower initial abundances, individual size, and leaf dry matter content had greater loss probabilities when species with lower initial abundances had greater colonization likelihood. The loss of species that were more closely related to other residents under decreasing precipitation in the late growing season did not alter phylogenetic overdispersion patterns, and the colonization of species that were more distantly related to residents under increasing precipitation in the late growing season shifted functional relatedness from clustering to randomness. Thus, the colonization of functionally dissimilar species decreased the strength of environmental filtering. Our study showed that phylogenetic and functional relatedness independently affected plant community structure. This finding suggests that evolutionary processes affect community assembly independently of ecological processes.

# Introduction

Climate changes have intensified hydrological cycles, causing the changes in precipitation patterns (Peng et al., 2013; IPCC, 2014). Changes in the amount and timing of precipitation may affect plant species coexistence (Willis et al., 2008; Lavergne et al., 2010; Yang et al., 2012; Li et al., 2020). Understanding phylogenetic community structure and trait-based community ecology is essential for predicting how precipitation changes structure communities (Silvertown et al., 2006; Duarte, 2011; Griffin-Nolan et al., 2018; Zhang et al., 2019). However, few studies have incorporated phylogenetic information on species traits distribution into analyses of the responses of community assembly to changing precipitation.

Changes in the local environment can affect species trait distribution (Pillar et al., 2009). Species that live together and experience similar environmental conditions likely share phenotypic traits because of environmental filtering (Weiher et al., 1998), whereas competitive exclusion tends to limit the similarity of species persisting in these environments (Webb et al., 2002; Cavender-Bares et al., 2009). Phenotypic traits likely covary with phylogenetic relatedness among species, and closely related species generally have similar phenotypic traits (Wiens and Graham, 2005). For example, extreme drought may allow only a limited number of species that can tolerate water stress to survive, leading to phylogenetic clustering if survived species comprise closely related species with similar traits. In contrast, phylogenetic overdispersion results if intense competition under increasing precipitation promotes the occurrence of distantly related species with divergent traits.

Most previous studies have reported that changes in phylogenetic and functional community structure mainly result from the extinction of species (Webb et al., 2002; Cavender-Bares et al., 2009; Bin et al., 2019). However, some studies have shown that the colonization of species that are distantly related to residents can lead to phylogenetic overdispersion (Li et al., 2015; Yang et al., 2017). Generally, the colonization of species that are functionally and phylogenetically similar to residents and/or the local extinction of species that are functionally and phylogenetically dissimilar to other residents may result in functional and phylogenetic clustering. Likewise, the colonization of species that are functionally and phylogenetically dissimilar to residents and/or the extinction of closely related species with similar traits with other residents may lead to functional and phylogenetic overdispersion. Thus, study of species colonization and extinction processes is essential for understanding the drivers of community structure. However, few studies have incorporated information on the functional and phylogenetic relatedness of locally lost resident species and the colonization of new species into analyses of community assembly processes.

Here, we conducted a six-year precipitation manipulation experiment in a temperate steppe in north China to examine how the structure and composition of plant communities respond to changes in precipitation in different periods of the growing season. Specifically, we proposed the following three hypotheses. First, decreasing precipitation results in functional/phylogenetic clustering due to water stress induced by the local disappear of species that are functionally and phylogenetically dissimilar to survived species (environmental filtering) (hypothesis 1a); alternatively, increases in precipitation result in functional/phylogenetic overdispersion if intense competition excludes closely related species (hypothesis 1b). Second, the colonization of species that are functionally/phylogenetically similar to residents leads to functional/phylogenetic clustering (hypothesis 2a), whereas the colonization of species that are functionally/phylogenetically dissimilar to residents leads to phylogenetic/functional overdispersion (hypothesis 2b). Third, phylogenetic relatedness may covary with functional relatedness given that species with shared ancestry often have similar phenotypic traits (hypothesis 3).

## Materials And Methods

### Site description

The study site was located in a semi-arid grassland at the Duolun Restoration Ecology Station (42°02'N, 116°17'E, 1324 m a.s.l.) in Inner Mongolia, China. Mean annual temperature was 2.1°C and mean annual precipitation was 383 mm (54-years average), with more than 90% of rainfall occurring between May and October (Niu et al., 2013). Soil is classified as chestnut, with 80–98% sand (0.02-2.0 mm) and an average bulk density of 1.31 g cm<sup>-3</sup> (Song et al., 2016). This semi-arid grassland was dominated by *Artemisia frigida* Willd., *Cleistogenes squarrosa* (Trin.) Keng, *Stipa krylovii* Roshev., *Potentilla acaulis* L. (Yang et al., 2021).

### Experimental Design

Using a randomized block design, we conducted a long-term precipitation manipulation experiment in the semi-arid steppe of Inner Mongolia, China. There are seven treatments, including a 60% decrease (DEP) or increase (IEP) in precipitation in the early growing season (from April 15<sup>th</sup> to June 30<sup>th</sup>), a 60% decrease (DLP) or increase (IEP) in precipitation in the late growing season (from July 1<sup>th</sup> to September 15<sup>th</sup>), and a 60% decrease (DP) or increase (IP) in precipitation during the entire growing season, as well as on control plots receiving ambient natural precipitation. Each treatment had five replicates, leading to 35 experimental plots. Buffer zones between plots were 1.5 m wide (Yang et al., 2021). Slat paneled shelter over experimental plots was used to exclude precipitation. Shelters were 4 × 4 m with a 3.5 × 3.5 m area at the center that was used to measure and survey, the 0.5 m edge was considered a buffering zone to avoid edge effects. The 3.5 × 3.5 m plot was divided into two parts, one 2 × 1 m section at the center for vegetation monitoring, and the other section for species traits and carbon flux measurement.

## Vegetation Monitoring

From 2015 to 2020, we estimated plant species richness and community cover in one 1 × 1 m permanent quadrant in each plot in early September when biomass had reached its peak level. The cover of each species in each plot was estimated as a percentage using a canopy interception technique based on 100 equally distributed grids (10 × 10 cm). The percent cover of each species was recorded in all of the grids, and total cover was calculated by summarizing the percent cover of all species in the quadrat to estimate the community cover in each quadrat (Zhang et al., 2020a).

## Trait Measurements

We chose 34 common species, which accounted for more than 95% of the

aboveground biomass, in each of the seven treatments for trait measurements. Only aboveground parts were sampled at flowering time from July 1 to August 20 in 2018. We randomly sampled 15 individuals per species for each treatment. Plant species height and biomass were measured for the 15 randomly selected individuals per species for each treatment. To measure the specific leaf area (SLA, the ratio of leaf area to leaf dry mass), we randomly sampled two fully developed, undamaged leaves from each of the 15 individuals per species for each treatment. The fresh leaves were scanned to measure leaf area using ImageJ (Schneider et al., 2012), followed by drying at 65°C for 48 hours and weighed using a Sartorius balance accurate to  $10^{-4}$  g. We calculated leaf dry matter content using relative leaf dry weight for each leaf of the 34 species. Plant nitrogen content was measured by digestion with concentrated  $H_2SO_4$  and 30%  $H_2O_2$  and colorimetric analysis using a Lachat Autoanalyzer for total nitrogen (EPA Method 10-107-06-2-A) with three replicates for each species (Lin et al., 2010; Zhang et al., 2020b).

## Data analysis

Abundance and trait-weighted net relatedness index (NRI) was calculated according to Yang et al. (2017) and Zhu et al. (2019). A positive NRI indicates phylogenetic clustering, whereas a negative NRI indicates phylogenetic overdispersion (Li et al., 2016). Locally lost species were defined as they were present in a plot in 2015 but absent in 2020 and new colonists species as they were absent in a plot in 2015 but present in 2020 based on Yang et al. (2017). We also classified species as having a loss likelihood from a plot if the relative abundance of these species was higher in 2015 than 2020. If the relative abundance of species was lower in 2015 than 2020, these species were defined as species with increased likelihood.  $\beta$ NRI/functional  $\beta$ NRI was used as a measure of the phylogenetic/functional similarities between locally lost/colonizing species and resident species of each plot (Yang et al., 2017). Negative  $\beta$ NRI indicates that the lost/colonizing species are more distantly related to the residents than by chance, whereas positive  $\beta$ NRI indicates the opposite (Webb et al., 2008).

Multivariate analysis of variance (MANOVA) was used to test the effects of DEP, DLP, DP, IEP, ILP, and IP on plant species richness, functional group richness, species colonization/loss, phylogenetic/functional net relatedness index (NRI/functional NRI), and phylogenetic/functional dissimilarity of colonizing and lost species ( $\beta$ NRI/functional  $\beta$ NRI). Post-hoc tests were used to test for significant differences in these variables among the seven treatments. Regression analysis was used to relate factors that have been suggested to affect abundance of species with loss or increased likelihood, including initial coverage of species in 2015, plant species height, leaf nitrogen content, specific leaf area, plant species biomass, and leaf dry matter content. We employed structural equation modeling (SEM) according to known effects to explain the drivers of plant species richness, NRI, and functional-NRI. The goodness of fit of the model was evaluated by chisquare test. SEM analyses were performed using AMOS 18.0 (Amos Development Co., Greene, Maine, USA). Other analyses were performed in R 2.14.0 and SPSS 16.0 (SPSS, Inc., Chicago, Illinois, USA).

## Results

### Species richness and Phylogenetic structure

Mean species richness was 16.4 species  $m^{-2}$  in the control plots. DLP and DP reduced species richness by an average of 3.2 (19.5%;  $p < 0.01$ ) and 3.8 species  $m^{-2}$  (23.2%;  $p < 0.001$ ), respectively. In contrast, DEP had no significant effect on species richness (Fig. 1a). ILP caused an increase in species richness of 3.8 species  $m^{-2}$  (23.2%;  $p < 0.05$ ), whereas neither IEP nor IP affected species richness.

NRI was lower than zero, indicating significant phylogenetic overdispersion (Fig. 1b). Changing precipitation had no effect on NRI, and average phylogenetic relatedness was stable among treatments (Fig. 1b). Functional NRI was greater than zero, indicating significant functional clustering (Fig. 1c). IEP and ILP decreased functional NRI and shifted phylogenetic relatedness from clustering to randomness. In contrast, DEP and DP significantly reduced functional NRI but did not alter the pattern of phylogenetic clustering. DLP and IP did not alter the functional NRI and average phylogenetic relatedness among species (Fig. 1c).

# Species Colonization And Loss

An average of 4.6 (SE = 0.5) species lost in the control plots from 2015 to 2020 (Fig. 2). Some of the grasses (*Agropyron cristatum* and *Leymus chinensis*), forbs (e.g., *Artemisia pubescens* and *Chamaerhodos erecta*), and legumes (*Medicago ruthenica* and *Gueldenstaedtia stenophylla*) with lower initial abundances, sizes, and leaf dry matter content disappeared under DP (Fig. 3a, b, c, d), leading to the loss of 6.8 (SE = 0.4) species. In contrast, the number of species loss under DEP, DLP, IEP, ILP, and IP did not differ from the control. An average of 2.8 (SE = 0.5) species colonized the control plots from 2015 to 2020 (Fig. 2). DLP decreased the colonization of drought sensitive forbs (e.g., *Chenopodium glaucum*) by 1.4 (SE = 0.4) species  $m^{-2}$  relative to the control from 2015 to 2020 (Fig. 2). In contrast, ILP increased forbs (*Artemisia scoparia* and *Potentilla acaulis*) and legumes (*Gueldenstaedtia stenophylla* and *Melissitus ruthenica*) colonization by 2.2 species  $m^{-2}$  relative to the control from 2015 to 2020. DEP, DP, IEP, and IP had no effect on species colonization. Species with lower initial coverage in 2015 had greater increased likelihoods in 2020 (Fig. 3g), whereas traits, such as species height, leaf nitrogen content, leaf dry matter content, SLA, and sizes, were not good predictors of increased probability in species abundance (Fig. 3h, i, j, k, l).

$\beta$ NRI between locally lost species and other resident species was significantly lower than zero in the control, IEP, ILP, and IP plots, indicating that lost species in this treatment were more distantly related to the other residents than expected by chance (Fig. 4a). DEP, DLP, and DP significantly increased  $\beta$ NRI but did not alter phylogenetic relatedness between lost species and other resident species.  $\beta$ NRI between colonists and residents in the control, DLP, ILP, and IP treatments was significantly lower than zero, indicating that colonists in these treatments were more distantly related to the residents than expected by chance.  $\beta$ NRI between colonists and residents in DEP, DP, and IEP did not differ from zero, indicating the phylogenetic randomness of species colonization (Fig. 4a).

Functional  $\beta$ NRI between lost species and other resident species was significantly greater than zero in the control and IEP, indicating that the traits of lost species in this treatment were more closely related to other residents than expected by chance (Fig. 4b). DP, ILP, and IP significantly and DLP marginally reduced the functional  $\beta$ NRI of lost species, which caused functional  $\beta$ NRI to be significantly lower than zero in DP, ILP, and IP; however, functional  $\beta$ NRI did not significantly differ from zero in DLP, indicating that the traits of lost species were more distantly related to other residents in DP, ILP, and IP but were random in DLP (Fig. 4b). Functional  $\beta$ NRI between colonists and residents in the control, DLP, DP, and IP did not differ from zero, indicating that the traits of colonists in these treatments were random. Functional  $\beta$ NRI in DEP, IEP, and ILP was significantly lower than zero, indicating that the traits of colonists in these treatments were more distantly related to the residents than expected by chance (Fig. 4b).

## Factors Affecting Phylogenetic And Functional Community Structure

Structural equation modeling (SEM) showed that changing precipitation affected species richness directly by altering soil moisture and indirectly by altering the number of colonizing species. Changing precipitation affected functional NRI by regulating soil moisture and thus the number of colonizing species and species richness (Fig. 6). Functional phylogenetic relatedness was independent of structural phylogenetic relatedness, and changes in species richness did not affect phylogenetic relatedness (Fig. 6).

## Discussion

Here, we assessed community assembly processes by combining data on species colonization and loss with information on phylogenetic and functional relatedness. Our study revealed four main findings. First, the decline in species richness under decreasing precipitation in the late and entire growing season can be attributed to the reduction in species colonization and the increase in species loss, respectively. In contrast, the increase in species richness under increasing precipitation in the late growing season is mainly caused by the increase in colonizing species. Second, trait and abundance-based mechanisms explained species loss probability when only abundance-based mechanisms explain the increased likelihood of species abundance. Third, loss of rare species more closely related to other residents weakened phylogenetic overdispersion but did not alter the phylogenetic pattern under decreasing precipitation in the entire growing season, which is in contrast to hypothesis 1b. Increased colonization of species that are more distantly related to the residents under increasing precipitation in the late growing season shifted functional relatedness from clustering to randomness, supporting hypothesis 2b. Finally, phylogenetic and functional relatedness act independently during community assembly processes; thus, rejected hypothesis 3.

## Response Of Species Richness To Changing Precipitation Timing

Our study showed that the decline/increase in species richness under decreasing/increasing precipitation in the late growing season was primarily caused by the decline/increase in colonized species, whereas the decline in species richness under decreasing precipitation in the entire growing season can be attributed to increased species loss. Abundance-based mechanisms, which assume rare species have a greater probability of becoming lost because of their small population sizes (Suding et al., 2005), are important for both species colonization and loss when trait-based mechanisms, which assume that species loss may be a function of specific traits that competitively favor some species (Yang et al., 2015), work only for species loss. Specifically, rare species, such as *Chenopodium glaucum* and *Chamaerhodos erecta*, are detrimental for survival under decreasing precipitation in the entire growing season because of their lower initial abundances and individual size at greater risk of loss under drought stress (Mudrak et al., 2016). Moreover, increased water stress under decreasing precipitation in the entire growing season intensifies competition for water from drought-insensitive species, enhancing species mortality rates of drought-sensitive species with lower leaf dry matter content (Mariotte, 2013; Hoover et

al., 2014). In contrast, increasing precipitation in the late growing season increases colonization likelihood by increasing the water availability, species germination rate, and seedling survival, whereas decreasing precipitation in the late growing season has the opposite effect (Zavaleta et al., 2003; Yang et al., 2011; Yang et al., 2017). These results are inconsistent with the light competition hypothesis, which suggests that increased competition for light enhances species loss (Dybzinski and Tilman, 2007; Hautier et al., 2009). Light limitation by itself is not a direct cause of plant mortality in this less productive (aboveground biomass:  $120 \text{ g m}^{-2}$ ) semi-arid grassland where water availability rather than light availability is the primary factor limiting plant growth. The findings highlight the importance of changing precipitation in the late growing season on species colonization process, which are vital for optimizing management strategies to protect biodiversity.

Precipitation in the early growing season will become increasingly important for plant growth given that precipitation at the start of the growing season determines the critical phenological phase of plants (Menzel et al., 2006; Suttle et al., 2007; Chelli et al., 2016). We previously found that decreasing precipitation in the early growing season reduces the biomass of grass and sub-shrubs (Zhang et al., 2020a). However, the effect of changing precipitation in the early growing season on species richness was small. This finding is consistent with the results of Denton et al. (2017) showing that spring drought does not affect plant species diversity. One possible explanation is that nominal precipitation during the late growing season in the plots that have a low precipitation in the early growing season promotes the restoration of diversity by increasing ephemeral plant colonization (Madrigal et al., 2009), counteracting the negative effect of decreasing precipitation during the early growing season on diversity, leading to neutral changes in diversity in these plots.

## Phylogenetic And Functional Community Structure

Changing precipitation affects plant traits and phylogeny by regulating soil water availability (Zhang et al., 2020a; Zhu et al., 2020). Decreasing precipitation in the entire growing season led to the loss of species with low leaf dry matter content (conserved trait, Table S1) because of the increased water stress (Mudrak et al., 2016). The loss of species with low leaf dry matter content, which is phylogenetic conserved and exhibits a clumped distribution, did not alter phylogenetic overdispersion patterns under decreasing precipitation in the entire growing season. The results indicate that species loss contributes little to the shift in the phylogenetic pattern (Fig. 6) and does not alter phylogenetic relatedness at the community level. Similarly, we did not find that species colonization alters phylogenetic community structure. However, we found that changing precipitation in late growing season affects community-weighted mean trait values and thus functional community structure. Reduced colonization of species with random trait distributions under decreasing precipitation in the late growing season did not alter functional clustering patterns. In contrast, the increased colonization of species that are more distantly related to residents under increasing precipitation in the late growing season shifted the pattern of functional relatedness from clustering to randomness. These results are consistent with Peay et al. (2012) showing that increasing dissimilarities between colonists and residents through biotic resistance

weakens the clumped trait distributions. These findings indicate that the colonization of species that are more distantly related to residents decreases the carrying capacity of the local habitat and thus weakens the extent of environmental filtering.

## **Phylogenetic Relatedness Is Independent Of Functional Relatedness**

Previous studies have shown that phylogenetic relatedness among plant species is an important driver of trait-based assembly processes (Wiens and Graham, 2005; Yang et al., 2012). Our study demonstrates that trait-based community assembly in the studied plant communities is independent of phylogenetic constraints on trait distributions. If the environmental tolerances of traits are phylogenetically conserved, then differences in the environment can act as filters, and closely related species with similar traits would be more likely to coexist. However, we did not observe this to be the case in this semi-arid grassland, at least with respect to the studied traits under increasing precipitation in the early and late growing season, in which the distribution of traits shifted from clustering to overdispersion or randomness (Fig. 2). Climate changes and biotic interactions may explain the observed patterns in the trait distribution (Geber and Griffen, 2003). Some aspects of the local environment that differ from those of the experimental treatments may dilute the treatment effects and cause changes in community structure. Biotic interactions induced by climate change may drive divergence in these traits and further alter community structure. These inferences suggest that closely related species do not necessarily have similar phenotypic traits, and this is more likely to be the case in fluctuating environments.

## **Conclusions**

Our study demonstrated that decreasing precipitation in the late and entire growing season reduced species richness by decreasing the number of new colonists and increasing the loss of resident species, respectively, whereas increasing precipitation in the late growing season enhanced species richness by increasing the number of new colonists. Species with lower initial abundances, individual size, and leaf dry matter content had greater loss probabilities when only abundance-based mechanisms explain species colonization likelihood. The loss of species that are more closely related to each other than expected by chance did not alter phylogenetic overdispersion patterns. Traits at the community level were significantly clustered, and the colonization of species that are more distantly related to residents under increasing precipitation in the late growing season shifted the pattern of functional relatedness from clustering to randomness. Our study also showed that phylogenetic and functional relatedness independently affected plant communities. This finding suggests that evolutionary processes affect community assembly processes independently of ecological processes.

## **Declarations**

## **Author contributions**

YZL conceived and designed the experiments; YZL wrote the paper; WMM and YJW performed the experiments; XR analyzed the data; ZT provided editorial advice.

## Data availability

The data that supports the findings of this study will be openly available in a data repository.

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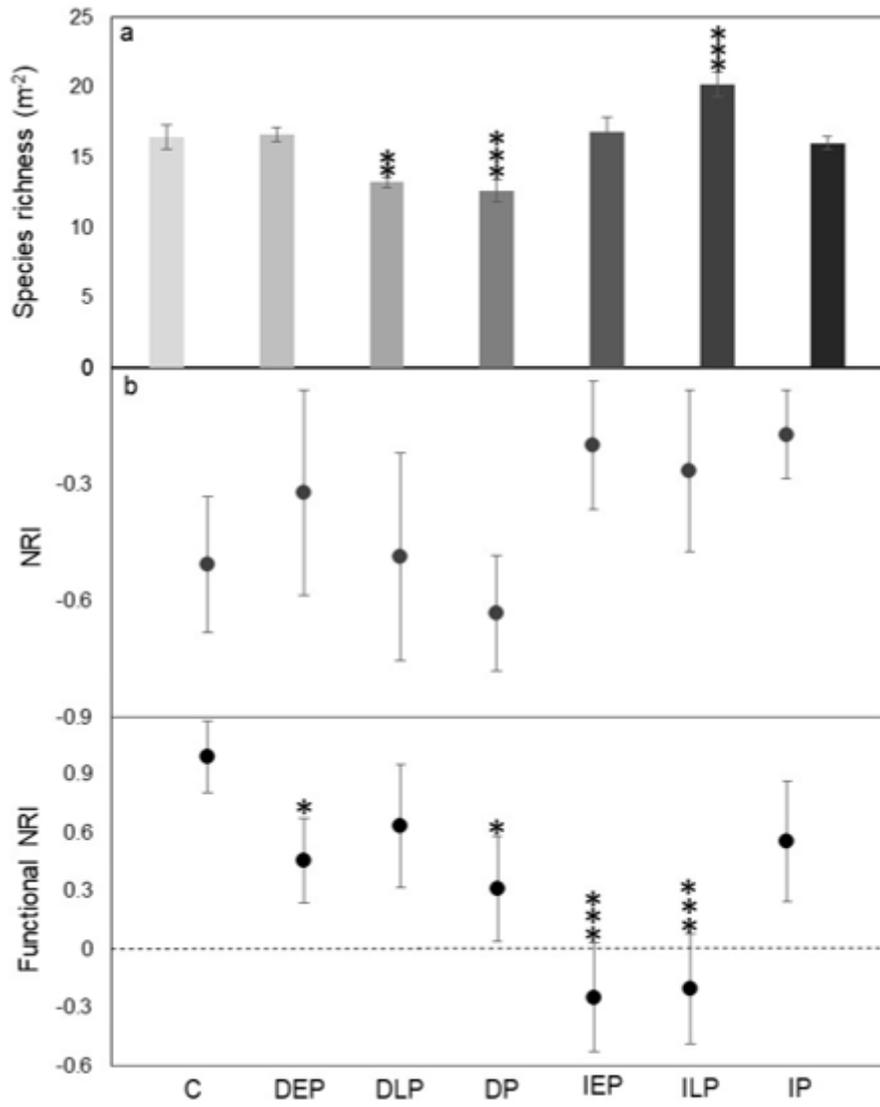
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## Figures



**Figure 1**

Effects of decreasing/increasing precipitation in the early (DEP/IEP), late (DLP/ILP), and entire (DP/IP) growing season on species richness, net relatedness index (NRI), and functional NRI in 2020. C represents the control. Error bars represents standard errors. \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

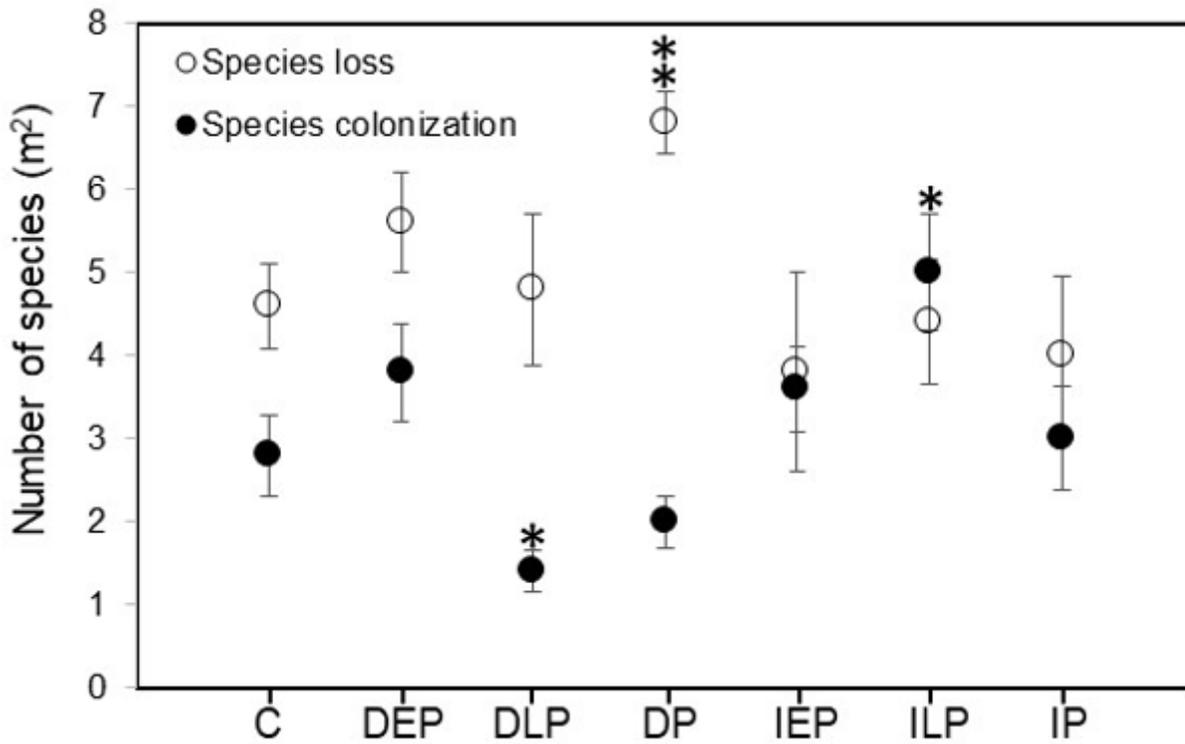
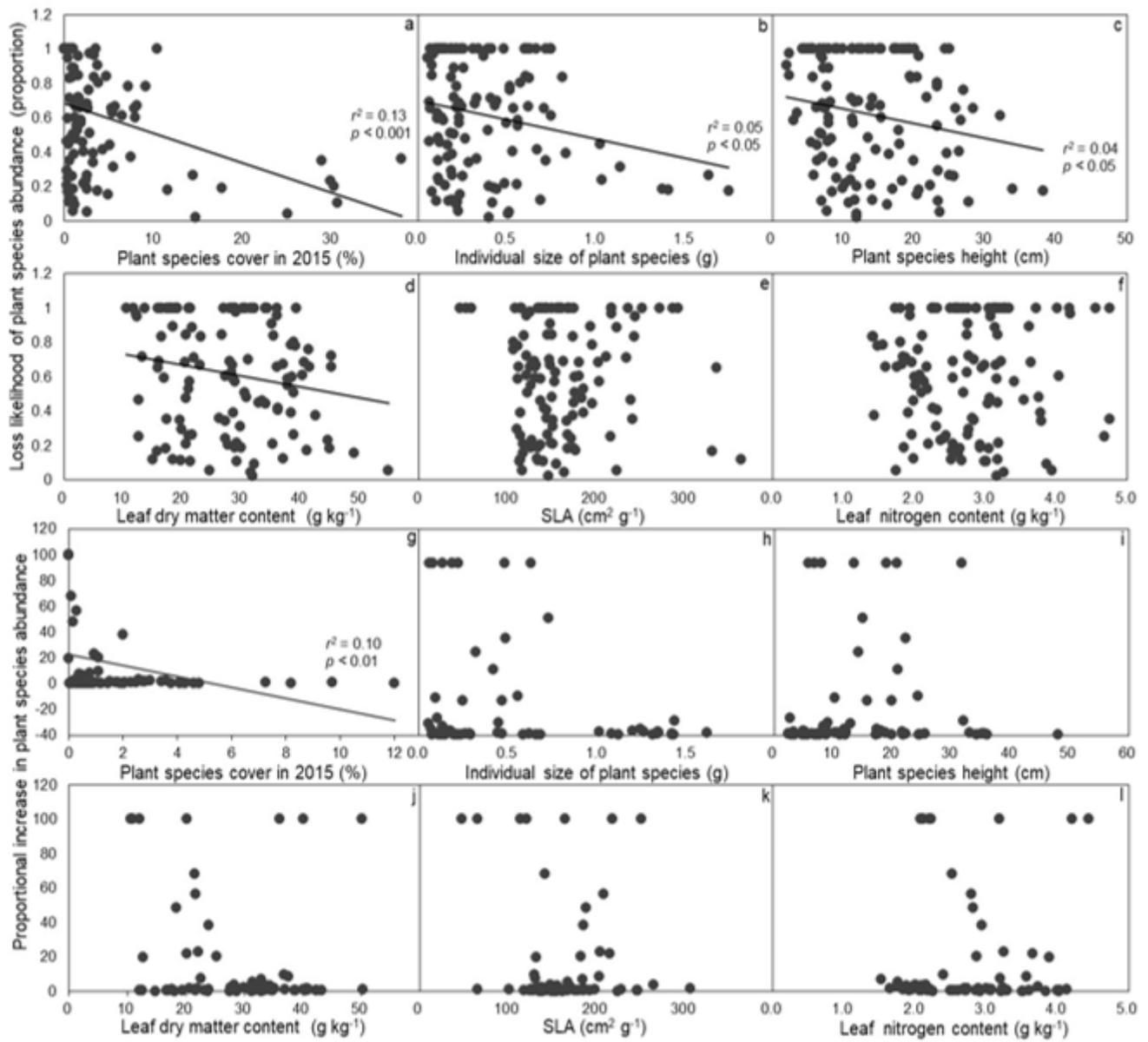


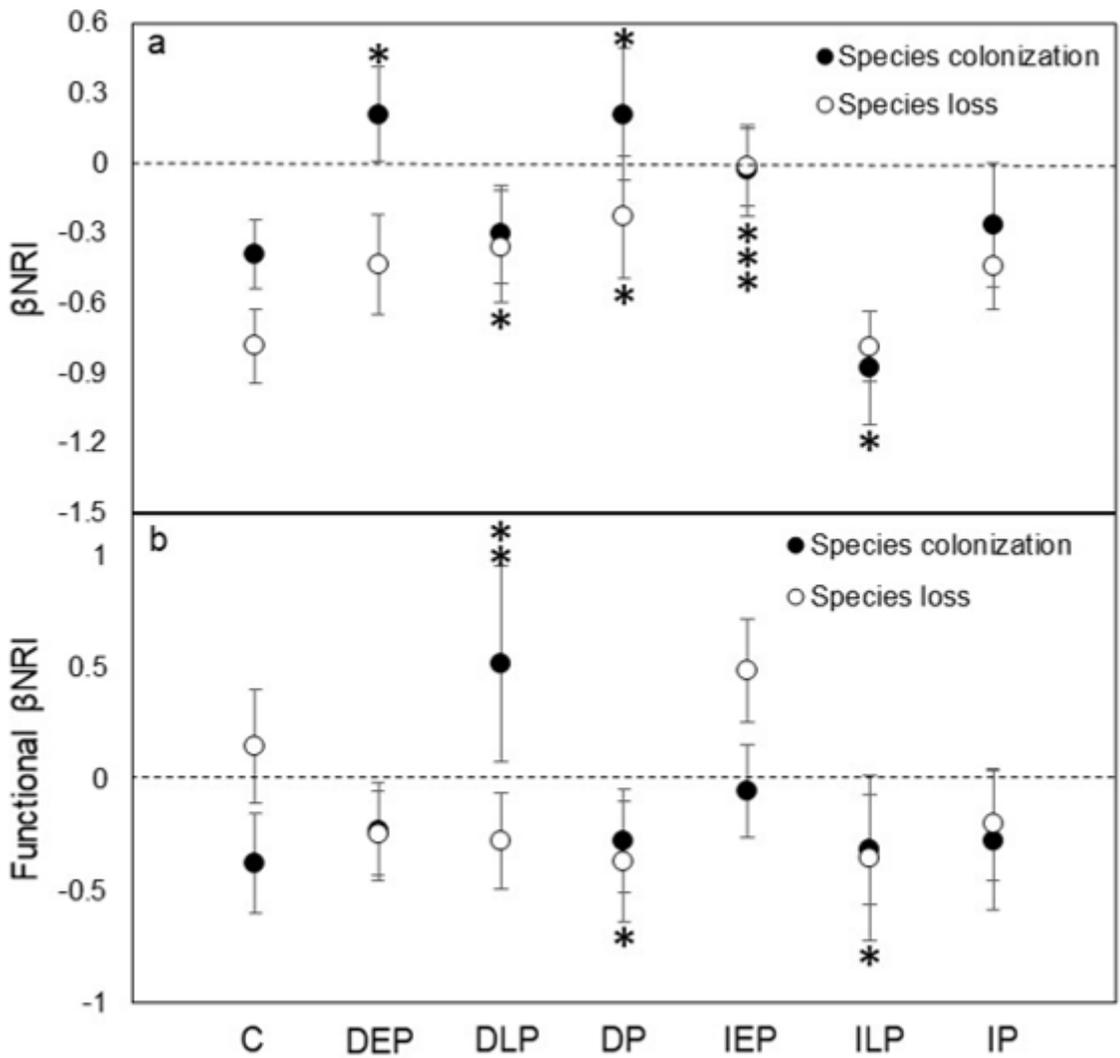
Figure 2

Effects of decreasing/increasing precipitation in the early (DEP/IEP), late (DLP/ILP), and entire (DP/IP) growing season on species loss and colonization. C represents the control. Error bars represent standard errors.



**Figure 3**

Species colonization and local loss as functions of initial abundance, leaf dry matter content, plant species height, leaf nitrogen content, specific leaf area, and individual size of plant species.



**Figure 4**

The phylogenetic/functional dissimilarity of colonizing species (solid circles) and locally lost species (open circles) to the resident species. The phylogenetic dissimilarity was calculated as  $\beta\text{NRI}$  by comparing the observed values to null models. Error bars represents standard errors. \* $P < 0.05$ , \*\* $P < 0.01$ .

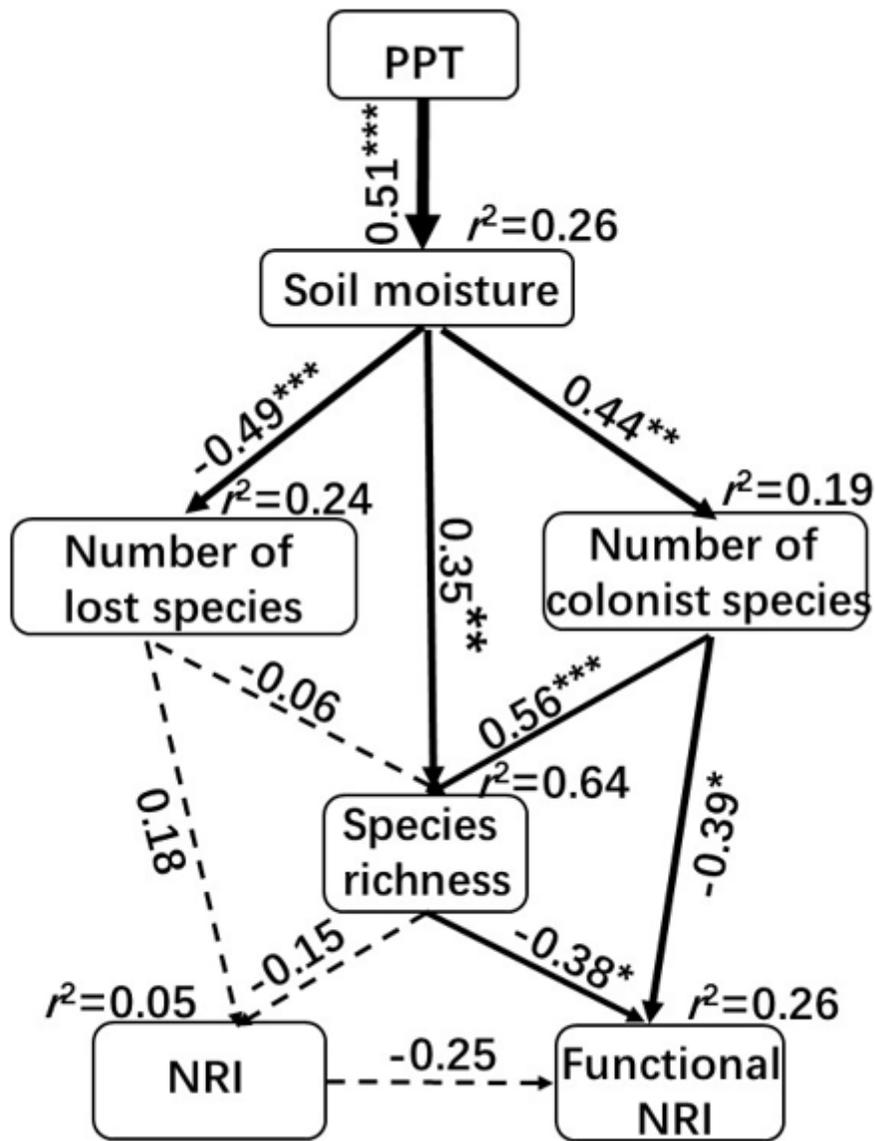


Figure 5

The result of structural equation modelling showing the causal effects of decreasing/increasing precipitation in different periods (PPT) on species richness, phylogenetic/functional net relatedness index (NRI/functional-NRI), number of colonizing species, and number of lost species via changing soil moisture. Arrows represent significant (solid) and non-significant (dashed) relationships. Width of arrows indicates the strength of the causal effect. Numbers above the arrows represent path coefficients ( $\beta$ , \*, \*\*, \*\*\* $p < 0.05, 0.01, 0.001$  respectively).  $r^2$  values represent the proportion of variance explained for each variable. Model fit summary for species richness:  $\chi^2 = 17.08, df = 12, p = 0.15$ .

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