

Dominance Structure Plays a Leading Role In Shaping Community Stability In The Northern Tibetan Grasslands

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Abstract

Dominant species may strongly influence biotic conditions and interact with other species, and thus are important drivers of community dynamics and ecosystem functioning, particularly in the stressed environment of alpine grasslands. However, the effects of dominant species and its derived dominance structure on the community stability remain poorly understood. We examined the temporal stability of above-ground productivity (2014-2020 year) and biotic stability mechanisms in the Northern Tibetan grasslands with changing species composition and dominance structure along a precipitation gradient. Our results showed that community stability was significantly higher in the alpine meadow than the other types of grasslands. This difference was mainly attributed to higher compensatory effect and selection effect of dominant species in the mesic meadows. Furthermore, dominant structure strongly affected community stability through increasing dominant species stability and species asynchrony. However, species richness had almost little effect. Our findings demonstrate that dominant species, as foundation species, may play leading roles in shaping community stability in the alpine grasslands, highlighting the importance of conserving dominant species for stable ecosystem functioning in these fragile ecosystems under increasing environmental fluctuations.

1. Introduction

Mounting evidence has documented that biodiversity increases community stability in the fluctuating environments, but the underlying mechanisms are complex and remain controversial (Loreau and de Mazancourt 2013). Exploring the biotic drivers of temporal community stability across diverse communities will facilitate the knowledge of biodiversity-ecosystem function relationships. Therefore, unraveling the biotic mechanisms is critical for understanding the biodiversity effects on ecosystem functioning and the stable provisioning of goods and services (Craven et al. 2018; Valencia et al. 2020).

Plant communities are often considered to be stable when they have low temporal variability in primary production. So far, there are several biotic mechanisms to explain how ecosystem stability is maintained under perturbations (Goodman 1975; Grman et al. 2010; Loreau and de Mazancourt 2013; Tilman 1980). First, species diversity has been intensively found to keep communities stable through “portfolio effect” (Chen et al. 2016; Tilman et al. 2012; Wang et al. 2020). Second, species interaction creates a “compensatory effect” among asynchronous species to balance between the increase and decrease of productivity in different species (Grman et al. 2010; Loreau and de Mazancourt 2013; Song and Yu 2015). Third, dominant species can beget a “selection effect” to stabilize communities due to its prominent contribution to the productivity of the overall communities (Donohue et al. 2016; Grman et al. 2010). Species dominance may promote stability if the relative abundances of dominant species are constant (Grman et al. 2010; Sasaki and Lauenroth 2011) or asynchronous (Valencia et al. 2020). These mechanisms may act alone or operate in combination, depending on the environmental context (Grman et al. 2010). The major drivers of stability and their relative importance in respective mechanisms remain elusive in different natural ecosystems (Valencia et al. 2020; Wang et al. 2020). Previous studies have examined extensively the importance of the richness effects and species asynchrony to community

stability. However, the effects of dominant species and dominance are less understood. Until more recently their stabilizing effects on stability are emphasized (Hillebrand et al. 2008; Polley et al. 2007; Sasaki and Lauenroth 2011; Valencia et al. 2020).

Dominant species may strongly influence biotic conditions and interact with other species, and thus are important drivers of community dynamics and ecosystem functioning (Grime 1998). Dominant species may affect community stability in at least two pathways (Song et al. 2019; Wayne Polley et al. 2007). First, dominant species play a disproportionate effect than other species on the community stability through selection effect (Hillebrand et al. 2008; Loreau and de Mazancourt 2013). Second, dominant species may enhance the compensatory effect by promoting the asynchrony among dominant species (Valencia et al. 2020; Zhang et al. 2018). In fact, dominant species may be more valuable to community stability in communities with few species than with many species (Wayne Polley et al. 2007). The changes in the abundance of dominant species will influence dominance structure, i.e., dominance (or evenness) in the communities, which may differentially modify species interaction and dominance hierarchies, with uncertain consequences on community dynamics and stability (Hillebrand et al. 2008; Klanderud and Totland 2005; Sasaki and Lauenroth 2011). Given dramatic changes in the dominance structure of communities in different environment, however, few studies have addressed the effects of dominance hierarchies and on maintaining community stability in different communities despite dominance is a measure of biodiversity (Grman et al. 2010; Hillebrand et al. 2008).

Northern Tibetan alpine grasslands are characterized by low temperature and cryophilic vegetation which shifts successively from alpine meadows to meadow steppes, steppes and desert steppes along a precipitation gradient ranging from over 600 mm in the east to less than 100 mm in the west (Zong et al. 2019). These grasslands, with relatively poor species richness but diverse functional groups of sedges, grasses, forbs and legumes, are dominated by sedges in the meadows, forbs in meadows steppe, legumes in the steppes and some grasses in desert steppes (Wu et al. 2013; Zhao et al. 2017; Zong et al. 2019). Dominants often act as nursery (or foundation species) and play a key role in determining functional structure and promoting biodiversity in alpine ecosystems (Cavieres et al. 2014; Elumeeva et al. 2017). Species diversity declines throughout the precipitation gradient from east to west, yet species dominance is greatest in meadows and steppes at both ends (Wu et al. 2014; Zhang et al. 2020; Zong et al. 2019). As a result, the components of species diversity, dominance structure vary from different types of grasslands, which may contribute differently to the community stability. This combination offers a natural framework to evaluate the relative importance of species richness, temporal asynchrony, and dominance as biotic mechanisms that stabilize community stability in a precipitation gradient.

In this study, we aimed to: 1) evaluate the patterns of community stability and the components of plant diversity, i.e. species richness, evenness, dominance, and species asynchrony in different types of grasslands; and 2) unravel biotic mechanisms, and their importance in modulating the temporal stability of aboveground productivity in the overall alpine grasslands on the Northern Tibetan Plateau. We focused on investigating the roles of dominant species and dominance structure as the direct or indirect biotic drivers of community stability. We hypothesized that community stability was primarily determined by

species asynchrony in the eastern alpine meadows with diverse species. Whereas, community stability was majorly shaped by the selection effect of the dominant species in the western desert steppes with poor species. In addition, dominant species might play a leading role in shaping community stability through dominance structure. To test the hypotheses, we measured aboveground biomass, species composition and abundance of each species over seven years (2014–2020) in the peak of growing season across the four types of grassland to unravel the biotic mechanisms underpinning diversity-stability relationships.

2. Materials And Methods

2.1. Experimental sites

This study was conducted in the alpine grasslands successively categorized as alpine meadow (AM), alpine meadow steppe (AMS), alpine steppe (AS), and alpine desert steppe (ADS) along a precipitation gradient ranging from over 600 mm in the east to 100 in the west on the northern Tibetan Plateau (29°53'-36°32'N, 78°41'-92°16'E). The Northern Tibet Plateau is characterized by plateau continental climate. Mean annual temperature (MAT) is below 0 °C and the highest monthly temperature is less than 10 °C in July (Xu et al. 2008; Zhang et al. 2020). The longitudinal difference in MAT is less than 2 °C (Table S1). An average altitude is about 4500 m (a.s.l.). Soil nutrient in the alpine grassland is relatively low, with soil organic matter of 1.0~4.0% and the total nitrogen (N) concentration ranging from 0.02–0.2%, respectively from the west to the east (Zhao et al. 2017; Zhao et al. 2020; Zong et al. 2019). In 2014, we established located plots in the counties of Nagqu, Baingoin, Nyima, and Gerze along the Northern Tibetan grasslands transect, representing four typical communities of AM, AMS, AS, and ADS, respectively for long-term plant community sampling. All the plots were fenced off to prevent trampling and grazing disturbance from stocks and large animals all year round. Species richness exhibits a decreasing trend from east to west (Sun et al. 2019). Dominant species are highly variable, varying from the sedges such as *Kobresia pygmaea* (C. B. Clarke), *Carex moorcroftii* Falc. ex Boott, and the grasses as *Stipa purpurea* Griseb. to different legumes and forbs, with sedges dominated in AM and grasses and legume dominated in AS and ADS (see detail in Table S2).

2.2. Sampling and measurements

Plant community survey was conducted in three 1.0 × 1.0 m² quadrats spacing at least 50 m randomly spread within each located plots in mid-August from 2014 to 2020, the peak growth of the alpine plants. The occurrence of plant species, species richness and species cover were recorded in each of the quadrats. Aboveground biomass of each species was clipped in the center of each quadrat with an area of 0.5 × 0.5 m². The quadrats for community survey and biomass sampling were randomly located but shifted each year to avoid repeated harvesting in the successive years. All shoots clipped were oven-dried at 60 °C for 48 h until they reached a constant weight and then weighed for dry mass. We considered the aboveground biomass of a community in the peak season as the aboveground net primary productivity (ANPP).

2.3. Variable calculations

Species relative abundance was calculated by dividing the aboveground biomass of the species with the aboveground biomass of the community (Song et al. 2019). Based on the averaged relative abundance across the years from 2014 to 2020, We treated the species those the averaged relative abundance was higher than 5% as dominant species in each type of grassland (Chen et al. 2016; Ma et al. 2020; Ma et al. 2017). In addition, plant species were also sorted into four functional groups: grasses, sedges, legumes, and forbs. The results indicated that the dominant species are dominated by sedges (*Kobresia pygmaea* (C. B. Clarke) and *Carex capillacea* Boott) and grasses (*Poa crymophila* Keng) in AM, forbs (*Artemisia wellbyi* Hemsl. et Pears. ex Deasy and *Leontopodium leontopodioides* (Willd.) Beauv.) and grasses (*Poa crymophila* Keng) in AMS, grasses (*Stipa purpurea* Griseb.) and Legumes (*Astragalus confertus* Benth. ex Bunge) in AS, grasses (*Stipa purpurea* Griseb.) and Legumes (*Oxytropis microphylla* (Pall.) DC.) in ADS, respectively (see detail in Fig S2 and Table S2).

The community stability was calculated as the ratio of the temporal mean of aboveground productivity (μ) to its standard deviation (σ) over time (Isbell et al. 2009; Yang et al. 2017). The temporal stability of the dominant species and non-dominant species was also calculated by the same method.

The portfolio effect was indicated by species richness (Beaumelle et al. 2020; Cadotte 2017; Chen et al. 2016). Species richness (SR) was calculated by averaging (over the observation years) the number of species occurring in the targeted quadrats. Meanwhile, the Simpson's dominance index (D), based on species relative biomass for each plot in each year (Smith and Wilson 1996). The species evenness was calculated as $(1/D)/SR$, then averaged evenness values over the study period to estimate a plot's evenness (Grman et al. 2010; Heip 1974).

The compensatory effect was indicated by the asynchrony of the community species (Grman et al. 2010; Song and Yu 2015; Valencia et al. 2020). The community-wide asynchrony of species was quantified as:

$$\phi_c = 1 - \phi_b = 1 - \frac{\delta^2}{\left(\sum_{i=1}^n \delta_i\right)^2}$$

Where ϕ_c is the community-wide asynchrony of species based on species aboveground biomass, ϕ_b is the community-wide synchrony of species, δ^2 is the variance of the community aboveground biomass and δ_i is the standard deviation of the aboveground biomass of species i in the n species community. The value of the asynchrony is more than zero when species fluctuate asynchronously, which indicates there is a significant compensatory effect (Valencia et al. 2020). The asynchrony of dominant species and non-dominant species was quantified by the same method.

We used the dominance and dominant species stability to exploring the selection effect of dominant species and dominance structure on the stability in these four grasslands (Grman et al. 2010).

2.4. Statistical analysis

To determine the patterns of community stability and plant diversity, we used the one-way analyses of variance (ANOVAs), followed by Duncan's test to examine the differences of community stability, dominant species stability, diversity (richness and evenness), dominance structure (dominance), and species asynchrony among the four types of the alpine grassland.

One-way ANOVA was used to test the differences of species asynchrony among dominant species, non-dominant species, and whole community species. Meanwhile, we further examined the difference between the non-dominant species and dominant species stability to determine the contribution of selection effect to the stability across the four types of the alpine grassland.

To determine the contribution of biotic mechanisms to the stability of alpine grasslands, we used Pearson correlation to test the coefficients between stability, asynchrony, dominant structure. We found that dominance, evenness, dominant species stability, and dominant species asynchrony had some influence on the selection effect and compensatory effect. Hence, we applied structural equation models (SEMs) to evaluate the contributions of species richness, asynchrony, and dominance to community stability across the alpine grassland. The model fit was tested using the model chi-square and its associated *P*-value. The SEMs were run by Amos software (Amos 17.0.2, Amos Development Corporation, Crawfordville, FL, USA). Statistical analyses were completed in SPSS 21.0 (SPSS Inc. Chicago, Illinois, USA), figures were produced in Origin 2021 (OriginLab Corporation), and maps were plotted in ArcGIS 10.7 (Environmental Systems Research Institute, ESRI).

3. Results

3.1 Patterns of community stability and plant diversity in different communities

Over the 7-year observation, species richness was significantly higher in AM and AMS than in AS and ADS (Fig. 1A). But evenness was significantly lower in AM than in the others (Fig. 1B). Despite AMS had higher species richness and evenness, it had the lowest dominance and dominant species stability, showing the lowest selection effect of dominant species on community stability. However, both AM and ADS showed higher dominant species stability than the other two (Fig. 1C, D). Meanwhile, the values of species asynchrony were close to 1, suggesting obvious compensatory effects among the coexisted species in all the four types of the alpine grassland. The highest species asynchrony was found in AM (Fig. 1E). Consequently, overall effects of species asynchrony led to significantly higher community stability in AM than in the other three alpine grasslands (Fig. 1F).

3.2 Patterns of asynchrony and stability in dominant and non-dominant species

There were no differences detected between the species asynchrony of the whole community and its components in the dominant or non-dominant species except in ADS (Fig. 2A~D), suggesting that

compensatory effects emerged between dominant species and non-dominant species in ADS. Higher asynchrony of the dominant species played an important role of dominant species in determining the compensatory effect among species in ADS. Moreover, we also compared stability between dominant species and non-dominant (subordinate species) and found that the stability was significantly higher in dominant species than in non-dominant species in all alpine grasslands (Fig. 3A~ D, $P < 0.05$). These results indicated that the dominant species with higher stability had greater contribution to community stability.

3.3 Contribution of biotic mechanisms to the stability of alpine grasslands

Dominance was positively correlated with the stability of dominant species (Fig. 4A), but evenness displayed a negative relationship with dominant species asynchrony (Fig. 4B). In addition, asynchrony of dominant species was positively correlated with the asynchrony of community species (Fig. 4C). Beyond that, Community stability was found to be correlated positively with dominant species stability (Fig. 4E) and community species asynchrony (Fig. 4F) but negatively with richness (Fig. 4D). Further, our structural equation modeling revealed that the contribution of the selection effect of dominant species and compensatory effect (especially of dominant species asynchrony) are much higher than the species richness on community stability (Fig. 5). These results clearly showed that dominance structure of dominant species played a critical role in determining community stability through affecting species asynchrony and the stability of dominant species, while species richness had little effect on community stability of the studied alpine grasslands only indirectly by increasing community species asynchrony.

4. Discussion

This long-time observational survey revealed that plant community stability declined along a precipitation gradient on the northern Tibetan grasslands. Overall, community stability was maintained by higher compensatory effect and selection effect through dominance structure, in which the roles of dominant species were crucial. In contrast, species richness had a little effect. These results supported our hypotheses that community stability was primarily determined by species asynchrony in the eastern alpine meadows with diverse species. Whereas, community stability was majorly shaped by the selection effect of the dominant species in the western desert steppes with poor species. In addition, dominant species might play a leading role in shaping community stability through dominance structure. Interestingly, dominant species played a leading role in shaping community stability across the alpine grassland with a distinct precipitation gradient.

4.1. Higher compensatory effect and selection effect in enhancing community stability

Our study revealed that plant communities, for example AM with higher species richness were more stable (Fig. 1A, F), in line with the results of the many studies (Isbell et al. 2009; Ives et al. 2000; Lehman

and Tilman 2000). However, it is not necessary the case in the alpine meadow steppes (AMS) with similar species richness (Fig. 1A, F), suggesting that species richness may not be decisive in deterring community stability in this study. Furthermore, we also found that the highest community stability in AM was associated with the highest species asynchrony (compensatory effect) and dominant species stability (selection effect) (Fig. 1D, E), which was corroborated by a great number of studies (Sasaki and Lauenroth 2011; Valencia et al. 2020). In contrast, the lower stability in AMS with similar species richness was mainly due to the offsetting effect of lower dominant species stability (Fig. 1A, D). More recently, the role of dominant species in maintaining community stability has been proven by several studies (Hillebrand et al. 2008; Wayne Polley et al. 2007).

It is generally acknowledged that species composition and plant functional traits may contribute to species asynchrony of in plant communities (Chi et al. 2019; Zhang et al. 2018; Zhou et al. 2019). First, species composition is the results of long-term effects of environment and climate (Zhang et al. 2018). On the northern Tibetan plateau, only a smaller number of species coexist and dominate the grassland communities (Song et al. 2019; White et al. 2020). A large difference in species composition occurs in the communities along the precipitation gradient (Table. S1, 2). In detail, the four types of the alpine grassland are composed of various dominant functional groups, i.e., sedges and grasses in meadows, but grasses and forbs in steppes, grasses and legumes in desert steppes, respectively (Table S2, Fig. S2). Different species groups demonstrate distinct adaptation to the abiotic or biotic factors such as rainfall, temperature, and soil nutrients (Loreau and de Mazancourt 2008; Loreau and de Mazancourt 2013; Valencia et al. 2020; Zhang et al. 2018). The differences in the fundamental niches of various species could produce asynchronous responses to environmental changes, which in turn lead to asynchronous population dynamics and more stable ecosystem properties (Chen et al. 2016; Loreau and de Mazancourt 2013; Valencia et al. 2020). Second, plant function traits can objectively reflect the adaptability of plants to external environment (Pontes et al. 2007; Song et al. 2008; Suding et al. 2005). And there are differences in the plant functional traits among functional groups, especially in root traits (Busso et al. 2001; Comas et al. 2013; Pontes et al. 2007). For example, the root system is shallow and fine in sedge specie *Kobresia pygmaea* (C. B. Clarke), large and deep in forbs like *Potentilla bifurca* Linn., but thick and deep in legumes such as *Astragalus confertus* Benth. ex Bunge (Song et al. 2019). Due to differentiation in the functional traits, different species exhibit respectively intrinsic rates of natural increase, which lead to differentiated performance to environmental perturbations (Loreau and de Mazancourt 2013). These differences may affect asynchronous population dynamics, and ultimately promote a more stable community (Grman et al. 2010; Loreau and de Mazancourt 2008; Song and Yu 2015; Zhao et al. 2017). Our results showed that there were richer species in different functional groups and more comprehensive utilization of resources in AM, and high levels of species asynchrony in all the four types of grassland (Fig. 1), but only the species-poor ADS had significant difference in asynchrony between dominant and non-dominant species (Fig. 2A, B, C, and D) based on the community structures of the four types of the alpine grassland (Table S2, Fig. S2). Although the dominant species or non-dominant species of the four types of the alpine grassland were different, the co-occurring species coexisted and kept high temporal asynchrony through niche segregation and resource compensation (Lawton and Strong Jr 1981; Roscher

et al. 2011; Song and Yu 2015). Consequently, the differences in community species composition and plant function traits maintained higher species asynchrony in grasslands under environmental perturbations (Chi et al. 2019; Xu et al. 2015; Zhou et al. 2019).

In the alpine grasslands, competition for limited resources among species in the communities has increased the abundance of some species while reducing the abundance of others (Li et al. 2020; Wu et al. 2020; Zong et al. 2019). Overall, dominant species were more stable than subordinate species in the alpine grasslands, particularly in AM and ADS (Fig. 3). The stable dominant species was also observed in other studies (Grman et al. 2010; Song and Yu 2015; Wayne Polley et al. 2007). Our result indicated that greater roles of dominant species could promote ecosystem stability, providing the evidence for mass ratio hypothesis and the high performance of dominant species in stabilizing ecosystem functioning (Grman et al. 2010; Tilman 1999; Wayne Polley et al. 2007). The reason is that the dominant species *Kobresia* sp. are major competitors because of benign climate and relatively abundant resources in AM, and the dominant legumes and grasses are mainly stress-tolerator species due to stressful climate and resources in ADS (Wu et al. 2014; Zong et al. 2019).

4.2. Importance of dominant species in stabilizing the stability of alpine grasslands

We found that dominant species stability (DSS) and community asynchrony (CAS) were both positively correlated with the community stability (CS) in the alpine grasslands (Fig. 4), in accordance with other studies (Sasaki and Lauenroth 2011; Song et al. 2019; Wayne Polley et al. 2007). In natural ecosystems, the functional attributes of communities are mainly determined by dominant species. Some studies have shown that the stability of dominant species is much higher than the stability of other subordinate species in the communities. Increasing the relative abundance of dominant species will increase the stability of the community (Sasaki and Lauenroth 2011; Wayne Polley et al. 2007). Structure equation modelling also showed dominance had a positive effect on the dominant species stability (Fig. 5). Meanwhile, dominant species asynchrony also had a positive effect on community stability through enhancing the dominant species stability and community asynchrony (Fig. 5). Therefore, dominance structure, especially those of dominant species might affect community stability through dominant species stability and asynchrony of dominant species.

Dominance rather than species richness determined the community stability. For example, the selection effect of dominant species and dominant species asynchrony improved community stability (Fig. 5), particularly in AM and ADS (Fig. 1D, F). Previous studies also have demonstrated that dominant species are more important than common species or rare species in regulating community stability (Sasaki and Lauenroth 2011; Song et al. 2019). Dominant species of alpine grasslands, such as *Kobresia* sp, legumes as foundation species, influenced dominance structure and regulating stability through dominant species effect. Therefore, higher dominance played a leading role in shaping community stability in the whole alpine grasslands. Despite some studies also found that increasing dominance could weaken the effect of the species richness on community stability (Ma et al. 2020; Sasaki and Lauenroth 2011; Wayne Polley

et al. 2007) or dominant population stability due to species synchrony (Song et al. 2019). Our result proved the importance of dominant species as foundational species for the function of community ecosystem (Lepš 2014; Sasaki and Lauenroth 2011; Song et al. 2019). What's more, some scholars also indicated that the functions and services of a community ecosystem were mainly determined by the properties of dominant groups (Grman et al. 2010; Lepš 2004), indirectly supporting the "mass ratio" theory of Grime (1998)).

Overall, resource availability gradient may shape the differentiation of biotic mechanisms underlying community stability. According to the stress gradient hypothesis, the strength or importance of mutualisms increases with increasing environmental stress, with species competition prevailing in benign environments while mutualism predominating in stressful environments (Bertness and Callaway 1994; Brooker et al. 2008; Chen et al. 2019). Therefore, species interaction may exhibit stronger competition in the eastern mesic alpine meadows, whereas more mutually facilitation in the western drier alpine desert steppes along the northern Tibetan precipitation gradient. Nevertheless, in any case when interacting species have similar competitive or stress-tolerant life-history traits and abiotic stress is a limiting resource factor (e.g., water), competitive interactions between neighbors can occur at both ends of the stress gradient (Bertness and Callaway 1994; Brooker et al. 2008). As a result, besides interspecific competitions led to the dominance of *Kobresia pygmaea* in AM (Miehe et al. 2019), intraspecific competition among neighbors of dominant species, for example *Stipa* sp. also ultimately resulted in high dominance of these dominant species in ADS (Fig. 6). But interspecies interactions and dominance brought about distinct mechanisms of stabilizing plant communities. In the eastern mesic AM, interactions among species did not only increase dominance and species richness but also drove niche differentiation because of relative abundance of resources (Chen et al. 2019; Sun et al. 2019), which led to higher roles of diversity, species asynchrony and selection effects of dominant species in maintaining stability. In contrast, in the western species-poor ADS, the beneficial effects of dominant species and selection effect explained the community stability. Eventually, the major mechanisms of community stability were relatively higher effects of species richness and asynchrony in the eastern alpine meadows but replaced by selection effects of dominant species stability in ADS (Fig. 6).

5. Conclusions

Overall, we found that the temporal stability of aboveground productivity declined with decreasing precipitation in the northern Tibetan grasslands. The drivers of community stability transited from relatively higher effects of species richness and species asynchrony in the eastern end to the more important selection effect of dominant species in the western end. In any case, dominance structure played a leading role in shaping community stability. Our study contributes to understanding the importance of dominance structure and the roles of dominant species in stabilizing ecosystems, highlighting the need for conserving native dominant species in maintaining stable ecosystem functioning in the alpine grasslands.

Declarations

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Conflicts of Interest

The authors declare no conflict of interest.

Author Contributions: GH collected, analyzed, and visualized the data, and wrote the manuscript. NZ and TCZ collected, analyzed, and visualized the data. MHS provided editorial advice and revised the manuscript. XZZ provided editorial advice. PLS conceived and designed the experiments, and revised and approved the final draft.

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Figures

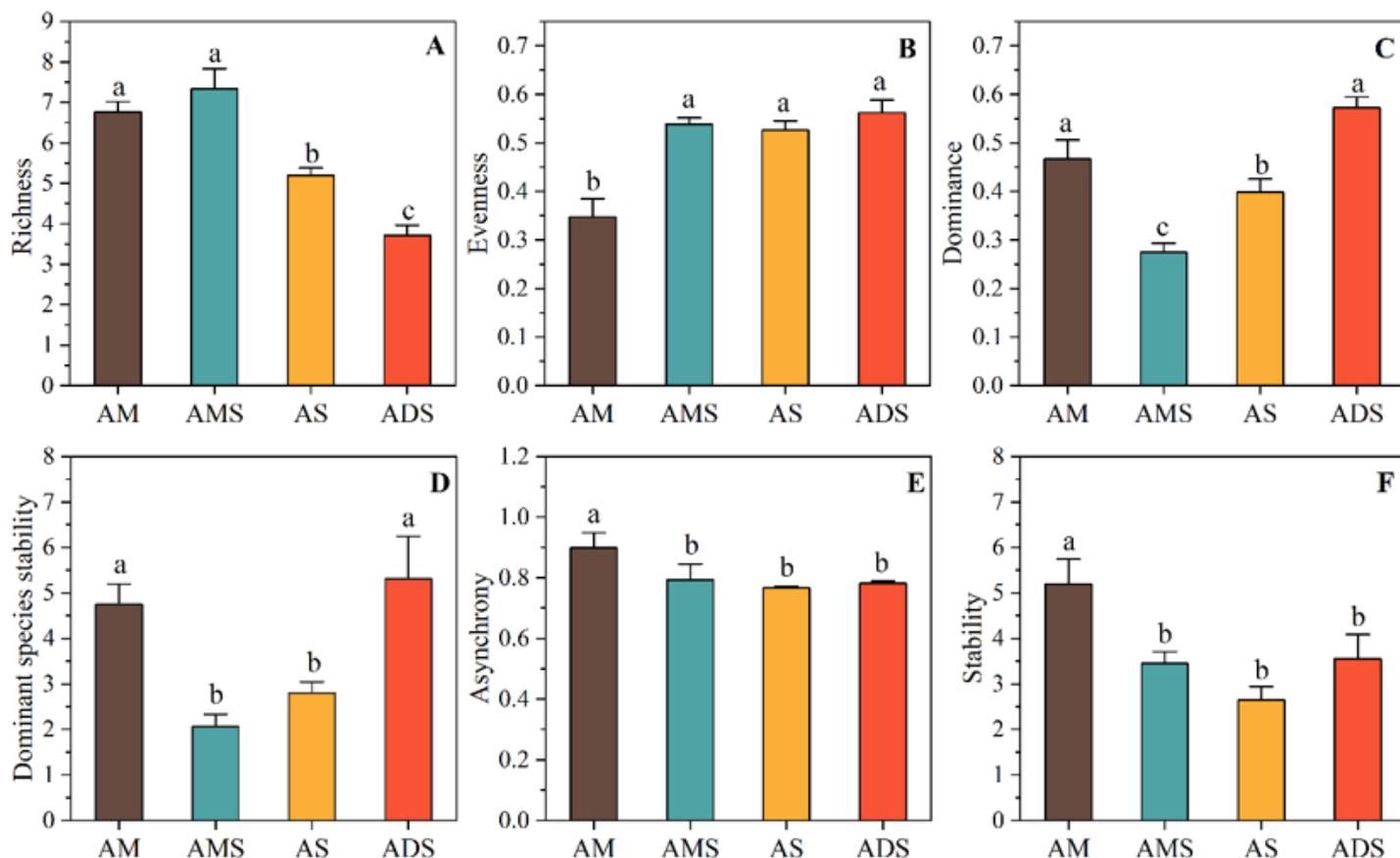


Figure 1

Richness (A), evenness (B), dominance (C), dominant species stability (D), asynchrony (E) and community stability (F) in the four major types of alpine grasslands (alpine meadow, AM; alpine meadow steppe, AMS; alpine steppe, AS and alpine desert steppe ADS). Data are shown in means \pm standard errors. Different letters represent significant differences at the $P < 0.05$ level based on Duncan's test.

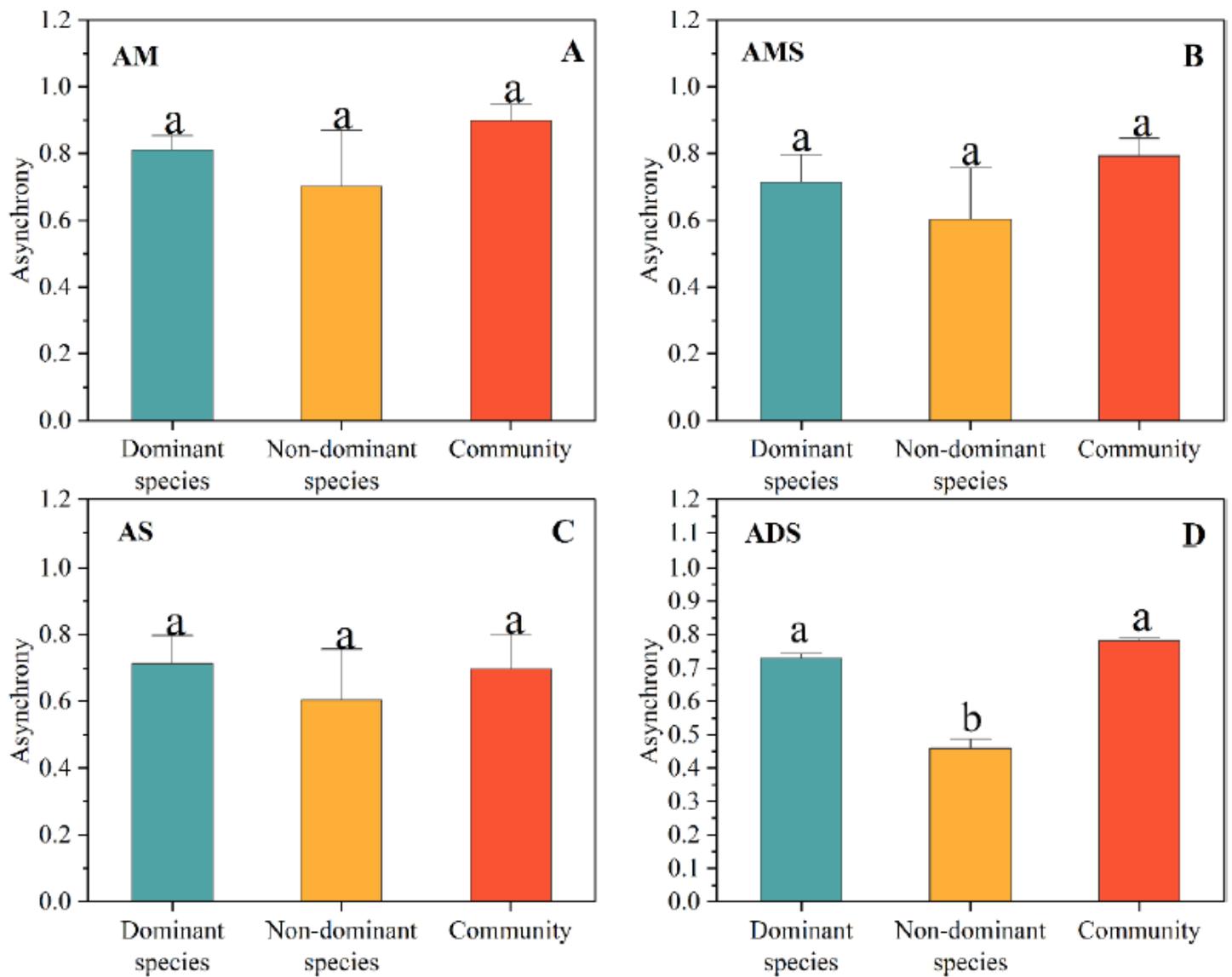


Figure 2

Asynchrony of dominant, non-dominant species and all species in corresponding plant communities in the four major types of alpine grasslands (alpine meadow, AM (A); alpine meadow steppe, AMS (B); alpine steppe, AS (C) and alpine desert steppe ADS(D)). Bars with different letters show significant differences among the different categories of species at the $P < 0.05$ level based on Duncan's test.

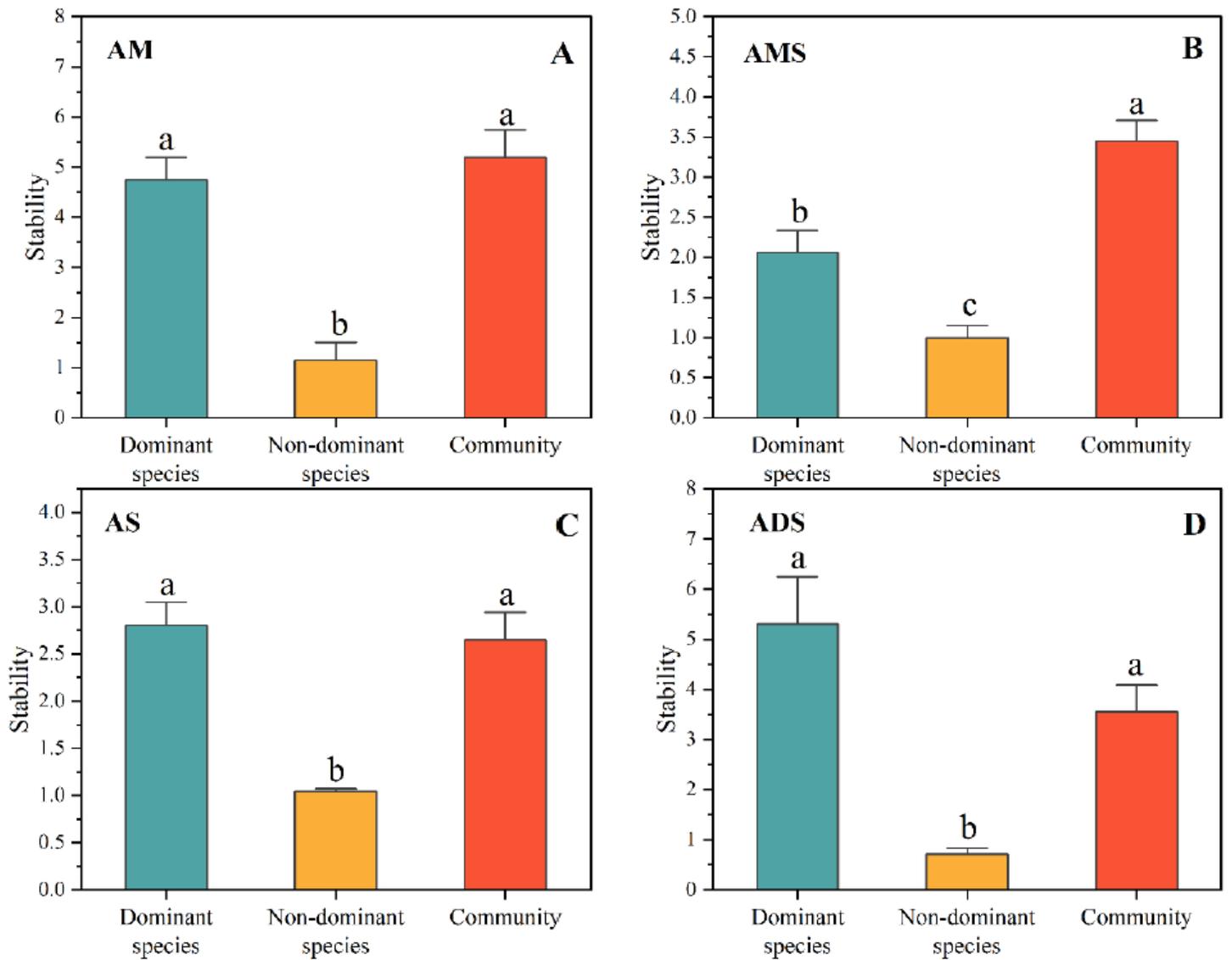


Figure 3

Stability of dominant, non-dominant species and all species in corresponding plant communities in the four major types of alpine grasslands (alpine meadow, AM; alpine meadow steppe, AMS; alpine steppe, AS and alpine desert steppe ADS). Bars with different letters represent significant differences among the different categories of species at the $P < 0.05$ level based on Duncan's test.

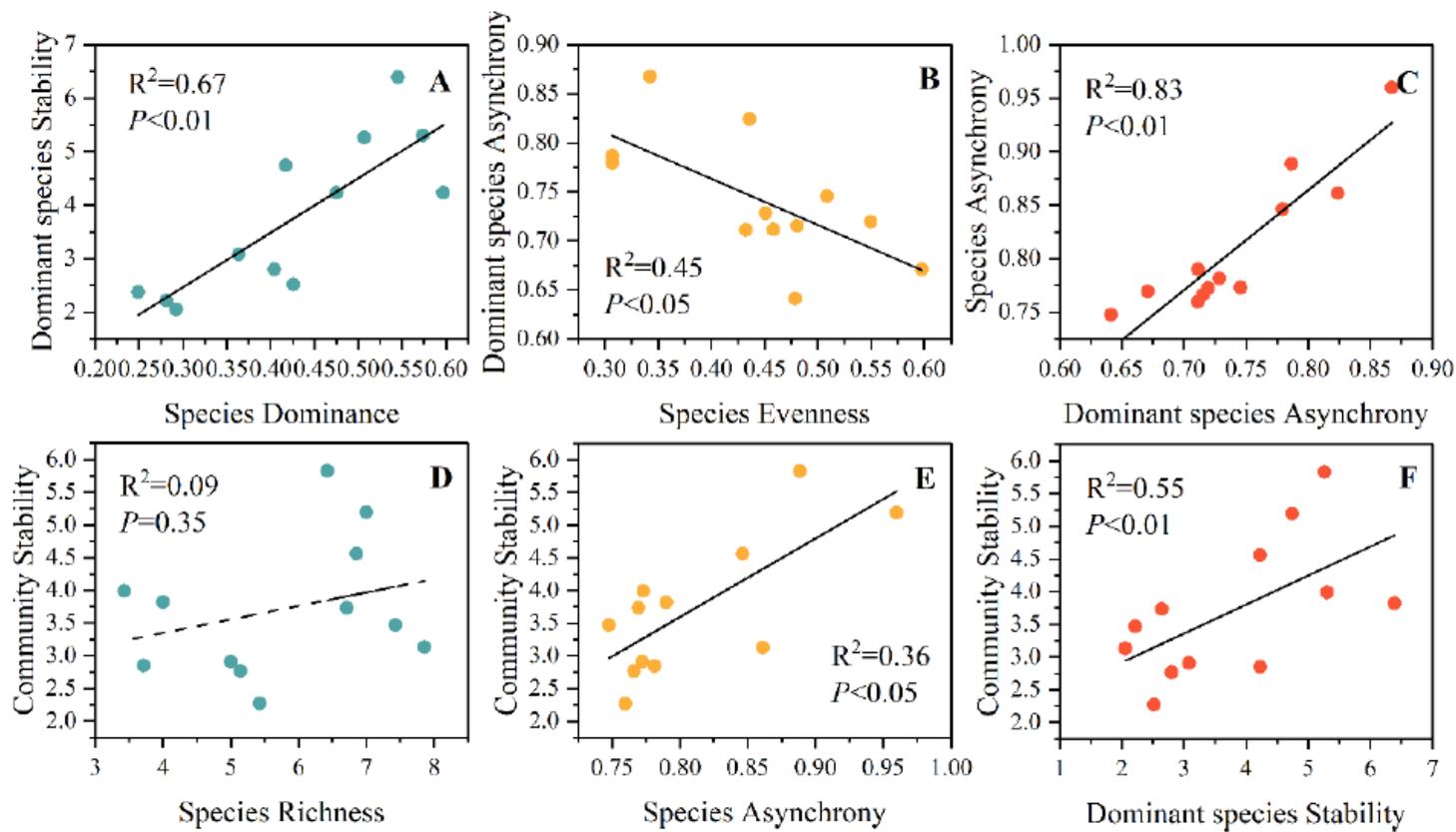


Figure 4

Correlations between species dominance and species richness (A), dominant species stability and species dominance (B), and species asynchrony and dominant species asynchrony (C). And community stability in relation to species richness (D), dominant species stability (E) and species asynchrony (F) respectively. Black solid lines represent significant linear relationships ($p<0.05$) and gray dashed lines represent non-significant linear relationships ($p>0.05$).

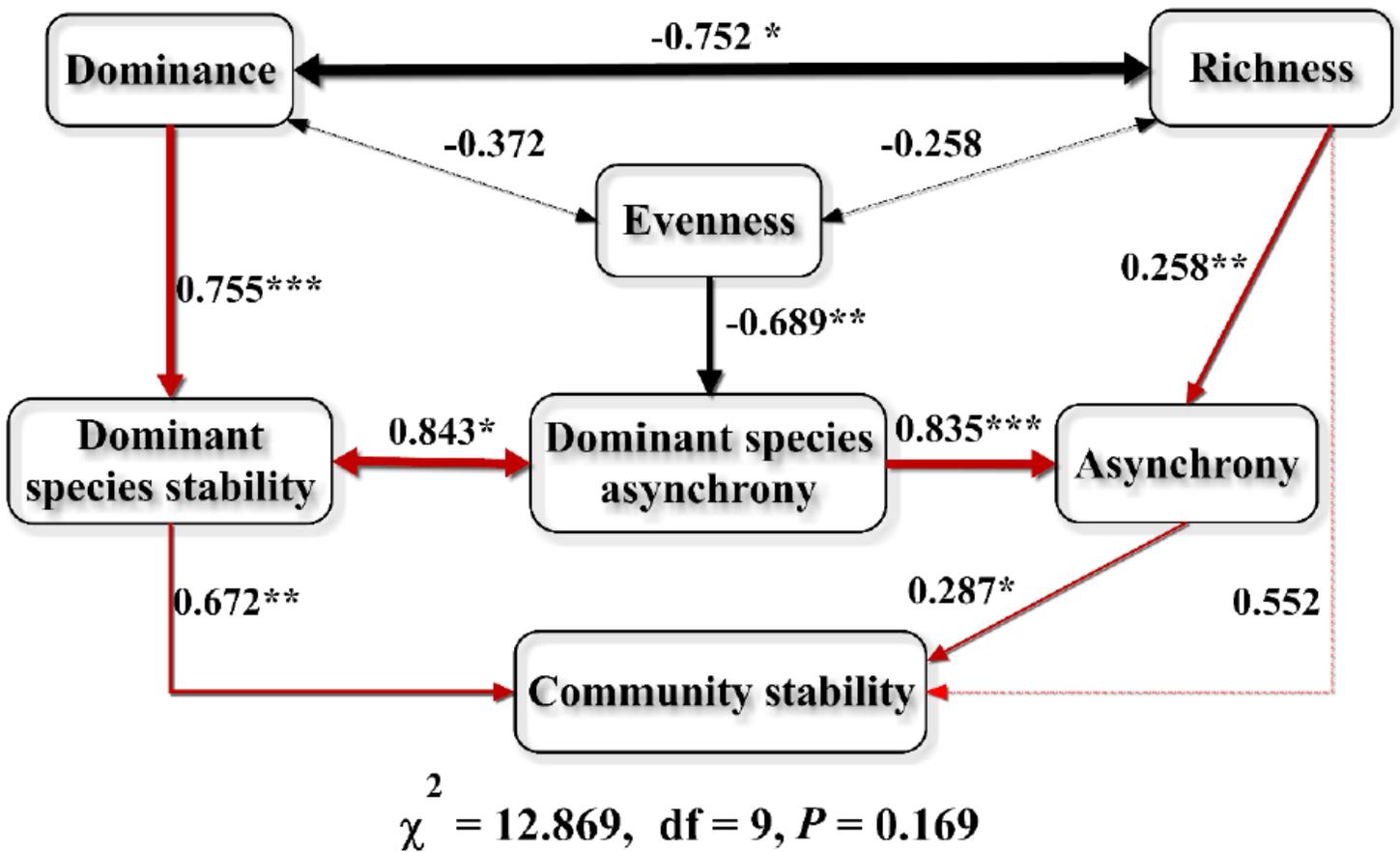


Figure 5

Structure equation modeling (SEM) examining the contributions of selection effect (dominant species stability) and compensation effect (asynchrony) to plant community stability. The thicknesses of arrows indicate the strength of the causal relationship, supplemented by a standardized regression coefficient. The red lines indicate positive correlation, black lines indicate negative correlation. Significance level: * $p < 0.05$. ** $p < 0.01$. *** $p < 0.001$. χ^2 , df , and p of the model fit are given.

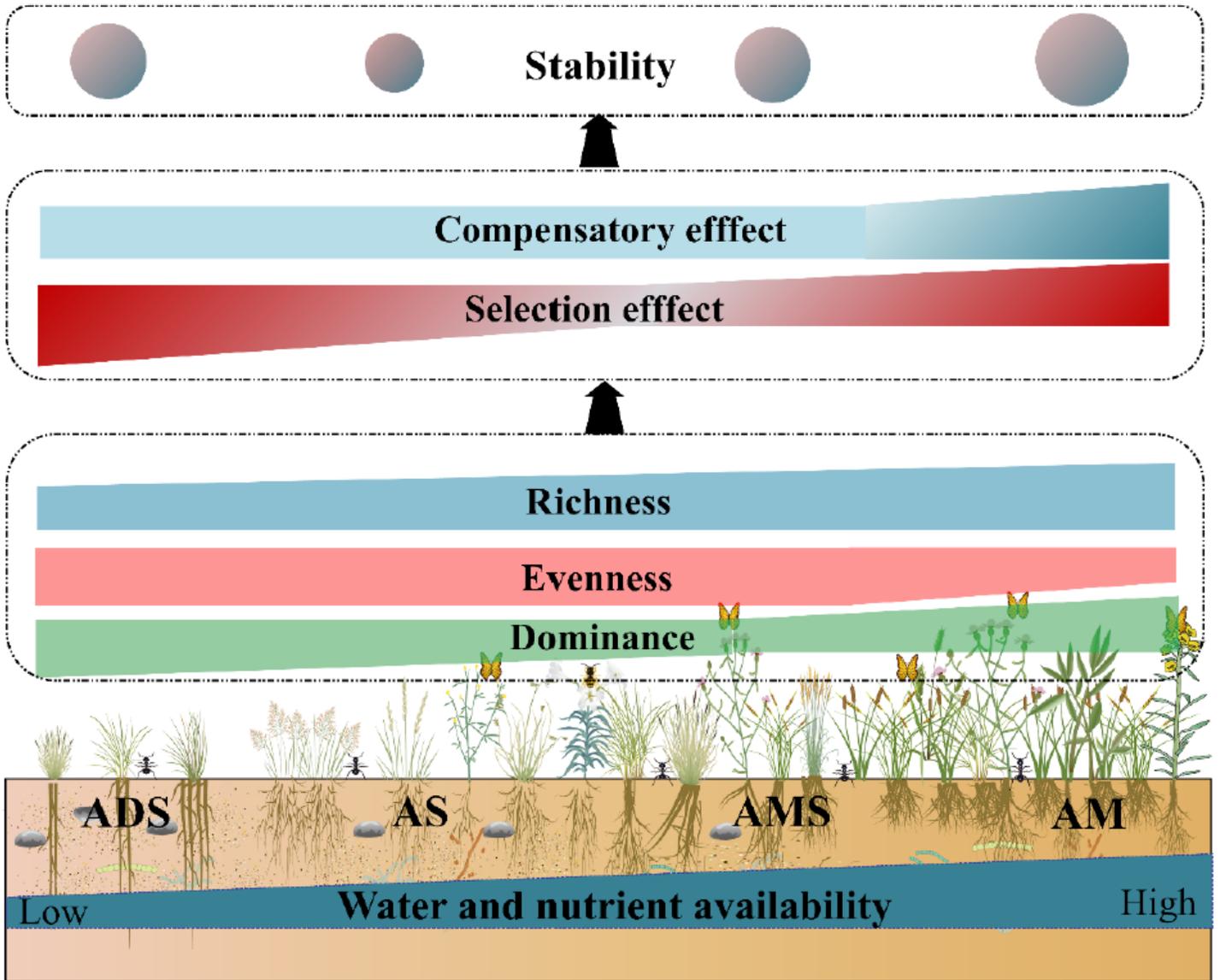


Figure 6

A schematic diagram of underlying stability mechanisms in the studied alpine grasslands. The width of the bar represents the strength of different effects

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