**Shrub canopy removal influences community assembly processes in shrub-encroached grassland in the Inner Mongolia steppe, China**

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**Abstract**

Understanding community assembly mechanism is essential for us to predict community dynamics and restoration process in the context of intensive human activities. In this study, we aimed to explore how the removal of shrub canopy influenced the community assembly in shrub-encroached grassland by both trait-based and phylogenetic approaches. We carried out an experiment of shrub canopy removal with three frequencies (no removal, removal once and twice a year) in a shrub-encroached grassland in China. We investigated community species composition under each treatment and collected plant functional traits for each species. We calculated the standard effect size (SES) of phylogenetic and trait-based functional diversity based on null model analysis to determine the dominant community assembly process. By phylogenetic analysis, the random process drove the community assembly, being independent of the removal frequencies and locations; while by trait-based approach, random process dominated the assembly in communities under ‘no removal’ treatment beneath shrub and under ‘removal twice a year’ treatment in shrub-interspace when using some certain single traits, and the limiting similarity process dominated the assembly in the rest communities. Removal of shrub canopy twice a year released more niches which promoted the performance of herbaceous species beneath shrub and promoted the settlement of annuals in shrub-interspace. Compared with phylogenetic analysis, the results of trait-based approach were more sensitive to the human activities. All these findings indicated that removal of shrub canopy twice a year would be an effective way for the restoration of shrub-encroached grassland.

**KEYWORDS**

Shrub removal frequency—Phylogenetic diversity—Trait-based functional diversity—Standard effect size-Community assembly

**INTRODUCTION**

Anthropogenic disturbance can affect the community assembly processes, such as increasing opportunities for recruitment, causing mortality or altering competitive inequalities (Chesson, 2000; Myers & Harms, 2009; Brandt, Seabloom, & Cadotte, 2019). Understanding the relative contribution of each mechanism is important for ecologists to predict the potential impacts and consequences of disturbance on community diversity and composition and then to understand the community succession and predict the trajectory of community dynamics in the future (Tilman, 2004; Myers & Harms, 2009; Marteinsdóttir, Svavarsdóttir, & Thórhallsdóttir, 2018; Brandt, Seabloom, & Cadotte, 2019). When deterministic processes such as limiting similarity and habitat filtering drive the community assembly, the plant traits such as height, leaf thickness, specific leaf area, leaf dry matter content can greatly modify a species’ abundance in given local environmental conditions, which is the core of niche models (Chesson, 2000; Cornwell & Ackerly, 2009; Díaz-Sierra, Verwijmeren, Rietkerk, de Dios, & Baudena, 2017). In contrast, when random processes dominate the community assembly, the number of seeds but not the plant traits will control species abundance in a certain community (Hubbell, 2001; Tilman, 2004; Arnillas & Cadotte, 2019), which is the core of neutral model. As for trait-based functional diversity approach, distances among species along a single trait axis or within a multivariate space with multi-traits were assessed to determine the community assembly (Marteinsdóttir, Svavarsdóttir, & Thórhallsdóttir, 2018; Lai, Chong, Yee, Tan, & van Breugel, 2020).

Recently, phylogenetic diversity approach, has proved helpful to explain the community assembly process (Webb, Ackerly, McPeek, & Donoghue, 2002; Webb & Donoghue, 2005; Cadotte, Carboni, & Tatsumi, 2019). Phylogenetic distance among species is easier to obtain and compute with the assumption that potential species ecological differences are proportional to the amount of time since they diverged from a common ancestor (Webb, Ackerly, McPeek, & Donoghue, 2002; Kraft & Ackerly, 2010; Cadotte et al., 2013). However, distance related lineages might converge on similar traits or strategies. For example, the species in Cactaceae and Euphorbiaceae have the synonymous adaptations to arid environments (Caddotte et al., 2013). Because the conserved evolution of traits is a foundational assumption of the phylogenetic approach, ecologists have increasingly recognized that implementing phylogenetic approach to assess the community assembly mechanism must assess the effect of phylogenetic signals on functional traits (Webb, Ackerly, McPeek, & Donoghue, 2002; Blomberg, Garland, & Ives, 2003; Mayfield & Levine, 2010). For a certain community, the community assembly mechanisms assessed by both phylogenetic and trait-based functional diversity approaches are conceptually similar as shown in many researches. However, a number of studies have shown the inconsistent results between both approaches (Cadotte & Davies, 2016; Lososová et al. 2016; Cadotte, Carboni, & Tatsumi, 2019). Therefore, there is a need to consider both sources of information in a complementary fashion to distinguish which approach is more sensitive to disturbance in order to predict accurately the community processes.

The phenomenon that the dominant species in typical steppe have changed from grass to shrub plants (hereafter shrub encroachment) has been widely reported in the arid and semi-arid regions around the world during the past century, with the increasing shrub plant density and abundance in the grassland regions (D'Odorico, Okin, & Bestelmeyer, 2012; Saintilan & Rogers, 2015). Shrub encroachment could increase the soil resources spatially heterogeneous, causing the fertile island by concentrating resources beneath shrub and depleting resources in shrub-interspace by runoff and soil erosion (Okin, Gillette, & Herrick, 2006, Ward et al., 2018). On the other hand, the existence of shrub canopy could reduce understory light and result in the reduction in understory cover and diversity of herbaceous species (Brantley & Young, 2009). In addition, shrub encroachment has not only affected a large area of the world’s drylands at the landscape-level, but also decreased the richness and diversity of the grassland and caused impoverishment and simplification of the herbaceous communities (Henrique et al., 2016; Sholto-Douglas, Shackleton, Ruwanza, & Dold, 2017; Zhou et al., 2019). Thus, it is extremely urgent to promote the restoration of grassland from shrub encroachment.

The physical removal of shrub canopy (hereafter shrub removal) as a disturbance is a popular and widely used technique to decrease the shrub cover and growth performance and to increase the opportunities of grass growth and restoration (Archer et al., 2011). A meta-analysis of 263 publications revealed that the consequences of shrub plant removal on community dynamics were variable and that the outcome of shrub removal would strongly depend on the environmental context (Ding & Eldridge, 2019). That is to say, the patterns that remaining species occupy the free space caused by shrub canopy removal would be site-specific. However, to our knowledge, no study has focused on the community structure and assembly beneath shrub and in shrub-interspace in shrub-encroached communities, not mention to the community dynamics and assembly after the restoration measures (Brandt, Seabloom, & Cadotte, 2019). Therefore, any advance would enhance our ability to predict the trajectory of community dynamics and to provide advice on how to manage the shrub-grassland from the viewpoint of ecology.

Here, we aimed to assess which mechanism dominated the community assembly at the location of both beneath shrub and in shrub-interspace under different treatments of shrub removal frequency. We carried out an experiment of shrub canopy removal with three frequencies (no removal, removal once and twice a year) for two years in the shrub-encroached grassland in the central part of Inner Mongolia Steppe, China. We investigated the community species composition in the plots both beneath shrub and in shrub-interspace under different treatments and collected plant functional traits for each species emerging in the survey. We calculated the standard effect size of phylogenetic and trait-based functional structure based on null model analysis to determine the community assembly mechanisms for each individual community. In addition, we would test whether the results estimated by phylogenetic and trait-based functional diversity approaches were similar to each other. We expected that this study would help us capture the herbaceous community succession trajectories, which would be of significance for understanding the community dynamics and assembly process after disturbance and providing guidance for the restoration of shrub-encroached grassland.

**MATERIALS AND METHODS**

**Study region**

The experiment was conducted in a shrub-encroached grassland (42°26’ N, 116°00’ E) at about 40 km north of Plain Blue Banner administrative subdivision of Xilingol League in the Inner Mongolia Autonomous Region, China. The study region has a semi-arid continental monsoon climate with annual precipitation of 350 mm and mean annual temperature of 1.5°C. Historically, the vegetation across this region was the typical steppe dominated by perennial grasses such as *Stipa grandis* and *Leymus chinensis*. The grassland has suffered degradation and changed from normal to shrub-encroached communities due to increasing extreme climate event and anthropogenic disturbance like overgrazing utilization (Peng et al., 2013). Before we conducted the treatments, shrub *Caragana microphylla* was the dominant species with the average length of short axis, long axis and height of *Caragana microphylla* patches being 3.6 m, 2.9 m and 0.83 m, respectively, and *Agropyron cristatum*, *Artemisia frigida* and *Cleistogenes squarrosa* were the constant companions.

**Experimental design and data collection**

In April of 2017, a quadrat of 400×500 m was fenced to prevent from grazing in the study region and a randomized block design of one-factor was carried out within the fenced area with different frequencies of the removal (no removal, removal once and twice a year) of *Caragana microphylla* canopy as the factor (hereafter removal frequency). We established nine 50×50 m blocks, with three blocks per treatment. During 2017 and 2018, *Caragana microphylla* canopy was removed by using gasoline brush cutter in the middle of May for removal once a year, and in the middle of May and August for removal twice a year.

*Functional groups and plant functional traits*

In the middle of August of 2018 before shrub clipping for the ‘removal twice a year’ treatment, we selected three *Caragana microphylla* shrub patches with an interval of 20 m along the diagonal line in each block. And then, a 0.5×0.5 m plot beneath a shrub and a 0.5×0.5 m plot in the shrub-interspace were selected for each shrub patch to investigate the species composition, density and aboveground biomass of each species. The species was classified into different functional groups (annuals, perennial forbs, perennial grasses and semi-shrubs) and the relative abundance of each functional group in a certain plot was calculated. The biomass was measured after drying at 80°C for 48 h, and community biomass was the sum of all species biomass in the plot.

Three plant functional traits, plant height, specific leaf area (SLA) and leaf dry matter content (LDMC), were measured for each species in this experimental area by following the standard protocols (Pérez-Harguindeguy et al., 2013). Plant height (cm) was measured as the maximum height of each species. Fully expanded and undamaged leaves collected outside the experimental plots were selected randomly to measure SLA and LDMC. Leaf water-saturated fresh biomass and dry biomass was measured by semi-analytic balance.SLA (m2 kg-1) was calculated as the leaf area divided by leaf dry mass, and LDMC (mg g-1) was calculated as the leaf dry mass divided by the water-saturated fresh mass. These traits could capture key ecological strategies related to competitive ability such as light interception, resource acquisition and utilization.

*Community light conditions*

To determine the community light conditions at the locations beneath shrub and in shrub-interspace, the surface light density (SLD) and bottom light density (BLD) of 3–5 cm above the soil surface were measured by using a LI-250A light meter (LI-COR, Lincoln, USA) between 10:30 and 11:30 on three sunny days during August 10–15, 2018. Light attenuation rate (LAR) was calculated as (SLD–BLD)/SLD × 100%.

**Data analyses**

*Phylogenetic diversity*

We constructed a genus-level phylogenetic tree via using all species observed in our survey by the online software Phylomatic (Webb and Donoghue, 2005), built on the taxon list against a background phylogeny of plant family and genus-level relationships and returned a trimmed phylogeny for the group (Zanne et al., 2014). We calculated the mean pairwise distance (MPD), and MPD consists of the mean phylogenetic distance between all pairs of species of the same assemblage and is considered a basal measure of the phylogenetic relationships of co-occurring species as it captures the largest branches of the phylogenetic tree (Webb, Ackerly, McPeek, & Donoghue, 2002).

We calculated the Blomberg’s *K* (Blomberg, Garland, & Ives 2003) of the phylogenetic signal for each trait examined to assess the effect of phylogenetic signals on functional traits. For a certain trait, *K* equal to, lower than and higher than 1 indicates that the variation in the trait follows a Brownian model of evolution, weak or less phylogenetic signal than expected from Brownian motion (convergence), and more or stronger phylogenetic signal than expected from Brownian motion (conservatism), respectively (Ackerly, 2009).

*Trait-based functional diversity*

We calculated the functional dispersion (FDis) in each community for single and multi-traits (Laliberté & Legendre, 2010).

FDis = /

*c* = /

where *aij* is the abundance of species *j* in plot *i*. *zij* is the distance of species *j* to the weighted centroid *c* in a certain plot. *Tj*is the mean trait value of species *j* measured in the study area, n is the number of species in a certain plot.

*Standardized effect size (SES)*

To determine which mechanism dominate the community assembly process, we calculated standardized effect size (SES) by comparing the observed MPD, single-FDis or multi-FDis to the corresponding expected value generated by 999 simulations based on Null model.

SES. X= (XObserved - ‾X Expected)/SD(X Expected)

where XObserved is the observed value of MPD, single-FDis or multi- FDis in each plot, ‾X Expected  and SD (X Expected) are the mean and standard deviation of the expected value generated by Null model simulation with 999 iterations, respectively.

For normally distributed data, the absolute value of SES lower than 1.96 locates in the 95% confidence interval, suggesting random pattern.Thus the deviation from expected values was denoted significance at 0.05 level if the SES value was higher than 1.96 or lower than -1.96. Accordingly, the value of SES is significantly lower than -1.96, suggesting clustering pattern; while the value of SES is significantly higher than 1.96, indicating over-dispersion pattern. In addition, a negative (positive) SES reflects a trend of clustering (over-dispersion). Combining the effect of phylogenetic signals on functional traits and the value of SES, we could judge the dominant community assembly mechanisms (Cavender-Bares, Kozak, Fine, & Kembel, 2009).

**Statistical analyses**

Data of SES.FDis of height in the communities beneath shrub were box-cox transformed to meet the normal distribution before analyzing. First, we used randomized block analysis to analyze the effect of shrub removal frequency and block on the SES.MPD, SES.FDis, relative abundance of each functional group, the above ground biomass of herbaceous species and LAR, and found that the effect of block only significantly influenced the relative abundance of annuls beneath shrub. Therefore, we then analyzed the effect of shrub removal frequency on each variable by one way ANOVA with Tukey HSD test.

We used the function *pd* and *multiPhylosignal* in the package *picante* to calculate MPD and Blomberg’s *K* (Kembel et al., 2010), the function *gowdis* in the package *FD* to calculate the FDis (Oksanen et al., 2018), the function *nullmodel* in the package *vegan* to assess the SES (Oksanen et al., 2018).The randomized-block design analysis was conducted using the *aov* function (Banakara & Popat, 2019). All analyses were performed using R 3.6.3 (R Core Team., 2019).

**RESULTS**

**Community structure, biomass and LAR**

In the communities beneath shrub, the factor of shrub removal frequency significantly influenced the relative abundance of perennial grasses and marginally significantly influenced the relative abundance of annuals (Table 1). The relative abundance of perennial grasses was significantly higher while the relative abundance of annuals was marginally significantly lower under the ‘removal twice a year’ treatment than under ‘no removal’ treatment (Table 1, Fig. 1A). In shrub-interspace communities, the factor of shrub removal frequency significantly influenced the relative abundance of annuals, perennial forbs and semi-shrubs (Table 1). The relative abundance of annuals was significantly higher while the relative abundance of semi-shrubs was significantly lower under ‘removal once a year’ or ‘removal twice a year’ treatments than that under ‘no removal’ treatment (Fig. 1B).

In the communities beneath shrub, community biomass was significantly influenced by the shrub removal frequency, and there was significantly higher community biomass under ‘removal twice a year’ treatment than that under any of the other two treatments. For the shrub-interspace communities, the effect of shrub removal frequency was not significant on community biomass (Table 1; Fig. 2A).

At the location beneath shrub, LAR was significantly influenced by the shrub removal frequency, and the highest LAR was recorded under ‘no removal’ treatment and the lowest LAR was noted under ‘removal twice a year’ treatment. At the location in the shrub-interspace, the effect of shrub removal frequency on LAR was not significant (Table 1; Fig. 2B).

**The distribution patterns of phylogenetic and trait-based diversity**

The absolute values of SES.MPD were lower than 1.96, being independent of shrub removal frequency and location (Tables 2&3, Fig. 3). The *K* values of the phylogenetic signal for each of the traits were lower than 1 (Table 4).

In communities beneath shrub, only the mean values of SES.FDis of height was significantly influenced by the shrub removal frequency, and the mean value under ‘no removal’ treatment was significantly lower than that under any of the other two removal treatments (Table 3, Fig. 4A). The proportions of SES.FDis of height higher than 1.96 were 2/9, 6/9 and 7/9 under ‘no removal’, ‘removal once a year’ and ‘removal twice a year’, respectively (Table 2). The proportions of SES.FDis of LDMC higher than 1.96 were 2/9, 6/9 and 6/9 under ‘no removal’, ‘removal once a year’ and ‘removal twice a year’, respectively (Table 2). No SES.FDis was lower than -1.96 for any of the three traits or multi-traits.

In the shrub-interspace communities, the factor of removal frequency significantly influenced SES.FDis of multi-traits and SES.FDis of SLA, and the lowest value of each variable was found under ‘no removal’ treatment (Table 3, Fig. 4B). The proportions of SES.FDis of height higher than 1.96 were 5/9, 5/9 and 2/9 under ‘no removal’, ‘removal once a year’ and ‘removal twice a year’, respectively (Tables 2 &3).

**DISCUSSION**

Both phylogenetic and trait-based diversity approaches would provide complementary information for community assembly mechanisms. Kraft and Ackerly (2010) firstly attempted to determine community process in the tropical forest plots by both approaches, and they found congruent results. It was the first attempt to assess the community assembly mechanisms of shrub encroachment after shrub removal disturbance by both trait-based and phylogenetic diversity approaches in the same study, and the results of these two approaches were significantly different. For example, the factor of shrub removal frequency did not significantly influence SES.MPD, and all SES.MPD were between -1.96 and 1.96, suggesting random process. However, shrub removal frequency could significantly influence the mean values of SES.FDis or influence the proportion with SES.FDis values higher than 1.96 no matter beneath shrub or in shrub-interspace. These results demonstrated that the trait-based approach was more sensitive to community dynamics after disturbance than the phylogenetic approach, which was consistent with the results in a grassland restoration experiment in USA (Khalil, Gibson, Baer, & Willand, 2018). Some researchers thought that the phylogenetic approach failed to detect some additional information because phylogenetic relatedness may integrate important ecological similarities between species (Gerhold, Cahill, Winter, Bartish, & Prinzing, 2015; Cadotte, Carboni, & Tatsumi, 2019). We thought that trait-based approach can better capture fine divergence in determining of community succession process because plant trait could response quickly to environmental changes while phylogenetic response need longer time. The Blomberg’s *K* of the phylogenetic signal for each of the functional traits was lower than one. This finding suggested that closely related genetic species did not show similar traits or that traits controlling the response of a species to the disturbance were conserved and shared deeper in the phylogeny (Cadotte & Davies, 2016; Lososová et al. 2016). Therefore, trait-based approach is necessary when community assembly mechanisms were assessed in a relatively short time after anthropogenic disturbance like our study.

In the following, we discussed further the results obtained by the trait-based functional diversity approach because no difference was found for SES.MPD among different treatments and phylogenetic approach showed the same results for all communities that random process dominated the community assembly. For trait-based functional diversity, the SES lower than -1.96 suggested habitat filtering process and the SES higher than 1.96 indicated limiting similarity process that dominated the community assembly.

**Community assembly beneath shrub**

Unexpectedly, no SES.FDis was found lower than -1.96 in no removal communities beneath shrub, which indicated that habitat filtering process did not dominate the assembly of these communities. As a matter of fact, the existence and expansion of *Caragana microphylla* canopy could provide refuge for certain plant species and limit the growth of some other species (Sholto-Douglas, Shackleton, Ruwanza, & Dold, 2017), thus we expected species or trait convergence (SES < -1.96) in communities beneath shrub under no removal communities. The following could provide some explanations for the unexpected findings. First, the growth and expansion of shrubs have achieved the stage to modify the physical environment and inhibited herbaceous community construction (Henrique et al., 2016). Second, the existence of shrub canopy reduced space available for the growth of herbaceous plants and intensified resource competition (Peng et al. 2013). Third, the existence of shrub canopy would intensify the magnitude of environmental alteration beneath shrub (Wright, Jones, Boeken, & Shachak, 2006) and inhibit subsequent plant establishment on the fertile island (Koyama, Sasaki, Jamsran, & Okuro, 2015). Fourth, some articles reported that extreme modification of the light environment, coupled with heavy shrub litter fall, might exclude potential competitors during thicket establishment (Brantley & Young, 2007). In the present study, we found the highest light attenuation rate (LAR) in no shrub removal beneath shrub. Fifth, annuals are viewed as opportunistic and they acquire resources as quickly as possible (Yé Lambiénou et al., 2015). We found that the relative abundance of annuals made up nearly 50% in the no removal communities, which would increase the change of random process.

The values of SES.FDis of plant height and LDMC were significantly higher than zero in the shrub removal communities, and they were significantly higher or more divergent than those in no removal communities beneath shrub, suggesting that limiting similarity played gradually more important role in influencing community assembly in the removal communities. Shrub removal released resources especially light (Fig. 2B) originally captured by shrub and then created more opportunity for the understory herbaceous species. Therefore, there was higher community biomass in removal communities than in no removal communities. As plant density and coverage increased in the shrub removal communities, competition for light and soil nutrient among species became more intense and resource utilization became more adequate. Communities with higher trait divergence are traditionally linked to higher competition between species, as species with similar traits are expected to have similar resource requirements and thus compete more intensely (Lavorel et al. 2007, Violle & Jiang, 2009). In the present study, shrub removal significantly increased the relative abundance of perennial grasses and marginally significantly decreased the relative abundance of opportunistic annuals, and shifted the community assembly process to a more deterministic one. In addition, the restoration of the perennial grasses is an important symbol of grassland restoration (Van Auken, 2000). We did not find any significant difference of SES.FDis between the two shrub removal treatments, while there was significantly higher community biomass in shrub removal twice a year communities than in shrub removal once a year communities. These results indicated that shrub canopy removal once a year could not completely alleviate the negative impact on the herbaceous species beneath shrub due to the fact that the resprout of shrub still competed for light with herbaceous species beneath shrub. Liu (2019) claimed that shrub canopy removal once a year would be non-effective on understory plant cover in the shrub grassland in the Inner Mongolia Steppe.

**Community assembly in shrub-interspace**

In shrub interspace communities, most of the values of SES.FDis of multi-traits, SLA and LDMC were between -1.96 and 1.96, suggesting that random process dominated the community assembly. The mean values of SES.FDis of multi-traits and SLA were higher in removal communities than in no removal communities, suggesting that plant-plant competition for soil resource increased in shrub removal communities.

In no removal and removal once a year communities, limiting similarity of plant height played an important role in affecting community assembly. In the removal twice a year communities, however, random process drove the community assembly. Plant height is closely related to the ability of capturing light. The removal of *Caragana microphylla* canopy twice a year impacted the pattern of light utilization in shrub interspace, which could be explained by the relatively higher abundance of annuals in removal twice a year communities than in other communities. Similar to the cushion plants, shrub canopy can act as wind shelters and affect sediment movement patterns, and is considered as seed traps especially trapping seeds dispersed by barochory and hydrochory (Haussmann, McGeoch, & Boelhouwers, 2009; Niknam, Erfanzadeh, Ghelichnia, & Cerdà, 2018). Seed density beneath shrub is significant higher than shrub-interspace (Niknam, Erfanzadeh, Ghelichnia, & Cerdà, 2018). In removal twice a year communities, more seeds beneath shrub would move out because of the destruction of the shelter structure caused by shorter the height of shrub canopy, and then germinate in the shrub interspace.

**CONCLUSION**

The present findings expanded our understanding of how the communities beneath *Caragana microphylla* and in *Caragana microphylla* shrub-interspace responded to the disturbance of shrub canopy removal. Community assembly mechanisms estimated by trait-based functional diversity approach were more sensitive than those estimated by phylogenetic diversity approach were. The increase of the effect of limiting similarity process in shrub removal communities could be explained by the decease of vacant niches which resulted from the increasing perennial grasses beneath communities and the increasing annuals in the shrub-interspace communities, and consequently, this trend would accelerate the recession of *Caragana microphylla* (Pierce et al., 2019; Liu et al., 2019). There was no significant difference in community structure and community assembly processes between two treatments of shrub canopy removal. However, considering the rate of restoration of grassland and the biomass, removal of shrub canopy twice a year would be more effective. These results may be useful for us to understand and make clear the effect of shrub canopy removal treatment on the grassland community dynamics, and more importantly, to provide an ecological basis for the development of an effective restoration strategy.

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**CONFLICT OF INTEREST STATEMENT**

The authors declare no competing interests.

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**Table 1.** The effects of shrub removal frequencies on the relative abundance of each functional group, community biomass and light attenuation rate (LAR) by one way ANOVA. *P*-values lower than 0.05 are in boldface.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  |  |  |  |  |  |  |
| **Variable** | | **Beneath shrub** | |  | **Shrub-interspace** | |
| *F* | *P* |  | *F* | *P* |
| **The relative abundance** | Perennial grasses | 4.905 | **0.016** |  | 1.314 | 0.287 |
| Annuals | 2.545 | 0.099 |  | 19.16 | **<0.001** |
| Perennial forbs | 0.339 | 0.716 |  | 3.516 | **0.046** |
| Semi-shrubs | 0.860 | 0.436 |  | 7.33 | **0.003** |
| **Community biomass** | | 18.22 | **<0.001** |  | 1.935 | 0.166 |
| **Light attenuation rate (LAR)** | | 58.93 | **<0.001** |  | 1.192 | 0.321 |
|  |  |  |  |  |  |  |

**Table 2.** The standard effect size (SES) of phylogenetic mean pairwise distance (MPD) and trait-based diversity for each plot calculated by Null model.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Standard effect size (SES) of variable | Treatment | Beneath shrubs | | |  | Shrub-interspace | | |
| SES<-1.96 | |SES|<1.96 | SES>1.96 |  | SES<-1.96 | |SES|<1.96 | SES>1.96 |
| Phylogenetic mean pairwise distance (MPD) | No removal | 0 | 9 | 0 |  | 0 | 9 | 0 |
| Removal once a year | 0 | 9 | 0 |  | 0 | 9 | 0 |
| Removal twice a year | 0 | 9 | 0 |  | 0 | 9 | 0 |
| Multi-traits functional dispersion (FDis) | No removal | 0 | 7 | 2 |  | 0 | 9 | 0 |
| Removal once a year | 0 | 6 | 3 |  | 0 | 8 | 1 |
| Removal twice a year | 0 | 8 | 1 |  | 0 | 9 | 0 |
| FDis of height | No removal | 0 | 7 | 2 |  | 0 | 4 | 5 |
| Removal once a year | 0 | 3 | 6 |  | 0 | 4 | 5 |
| Removal twice a year | 0 | 2 | 7 |  | 0 | 7 | 2 |
| FDis of specific leaf area | No removal | 0 | 5 | 4 |  | 0 | 8 | 1 |
| Removal once a year | 0 | 6 | 3 |  | 0 | 8 | 1 |
| Removal twice a year | 0 | 5 | 4 |  | 0 | 8 | 1 |
| FDis of leaf dry matter content | No removal | 0 | 7 | 2 |  | 0 | 7 | 2 |
| Removal once a year | 0 | 3 | 6 |  | 0 | 9 | 0 |
| Removal twice a year | 0 | 3 | 6 |  | 0 | 9 | 0 |

**Table 3.** The effects of shrub removal frequency on the standard effect size (SES) of phylogenetic and trait-based diversity by one way ANOVA. *P*-values lower than 0.05 are in boldface.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  |  |  |  |  |  |
| Standard effect size (SES) of variable | Beneath shrub | |  | Shrub-interspace | |
| *F* | *P* |  | *F* | *P* |
| Phylogenetic mean pairwise distance | 1.200 | 0.319 |  | 0.235 | 0.793 |
| Multi-traits functional dispersion (FDis) | 0.375 | 0.691 |  | 8.037 | **0.002** |
| FDis of height | 4.893 | **0.017** |  | 0.783 | 0.468 |
| FDis of specific leaf area | 0.402 | 0.674 |  | 4.991 | **0.015** |
| FDis of leaf dry matter content | 0.599 | 0.557 |  | 0.054 | 0.948 |
|  |  |  |  |  |  |

**Table 4.** Blomberg’s *K* of the phylogenetic signal for each of the functional traits. *P*-values lower than 0.05 are in boldface.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  |  |  |  |  |
| Trait |  | *K* |  | *P* |
| Plant height |  | 0.015 |  | **0.028** |
| Specific leaf area, SLA |  | 0.038 |  | 0.566 |
| Leaf dry matter content, LDMC |  | 0.343 |  | **0.005** |