

Above- and belowground biodiversity jointly drive ecosystem stability in natural alpine grasslands on the Tibetan Plateau

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Funding information

the National Nature Science Foundation of China, Grant/Award Number: 31630009; the Second Tibetan Plateau Scientific Expedition and Research (STEP) Program, Grant/Award Number: 2019QZKK0302; the Qinghai Innovation Platform Construction Project: Qinghai Provincial Key Laboratory of Restoration Ecology of Cold Area, Grant/Award Number: 2017-ZJ-Y20; the Strategic Priority Research Program—"Climate Change: Carbon Budget and Relevant Issues" of the Chinese Academy of Sciences, Grant/Award Number: XDA05050404

Editor: Anne Bjorkman

Abstract

Aim: Most existing studies that examined the biotic mechanisms of ecosystem stability have focused on aboveground biodiversity. Whether and how belowground biodiversity affects the stability of natural ecosystems is largely unknown. In the present study, we investigated the relationships between above- and belowground biodiversity and the temporal stability of grassland biomass production across a large gradient of soil and climatic conditions.

Location: Tibetan Plateau.

Time period: 2001–2016.

Major taxa studied: Alpine grass and soil bacteria, arbuscular mycorrhiza (AM) fungi and fauna.

Methods: We coupled a field biodiversity survey conducted in 54 alpine grassland ecosystems across the Tibetan Plateau with a satellite-sensed proxy (enhanced vegetation index, EVI) of ecosystem productivity during 2001–2016. The temporal stability of primary productivity was calculated as the ratio of the mean annual peak EVI to the standard deviation of the annual peak EVI over this period. Plant diversity was determined using a classic vegetation survey approach, soil bacterial and AM fungal diversity were measured using a high-throughput sequencing approach, and soil fauna was counted and identified at the order level after being extracted using a modified Berlese–Tullgren method.

Results: Our results demonstrated that both above- and belowground biodiversity were positively associated with ecosystem stability. Belowground biodiversity not only affected ecosystem stability directly, but also influenced it indirectly through plant diversity and soil fertility. Furthermore, soil pH, climate and its variability strongly influenced soil biodiversity, which in turn influenced ecosystem stability.

Main conclusions: Our study demonstrates the indispensable role of belowground biodiversity in regulating ecosystem stability, emphasizing the necessity of conserving this 'hidden' biodiversity in fragile alpine ecosystems facing ongoing environmental change.

KEYWORDS

alpine grassland, belowground biodiversity, climate, ecosystem stability, EVI, natural ecosystem, soil pH, Tibetan Plateau

1 | INTRODUCTION

Evidence from theoretical, observational and experimental studies has demonstrated that higher biodiversity tends to promote ecosystem functioning and stability in the face of a changing environment (Craven et al., 2018; Garcia-Palacios et al., 2018; Gilbert et al., 2020; Hautier et al., 2015; Oehri et al., 2017; Tilman et al., 2006). The majority of these studies, however, have focused solely on aboveground biodiversity (e.g. plant diversity), neglecting the potentially important role of belowground biodiversity for ecosystem stability (Yang et al., 2018). Because of our limited understanding of this 'unseen' belowground biodiversity, whether and how soil biodiversity influences ecosystem stability remains unknown, especially in natural ecosystems. The lack of such knowledge constrains our understanding of the functional consequences of biodiversity loss, and hampers our ability to accurately predict the consequences of realistic scenarios of biodiversity change caused by ongoing global environmental change.

Soil biota includes millions of species and billions of organisms ranging from microscopic bacteria and fungi to macroscopic organisms (e.g. earthworms, ants and moles), all being found within a single ecosystem (Bardgett & van der Putten, 2014), and it therefore represents one of the largest reservoirs of biological diversity on Earth (Decaens, 2010). Soil biodiversity plays an important role in promoting the ecological processes of decomposition and nutrient cycling, and in facilitating plant nutrient acquisition and their tolerance to stress factors, consequently affecting plant performance and functioning of terrestrial ecosystems (Bardgett & van der Putten, 2014; Delgado-Baquerizo et al., 2020; Jing et al., 2015; Wagg et al., 2014, 2019). Furthermore, a growing body of literature has demonstrated the role of soil biodiversity as one of the primary drivers of plant population and community properties through plant-soil feedbacks (Bardgett & van der Putten, 2014; Bradford et al., 2002; De Deyn et al., 2003; Tederloo et al., 2020; Teste et al., 2017; van der Heijden et al., 1998). Based on the results of these studies, potential mechanistic pathways by which soil biodiversity influences ecosystem stability have been proposed (Powell & Rillig, 2018; van der Heijden et al., 2008; Yang et al., 2018). For instance, soil biota may influence ecosystem stability through direct or indirect regulation of plant diversity and community composition, aboveground net primary productivity mediated by plant water and nutrient uptake, soil nutrient supply, and species compensatory dynamics under temporally varying environmental conditions (Yang et al., 2018). Although one or a few of these potential mechanisms have been examined

in small-scale experiments (Pellkofer et al., 2016; Yang et al., 2014, 2016), they have rarely been explored across large scales, and thus across different climatic and soil environmental conditions.

The temporal stability of plant productivity is generally quantified as the ratio of the temporal mean of productivity to its standard deviation (*SD*; Craven et al., 2018; Hautier et al., 2015; Tilman et al., 2006). However, at a large scale, obtaining a long time series of plant productivity measured continuously is a great challenge. Remote sensing provides a potential approach to inferring ecosystem stability across large spatial and temporal scales using vegetation indices, such as the enhanced vegetation index (EVI) or normal difference vegetation index (NDVI). Several recent studies conducted at regional or global scales have explored the relationships between biodiversity and stability by coupling these vegetation indices with field plant diversity inventories (Garcia-Palacios et al., 2018; Oehri et al., 2017; van Rooijen et al., 2015); soil biodiversity, however, was not considered in these studies.

In the present study, we explored whether and how soil biodiversity [i.e. arbuscular mycorrhiza (AM) fungal richness, bacterial operational taxonomic units (OTUs) and faunal richness] and plant species richness influence ecosystem stability at a regional scale. We coupled a field survey of plant and soil biodiversity conducted in 54 alpine grassland ecosystems across the Tibetan Plateau with a satellite-sensed proxy of ecosystem productivity. The Tibetan Plateau covers approximately 25% of the Chinese land surface, with 64% of this region occupied by alpine grasslands (Wu, 1980). Furthermore, the Tibetan Plateau has been experiencing rapid warming at a rate of 0.2 °C per decade over the past 50 years, coupled with increasing interannual variation in precipitation (Chen et al., 2013). This may jeopardize essential ecosystem services for livestock production and, therefore, human well-being in this area. Specifically, we aimed to answer the following questions: (a) Is belowground biodiversity a significant predictor of ecosystem stability? (b) What are the relative contributions of above- and belowground biodiversity to ecosystem stability? (c) What are the direct and indirect pathways by which above- and belowground biodiversity influence ecosystem stability?

2 | METHODS

2.1 | Study sites

We surveyed 54 alpine grassland sites during the peak growing season (July–August) in 2011 across the Tibetan Plateau (Figure 1).

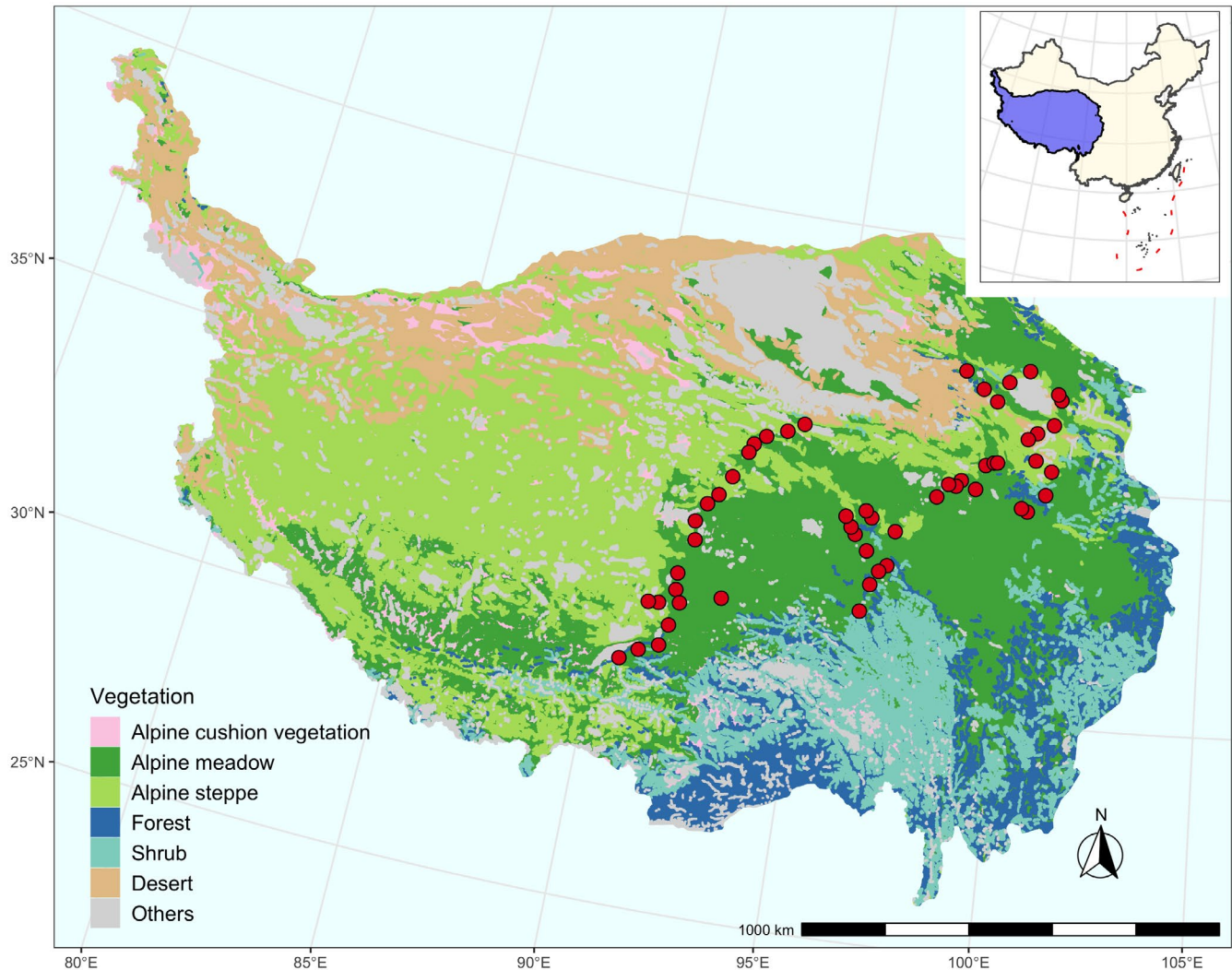


FIGURE 1 Locations of the sampling sites across the Tibetan Plateau, shown on the background of China's vegetation atlas (Chinese Academy of Sciences, 2001)

These sampling sites cover an area of over 1,000,000 km² in the north-eastern and central Tibetan Plateau. The 54 sites were located in two major vegetation types (alpine meadow and steppe). These sites comprise a reasonable representation of the geographic and climatic conditions currently found in the Tibetan Plateau, with elevation, mean annual temperature and precipitation ranging from 2,938 to 5,228 m, -4.79 to 3.51 °C and 139.70 to 653.70 mm, respectively. For more details, see the materials and methods in Jing et al. (2015).

2.2 | Above- and belowground biodiversity

At each study site, within a 100 m × 100 m plot, 10 subplots of 1 m × 1 m in size spaced by 10 m were selected along a 100-m transect, of which three (subplots 2, 6 and 10) were used to quantify local species richness, and five (subplots 1, 3, 5, 7 and 9) were used to measure soil fertility and pH. We defined aboveground plant diversity as the total number of plant species of the three species richness subplots (2, 6 and 10). Within each of the soil fertility and pH

subplots (1, 3, 5, 7 and 9), 5–7 soil cores (5 cm in diameter) were collected at 5 cm depth, bulked, and homogenized in the field. Then, one subset of soil samples was taken into the laboratory to be air-dried, sieved (2-mm mesh), and ground to a fine powder using a ball mill. The other subset of soil samples for molecular analysis was packed in polyethylene bags, immediately stored in a portable refrigerator powered with a car battery and then, stored in the lab at -20 °C until processing.

Soil DNA was extracted using a FastDNA Spin kit (Bio 101, Carlsbad, CA, USA) and amplified using the V4–V5 hypervariable regions of the 16S ribosomal RNA (16S rRNA) for bacteria and the 18S ribosomal RNA (18S rRNA) gene fragment for AM fungi. Samples for soil bacteria and AM fungi were sequenced on the Roche FLX454 pyrosequencing instruments (Roche Diagnostics Corp., Branford, CT, USA) at the Beijing Genomics Institute (BGI-Shenzhen, China). The molecular and bioinformatic analyses were performed following the protocol described by Jing et al. (2015).

Soil faunal biodiversity was assessed by sampling and homogenizing three soil cores within each plot (3.5 cm in diameter, 0–15 cm in depth).

Cores were carried into the laboratory, and then soil fauna was extracted using a modified Berlese–Tullgren apparatus (for more details, see Jing et al., 2015). Specifically, soil samples for microarthropods, which prefer dry environments, were extracted through Tullgren funnels for 48 hr (dry funnel method), while soil samples for nematodes and enchytraeids, which prefer wet environments, were wrapped in nylon cloth and extracted through Berlese funnels for 48 hr (wet funnel method). They were counted, identified at the order level, and preserved in 75% ethyl alcohol.

2.3 | Ecosystem stability

We used the EVI, which is similar to the NDVI, as the proxy of above-ground net primary productivity. Using the R package MODISTools (Tuck et al., 2014), EVI data for each site were acquired from the MOD13Q1 product with a spatial resolution of 250 m × 250 m and a temporal resolution of 16 days (23 times per year). We noted that the inconsistent area covered by the field survey plot (100 m × 100 m) and by the moderate resolution imaging spectroradiometer (MODIS) EVI pixel size (250 m × 250 m) may cause a scale mismatch. In order to reduce the effects of this spatial mismatch, we strictly selected the survey plot in an evenly distributed and homogeneous grassland at the larger landscape scale based on our field observations; second, we obtained the EVI data for each site according to its longitude and latitude information to avoid spatial bias. Additionally, Garcia-Palacios et al. (2018) showed that in global dryland ecosystem the homogeneous field survey plot (30 m × 30 m) can avoid scale mismatch with remote sensing data (250 m × 250 m). Therefore, compared to dryland ecosystems, MODIS EVI data from more homogeneous alpine grassland ecosystems can truly represent the productivity of our field survey plots.

The EVI time series were smoothed using the function *PhenoDeriv* in the R package *greenbrown* to determine the growing season start (SOS), end (EOS), and length (Forkel et al., 2015). Peak growing season activity (peak EVI), as a proxy of primary productivity, was estimated as the maximum EVI in the SOS and EOS time. Using the 16 annual peak EVIs, we quantified the temporal stability of primary productivity as the ratio of the mean annual peak EVI calculated from 2001 to 2016 (mean peak EVI) to the *SD* of the annual peak EVI (*SD* of peak EVI) over this period.

2.4 | Climatic and soil variables

We obtained annual climatic conditions (monthly mean temperature and precipitation) from the same period of ecosystem stability measurements (2001–2016) using the climatologies at high resolution for the earth's land surface areas (CHELSA) dataset (version 1.2, available at <http://chelsea-climate.org>) at a 30 arcsec resolution. Climate conditions and variability were assessed using four indices: (a) mean annual precipitation (Mean_Prec), (b) interannual rainfall variability (*SD* of annual precipitation, *SD_Prec*), (c) mean annual temperature (Mean_Temp), and (d) interannual temperature variability (*SD* of annual temperature, *SD_Temp*).

We summarized soil parameters at each site using soil organic carbon (SOC), total nitrogen and phosphorus (STN and STP), and pH. Using a CHN elemental analyser (2400 II CHN elemental analyser, PerkinElmer, Boston, MA, USA), we measured total soil carbon and nitrogen. We determined total soil phosphorus by the molybdenum blue method with an ultraviolet-visible spectrophotometer (UV-2550, Shimadzu, Kyoto, Japan). Soil CaCO₃ was analysed volumetrically on ground subsamples using a calcimeter (Eijkkamp, Netherlands). SOC was then quantified as the difference between total soil carbon and carbon bound in soil CaCO₃. Finally, we measured soil pH in a 1:5 ratio of fresh soil to deionized water slurry on a pH meter (Seven-Compact S220, Mettler-Toledo AG, Switzerland).

Due to the significant correlations between climatic and soil variables (Supporting Information Figure S1), principal component analyses (PCA) were conducted with these environmental variables; the first four principal components (PC1, PC2, PC3 and PC4) captured 92.24% of the total variation in these variables (Supporting Information Figure S2).

2.5 | Statistical analyses

To make model coefficients comparable in multi-predictor regressions, we standardized the response variables and all predictors using the z-score (overall mean of 0 and *SD* of 1) prior to analyses. Predictor variables were log- or square root (*sqrt*)-transformed when necessary before the z-score transformation to improve homoscedasticity.

First, we assessed the relationships between above- and below-ground biodiversity and ecosystem stability and its two components, namely, mean peak EVI and *SD* of peak EVI, using bivariate ordinary least-square regressions. Under field conditions, geographic and environmental variables also affect the diversity of ecosystems and their stability, and may therefore obscure the relationships between them. Then, we conducted multiple regression analyses to evaluate the influences of geographic and environmental variables, and above- and below-ground biodiversity variables on ecosystem stability and its two components. Since multivariate analyses can be confounded by collinear predictor variables, we first removed the collinear predictors (i.e. elevation in this study) as suggested by variance inflation factors. Then we built a full model with ecosystem stability and its two components as the response variables and the 11 geographic, environmental (four components of PCA of climatic and soil variables), and above- and below-ground biodiversity (plant species richness, soil AM fungal richness, soil bacterial OTUs, and soil faunal richness) variables as predictors. We conducted a model selection procedure based on corrected Akaike information criterion (AIC_c) selection ($\Delta AIC_c < 2$) on the full model to select the best predictors supported by the data. This procedure was performed using the *dredge* function in the R package *MuMIn*. AIC_c measures the relative goodness-of-fit of a given model; the lower its value, the more likely it is that this model is correct. Additionally, to evaluate the variance explained by each predictor variable in the best model, we employed the averaged over ordering method (the *lmg* metric, similar to hierarchical partitioning) to decompose *R*² using the

R package `relaimpo` (relative importance for linear regression). We included the latitude and longitude of the sampling sites to account for the spatial structure of our dataset. Because of the intrinsic circularity of longitude in the models, we used the sine and cosine of the longitude to avoid any bias.

To account for the potential effect caused by spatial autocorrelation, which could affect the interpretation of regression models (Borcard et al., 2018), we used Moran's I values to quantify the residual spatial autocorrelation of the best model. The Moran's I value of the best model for ecosystem stability and its components, respectively, was -0.028 ($p = .52$), -0.086 ($p = .77$) and -0.014 ($p = .46$), indicating little spatial autocorrelation.

Finally, using structural equation modelling (SEM), we assessed the direct and indirect relationships between above- and belowground biodiversity, soil pH, soil fertility, climate and its interannual variability, and ecosystem stability and its two components. To reduce the number of variables included in the SEM model as recommended for small sample sizes (Grace, 2006), we removed the effects of spatial variables such as longitude, latitude and elevation. Traditionally, patterns of belowground biodiversity are often explained by the 'plant diversity hypothesis', which states that higher plant diversity increases microclimatic variability and habitat complexity in soil structure and root architecture (Hooper et al., 2000; Waldrop et al., 2006). However, increasing evidence indicates that belowground biodiversity is commonly the key factor regulating plant community dynamics, and thereby plant coexistence and diversity (Bardgett & van der Putten, 2014; Bradford et al., 2002; De Deyn et al., 2003; Tedersoo et al., 2020; Teste et al., 2017; van der Heijden et al., 1998). We, therefore, constructed three types of SEM models, the first including the direct effect of belowground biodiversity on plant diversity (Supporting Information Figure S3a), the second considering the direct effect of plant diversity on soil biodiversity (Supporting Information Figure S3b) and the third containing their correlation due to the complex cause and effect between them (Supporting Information Figure S3c). In the present study, we only report results for the first SEM model in the main text, because the priori hypothesis for this model is consistent with the conceptual framework introduced by Yang et al. (2018) for understanding how soil biota affects ecosystem stability, and because the three types of SEM model yield qualitatively similar results (Figure 3; Supporting Information Figures S7 and S8). We first constructed an initial full model including all possible pathways, and then removed non-significant pathways with small path coefficients until a final model remained for which there was no significant deviation between the observed and model-implied covariance among the variables (χ^2 test; $p > .05$). These models were fitted with the maximum likelihood method, using the R package `lavaan`. All statistical analyses were performed using R 3.6.2 (R Core Team, 2019).

3 | RESULTS

Bivariate regression analyses indicated that plant species richness, soil bacterial OTUs and soil faunal richness were all significantly and

positively associated with the mean peak EVI (Supporting Information Figure S4). Additionally, soil bacterial OTUs and soil faunal richness, respectively, also had a significantly and near-significantly positive relationship with the SD of peak EVI (Supporting Information Figure S5). Consequently, plant species richness showed a significant and positive relationship with ecosystem temporal stability (Figure 2a), and soil AM fungal richness had a marginally significant positive relationship with ecosystem stability (Figure 2b). Conversely, neither soil bacterial OTUs nor soil faunal richness was related to ecosystem stability (Figure 2c,d).

Even after accounting for the strong influences of geographic, soil and climatic variables, above- and belowground biodiversity were still found to be strongly related to ecosystem stability (Table 1; Figure 3a), despite their relatively weaker effects on its two components, namely, the mean peak EVI and SD of peak EVI (Supporting Information Table S1 and Figure S6). Model selection indicated that in the 11 best models ($AIC_C < 2$) selected, nine models contained above- and belowground biodiversity simultaneously (Table 1). The best statistical model (based on corrected AIC_C value, $AIC_C = 138.6$; listed as the first model in Table 1), including both above- (plant species richness) and belowground (soil AM fungal richness) measures of biodiversity, accounted for 43% of the variation in ecosystem stability (Figure 3a). More importantly, compared with environmental variables (climate and soil, 42%), above- and belowground diversity metrics accounted for a higher proportion (54%) of the explained variance in ecosystem stability (Figure 3b). The best multi-predictor model demonstrated that PC2 (representing positive climatic variability), plant species richness and soil AM fungal richness had positive and significant influences on ecosystem stability, whereas PC4 (corresponding to positive mean annual temperature, MAT) had the opposite effect on ecosystem stability (Figure 3a).

Our SEM model explained 43% of the variation in ecosystem stability (Figure 4a), 81 and 71% of the variation in its components, the mean peak EVI and SD of peak EVI (Figure 4b), respectively, with similar quantities being explained by their best multi-predictor models (Table 1; Figure 3; Supporting Information Table S1 and Figure S6). Effects of soil biodiversity on ecosystem stability followed two paths: first, soil AM fungi had a direct strong and positive effect on ecosystem stability by increasing the mean peak EVI (Figure 4b), although soil bacteria and fauna had weak impacts on it; second, soil biodiversity had an indirect positive influence on ecosystem stability via its positive effects on plant species richness, despite these effects being not statistically significant due to the weak correlations between them (Figure 4b); soil biodiversity may have a weak negative impact on ecosystem stability through increasing soil fertility by soil fauna, because soil fertility had an equal positive effect on the SD of peak EVI and mean peak EVI (Figure 4b; standardized path coefficient: $.63$ vs. $.69$). Our SEM model also indicated that the significant positive impact of plant species richness on ecosystem stability was mainly through reducing the SD of peak EVI, rather than increasing the mean peak EVI (Figure 4b), which was also supported by the best multivariate models (Supporting Information Figure S6). Additionally, climatic

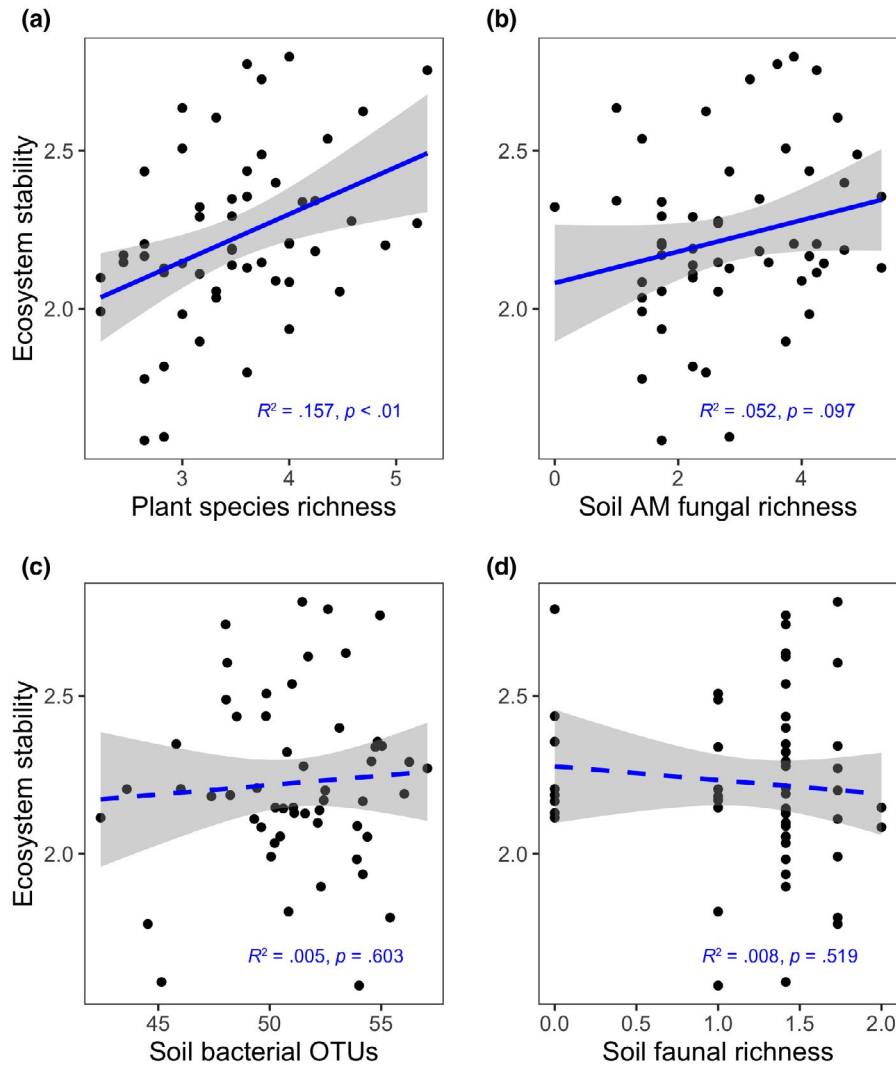


FIGURE 2 Bivariate relationships between ecosystem stability and plant species richness (a), soil arbuscular mycorrhiza (AM) fungal richness (b), soil bacterial operational taxonomic units (OTUs) (c) and soil faunal richness (d) in alpine grasslands on the Tibetan Plateau. Shaded areas represent 95% confidence intervals. Note above- and belowground biodiversity metrics were all square root (sqrt)-transformed. Solid line, $p < .1$; long-dash line, $p > .1$

variability, indicated by the SD of annual temperature, had a direct marginal and positive influence on ecosystem stability by reducing SD of peak EVI to a greater extent than mean peak EVI (standardized path coefficient: $-.31$ vs. $-.18$; Figure 4b). Furthermore, ecosystem stability was strongly determined by the SD of peak EVI relative to the mean peak EVI (Supporting Information Figure S10); the mean annual temperature had the opposite effect on ecosystem stability mainly by increasing the SD of peak EVI (Figure 4b). The lack of a direct effect of interannual rainfall variability on ecosystem stability in our SEM models may be ascribed to the quadratic relationship between them revealed by the bivariate regression analysis (Supporting Information Figure S9f). Lastly, owing to its almost equal influences on both the mean peak EVI and SD of peak EVI (standardized path coefficient: $-.22$ vs. $-.30$; Figure 4b), soil pH did not directly affect ecosystem stability (Figure 4a; Supporting Information Figure S9d). However, soil pH affected ecosystem stability indirectly by altering above- and

belowground biodiversity, and soil fertility. Specifically, soil pH had a positive influence on soil AM fungal richness, and negative effects on soil bacteria and plant species richness, which promote ecosystem stability, and on soil fertility, which reduces ecosystem stability (Figure 4a).

4 | DISCUSSION

Our study provides empirical evidence that belowground biodiversity contributes to the temporal stability of ecosystem productivity. After considering soil and climatic variables, the best-performing model including both aboveground and belowground biodiversity accounts for 43% of the variation in ecosystem stability. This value is larger than those [29%: van Rooijen et al. (2015), 16%: Oehri et al. (2017) and 29–33%: Huang et al. (2016)] in several previous large-scale studies that evaluated ecosystem stability using remote sensing

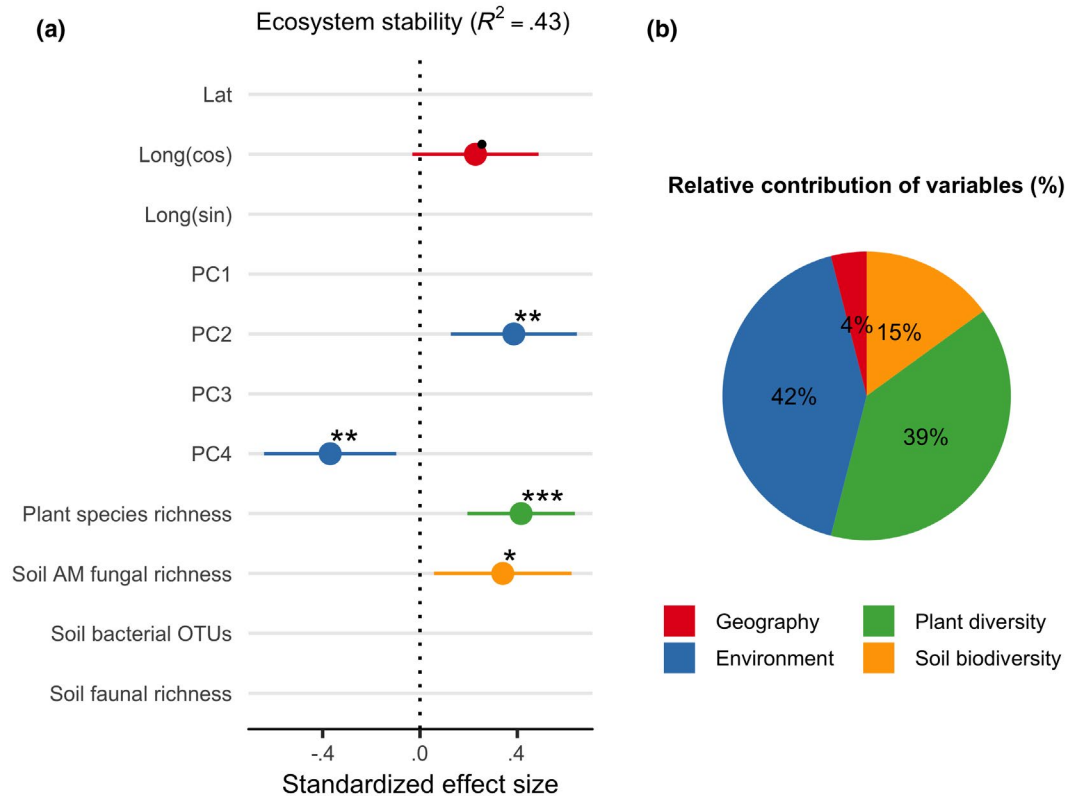


FIGURE 3 Standardized effect size (a) and relative contribution (b) of multiple predictors of the best-fit model (the first model in Table 1) for ecosystem stability in alpine grasslands on the Tibetan Plateau. The standardized effect sizes (standardized regression coefficients) are shown with their 95% confidence intervals, and the relative contribution (%), the variance explained by each predictor variable, is evaluated using the averaged over orderings method (the lmg metric in relaimpo R package). Significance level: • $p < .10$. * $p < .05$. ** $p < .01$. *** $p < .001$. AM = arbuscular mycorrhiza; OTUs = operational taxonomic units; PC = principal component

TABLE 1 Best-fitting regression models of ecosystem stability in alpine grasslands across the Tibetan Plateau. Each column represents a different predictor variable [red, geographic variables; blue, environmental variables; green, plant species richness; yellow, soil biodiversity including soil arbuscular mycorrhiza (AM) fungi, bacteria and fauna]. The best 11 models are presented, ranked according to the corrected Akaike information criterion (AIC_c). AIC_c measures the relative goodness-of-fit of a given model; the lower its value, the more likely it is that this model is correct. Unshaded cells indicate variables that were not included in a particular model. The first model of the table is the best model including both above- and belowground biodiversity

Geographic			Environmental				Soil biodiversity			R^2	AIC_c	ΔAIC_c	w_i	
Lat	Long(cos)	Long(sin)	PC1	PC2	PC3	PC4	Species richness	AM fungi	Bacteria					Fauna
	■			■		■	■	■			.4270	138.6	0.00	.146
	■			■		■	■	■			.4528	138.9	0.27	.127
			■	■		■	■	■			.4210	139.2	0.56	.110
			■	■		■	■	■	■		.4489	139.3	0.66	.105
	■		■	■		■	■	■			.3897	139.4	0.76	.100
	■		■	■		■	■	■			.4451	139.6	1.03	.088
			■	■		■	■	■			.3813	140.1	1.49	.069
			■	■		■	■	■			.3511	140.1	1.53	.068
	■	■	■	■		■	■	■			.4675	140.3	1.70	.063
	■		■	■		■	■	■	■		.3776	140.3	1.72	.062
	■		■	■		■	■	■	■		.4378	140.3	1.73	.062

Note: ΔAIC_c = difference between the AIC_c of each model and that of the best model; w_i = Akaike weights; PC1, PC2, PC3 and PC4 = first, second, third and fourth components of a principal components analysis performed with soil and climatic variables; Lat = latitude; Long(cos) and Long(sin) = cos- and sin-transformed longitude, respectively.

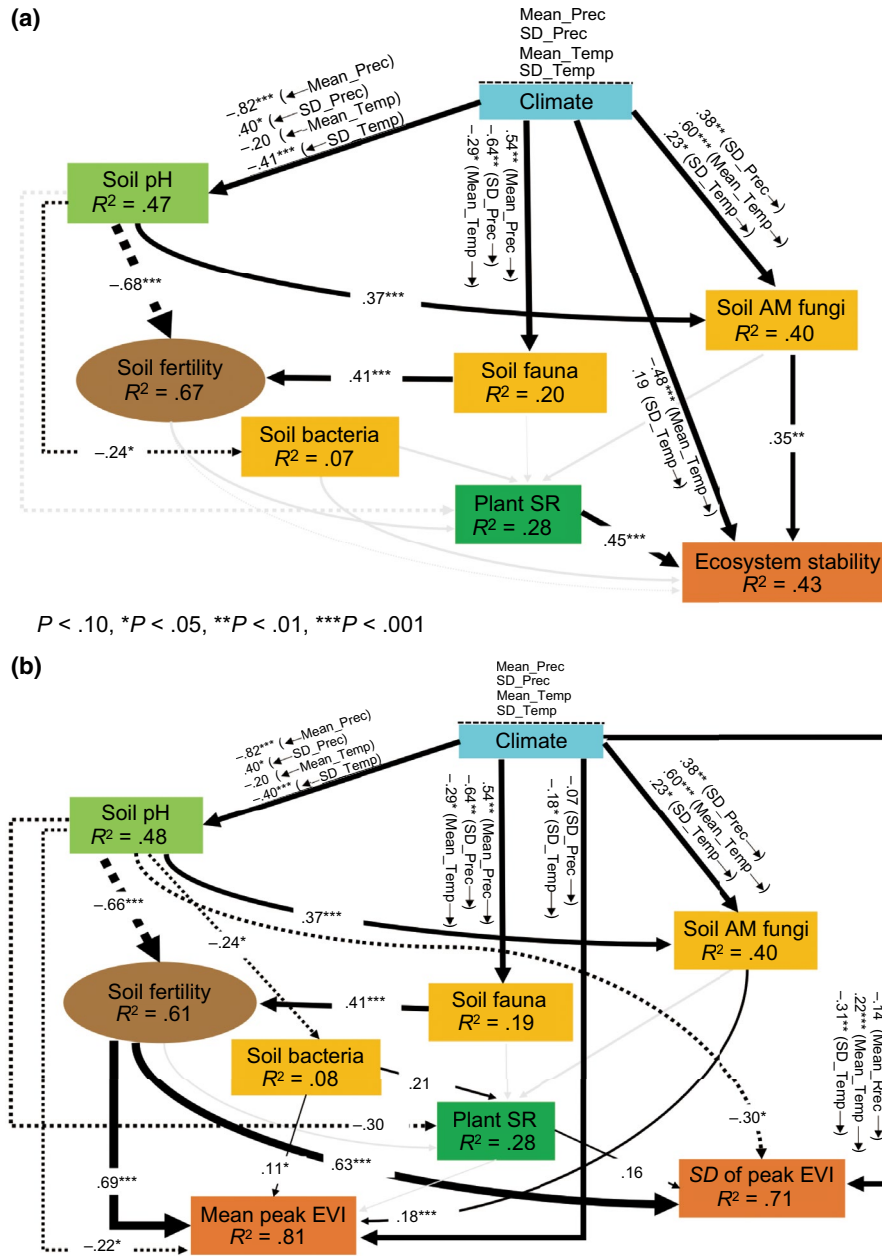


FIGURE 4 Relationships between environment variables, above- and belowground diversity, and ecosystem stability (a, $\chi^2 = 24.631$, $df = 34$, $p = .881$) and its components, mean peak enhanced vegetation index (EVI) and SD of peak EVI (b, $\chi^2 = 25.501$, $df = 39$, $p = .953$) in alpine grasslands across the Tibetan Plateau. For graphical simplicity, we put climatic predictors [mean annual precipitation (Mean_Prec), interannual precipitation variability (SD_Prec), mean annual temperature (Mean_Temp) and interannual temperature variability (SD_Temp)] into the same box in the structural equation modelling (SEM). Soil fertility, the latent variable, was composed of soil organic carbon (SOC), soil total nitrogen (STN) and soil total phosphorus (STP). The weight of the arrows indicates the strength of the causal relationship, supplemented by a standardized path coefficient. Significance level: $\bullet p < .10$. $*p < .05$. $**p < .01$. $***p < .001$. AM = arbuscular mycorrhiza; SR = species richness

approaches, but lower than that in a study from global drylands explaining 73% of the variation in ecosystem stability (Garcia-Palacios et al., 2018). Furthermore, the above- and belowground biodiversity considered in our study was more important than soil and climatic features (54 vs. 42%), suggesting that the stabilizing role of biodiversity is ubiquitous and strong in natural ecosystems.

Consistent with the accumulating evidence in most existing studies (Craven et al., 2018; Garcia-Palacios et al., 2018; Hautier

et al., 2015; Isbell et al., 2009; Oehri et al., 2017; Tilman et al., 2006), our study revealed that plant species richness promotes ecosystem stability. However, combining soil biodiversity with plant diversity increased the predictive power of biodiversity on ecosystem stability. A recent study has demonstrated the important role of soil biodiversity in the resistance of multifunctionality (e.g. soil carbon, nitrogen and phosphorus cycling) to global change in dryland ecosystems (Delgado-Baquerizo et al., 2017). Our study is unique in that

we simultaneously considered the influences of both aboveground and belowground biodiversity, accounting for 43% of the observed variation in ecosystem stability across sites, although soil biodiversity had a lesser effect on ecosystem stability than plant diversity (15 vs. 39%). The simultaneous influence of above- and belowground biodiversity emphasizes the need to change from only considering aboveground biodiversity as conducted in most stability studies to include plant and soil biodiversity together to understand their combined effects on the stability of terrestrial ecosystems.

Soil biodiversity affected ecosystem stability via multiple direct and indirect pathways through soil nutrient availability or plant species richness. However, the strength and direction of these effects varied among soil biota groups. As a major contributor to plant performance and plant community structure (Tedersoo et al., 2020; Teste et al., 2017; van der Heijden et al., 2008), AM fungi may influence ecosystem stability by regulating plant diversity, since there are strongly positive linkages between plant diversity and ecosystem stability, as demonstrated in the aforementioned studies. In contrast to the significantly positive relationship between AM fungal richness and plant species richness found in a native North American grassland (Hiiesalu et al., 2014), we only detected a weakly positive association between them. This implies that the ability of AM fungi to stabilize the temporal production of alpine grasslands, mediated by plant diversity, may be not the main pathway, or may be undetectable at the large regional scale that we studied. Additionally, several studies conducted at local scales (Pellkofer et al., 2016; Yang et al., 2014, 2016), found that AM fungi contributed to stabilizing the biomass production of plant communities over time by increasing asynchrony among plant species, which has been identified as a key mechanism driving ecosystem stability (Loreau & de Mazancourt, 2013). This mechanism may have operated in our study, although it is challenging to demonstrate the operation of this mechanism in natural ecosystems across large geographic scales. Future experiments across different sites are needed to look into the role of species asynchrony in our study. Moreover, in our study, the significant and positive influence of AM fungi on alpine ecosystem stability was mainly through markedly increasing the temporal productivity of the ecosystem. This is probably caused by the external mycelium of AM fungi increasing water and nutrient uptake and reducing nutrient losses via leaching (Bender et al., 2015; Tedersoo & Bahram, 2019; van der Heijden et al., 1998, 2015; Wagg et al., 2014).

Available evidence also indicates that free-living soil biota may contribute to ecosystem stability by directly or indirectly regulating plant diversity (Bradford et al., 2002; De Deyn et al., 2003; van der Heijden et al., 2008). For example, De Deyn et al. (2003) reported that soil invertebrate fauna directly promoted plant diversity by suppressing the biomass of the dominant plant species. In contrast, we found that free-living soil bacteria and fauna had relatively weak influences on plant diversity. Additionally, similar to soil AM fungi, soil bacteria also had a direct yet non-significant impact on ecosystem stability by significantly enhancing the mean productivity. We found that soil fauna markedly enhanced soil fertility; however, soil fertility had nearly the same effects on mean productivity and its variability,

and hence there was no indirect influence of soil fauna on ecosystem stability mediated by soil fertility. Our findings suggest that not all soil organisms are equally important for the stability of ecosystem functioning.

In complex natural systems, environmental factors vary greatly across space and time, and thus these abiotic factors can be even more important in driving ecosystem stability than biodiversity (Gilbert et al., 2020; van der Plas, 2019). Our results demonstrated that abiotic (soil and climate) factors explained 42% of the observed variation in ecosystem stability, providing direct evidence that in naturally assembled communities climate (and its temporal variability) and soil pH may be key drivers of ecosystem stability. Consistent with an experimental study in this region (Ma et al., 2017), MAT showed an apparent negative impact on the stability of the alpine ecosystem by increasing interannual variation in productivity (Figure 3; Supporting Information Figure S9g). This result suggests that projected increases in MAT [1.5 to 4.5 °C by the end of the 21st century (IPCC, 2013)] will decrease the ability of alpine ecosystems to maintain the stability of functioning related to primary productivity. Conversely, interannual temperature variation had a significant positive effect on ecosystem stability (Supporting Information Figure S9h), despite the effect being marginal in our SEM models. Consistent with a study from global drylands (Garcia-Palacios et al., 2018), interannual variation in rainfall had a significant hump-shaped relationship with ecosystem stability (Supporting Information Figure S9f), indicating that alpine ecosystems under an intermediate level of interannual rainfall variability were most stable. However, conversely, the nonlinear relationship may also imply that once a threshold in climatic conditions is reached, ecosystem stability abruptly declines. This may be an important factor leading to the degradation and desertification of alpine grassland ecosystems across the Tibetan Plateau in recent decades (Liu et al., 2018). These positive impacts of interannual variability in climate on the ecosystem stability of alpine grasslands are interesting findings, especially in an era of increased climatic variability (Stott, 2016). Nevertheless, our results conflicted with several previous studies in temperate grasslands (Craven et al., 2018; Hallett et al., 2014; Zhang et al., 2018), while Ma et al. (2017) found that changes in precipitation did not alter the biomass temporal stability of an alpine ecosystem. The conflicting results from our study and previous research may reflect the differences in climate variation among regions (Gilbert et al., 2020). Our SEM analyses also revealed the complex and indirect effects of climate and its variability on ecosystem stability through belowground biodiversity, which was positively related to ecosystem stability. These results suggest that conserving the 'hidden' diversity of soil organisms may be crucial for sustaining the provision of ecosystem services under more frequent climate variability in the future on the Tibetan Plateau.

Compared with climate and other soil variables, we found that soil pH mainly affected ecosystem stability indirectly via soil fertility and above- and belowground biodiversity. This is similar to the finding in drylands across the globe that soil pH controlled the effects of particular microbial taxa on multifunctionality resistance to global change (Delgado-Baquerizo et al., 2017). Yang et al. (2012) found

that soils from the Tibetan Plateau had experienced a decreasing pH trend during the past 20 years. Soil pH is a major driver of the microbial composition in terrestrial ecosystems (Bahram et al., 2018; Delgado-Baquerizo et al., 2018; Tedersoo et al., 2014). Such a change in the future caused by the increasingly intensive human activity on the plateau and its surrounding area would have a great impact on above- and belowground biodiversity, and their feedbacks (that is, plant–soil feedback), and consequently alter ecosystem stability.

Our results demonstrate that a positive linkage between above- and belowground biodiversity and ecosystem stability is significant across the natural alpine ecosystems of the Tibetan Plateau. This relationship is much stronger than the relationship between stability and environmental features. Our study provides quantitative evidence that belowground biodiversity is significantly related to ecosystem stability at a large regional scale in natural ecosystems. Belowground biodiversity affected ecosystem stability via multiple direct and indirect pathways mediated by soil fertility and plant diversity, although the indirect influences were relatively weak. Moreover, above- and belowground biodiversity also mediated the influences of soil pH alongside climate and its variability on ecosystem stability. Together, our findings suggest that simultaneously considering above- and belowground biodiversity is crucial for predicting how the loss of biodiversity caused by human-induced global change affects ecosystem stability and stresses the necessity of conserving this 'hidden' belowground biodiversity in vulnerable alpine ecosystems when facing ongoing environmental change.

ACKNOWLEDGMENTS

The authors are very grateful to Dr Anne Bjorkman and the anonymous referees whose constructive comments substantially improved the manuscript. This study was supported by the National Nature Science Foundation of China (31630009), the Second Tibetan Plateau Scientific Expedition and Research (STEP) Program (2019QZKK0302), the Qinghai Innovation Platform Construction Project: Qinghai Provincial Key Laboratory of Restoration Ecology of Cold Area (2017-ZJ-Y20), and the Strategic Priority Research Program – 'Climate Change: Carbon Budget and Relevant Issues' of the Chinese Academy of Sciences (XDA05050404).

AUTHOR CONTRIBUTIONS

L.C. conceived the ideas, analysed the data and wrote the draft; L.C., X.J., Y.S. and J.W. conducted the fieldwork and laboratory analyses; L.J., J.-S.H. and H.C. made valuable comments on the draft; all authors contributed critically to the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available through figshare (<https://figshare.com/s/185cafb271921b1ee6ff>).

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BIOSKETCH

Litong Chen is interested in investigating biodiversity patterns and the linkages between biodiversity and ecosystem functioning through large-scale field inventories and manipulated experiments in alpine grasslands in the Tibetan Plateau.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

How to cite this article: Chen L, Jiang L, Jing X, et al. Above- and belowground biodiversity jointly drive ecosystem stability in natural alpine grasslands on the Tibetan Plateau. *Global Ecol Biogeogr.* 2021;00:1–12. <https://doi.org/10.1111/geb.13307>