

# Direct and indirect effects of temperature and precipitation on alpine seed banks in the Tibetan Plateau

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**Abstract.** Plant community responses to global environmental change focus primarily on aboveground vegetation; however, the important role of the seed bank is frequently neglected. Specifically, the direct and indirect effects of changes in temperature and precipitation on seed banks remain poorly understood, yet seed banks provide a vital source of ecosystem resilience to global environmental change. We used a structural equation model to explore the direct and indirect effects of temperature, precipitation, and other biotic and abiotic factors on soil seed bank community composition using 1,026 soil seed bank samples from 57 sites along an elevation gradient that served as a space-for-time substitution for changing climate in the Tibetan Plateau. Seed bank richness was negatively correlated with both precipitation and temperature, but neither climate factor affected seed bank density. Temperature was also negatively correlated with vegetation species richness, which was positively correlated with seed bank richness and density. Both precipitation and temperature were positively correlated with soil total N, and total N was negatively correlated with vegetation richness. Both precipitation and temperature were negatively correlated with soil pH, and soil pH was negatively correlated with vegetation richness, but positively correlated with seed bank richness and density. Increasing precipitation and temperature would decrease seed bank diversity through direct effects as well as indirectly by decreasing vegetation diversity. Soil pH and total N emerged as the most important soil abiotic factors for seed bank diversity. Increasing precipitation and temperature under climate change may increase the extinction risk of some species in the seed bank by altering bet-hedging and risk-spreading strategies, which will degrade natural restoration ability and ultimately ecosystem resilience. This research is important because it identifies the potential underlying mechanistic basis of climate change impacts on seed banks through effects of aboveground vegetation and belowground biotic and abiotic factors.

**Key words:** climate change; diversity; elevation; plant community; precipitation; soil seed bank; temperature.

## INTRODUCTION

Climate change is predicted to have significant consequences for both temperature and precipitation globally (IPCC 2014). In general, temperatures will increase in nearly all terrestrial ecosystems, whereas climate change will result in increases in mean annual precipitation in some regions and decreases in others (Trenberth 2011). As a consequence, the impacts of global change on the interactive effects of precipitation and temperature will vary spatially. Increasing evidence has demonstrated that both temperature and precipitation change have potentially large impacts on species and/or aboveground vegetation structure, composition, and dynamics (e.g., Knapp et al. 2002, Walther et al. 2002, Klein et al. 2004).

Although the impacts of climate change on aboveground vegetation have been intensively studied (Elmendorf et al. 2012, Franklin et al. 2016), the influence of climate change on soil seed banks, a potentially stabilizing component of ecosystems, is much less well understood (Ooi et al. 2009). Climate change not only influences vegetation growth and distribution, but it also affects potential vegetation as represented in species composition of soil seed banks. In order to predict the long-term consequences of climate change, it is necessary to assess how variation in both precipitation and temperature effects not only aboveground vegetation but the composition of the soil seed bank. Understanding how soil seed banks are influenced by temperature and precipitation can therefore give insights into the effects of climate change on long-term vegetation dynamics and resilience. Moreover, understanding how climate change affects vegetation dynamics in extreme environments, such as the Tibetan Plateau, is vital because these extensive ecosystems already experience climate extremes in

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which most species are already near their physiological limits.

The Tibetan Plateau is regarded as the third pole of the earth, and it is the highest plateau in the world (4,000 m above sea level). This region has undergone significant climate warming in recent decades (e.g., Kuang and Jiao 2016), and the warming rate is almost 1.5 times that of global warming (Zhang et al. 2013). Moreover, annual precipitation has increased in most areas in the Tibetan Plateau over recent decades, and precipitation is increasingly more variable as some regions are becoming wetter, while others are drier (Kuang and Jiao 2016). Cold, high-altitude, alpine vegetation and ecosystems are inherently fragile (Elmendorf et al. 2012) and particularly vulnerable to climate change (Klein et al. 2004). Thus, this region is ideal for understanding the direct and indirect effects of temperature and precipitation change on vegetation and soil seed bank communities under rapid climate change.

Soil seed banks represent a fundamental mechanism to conserve genetic diversity and enhance coexistence in variable environments (Fenner and Thompson 2005), and seed dormancy acts as a bet-hedging strategy and risk-spreading mechanism supplied by persistent seed banks to reduce stochasticity in response to environmental perturbations (Venable 2007). Cold and unstable climatic conditions of alpine environments favor persistent seed banks (e.g., Walck et al. 2005). Consistent with this theory, (Ma et al. 2010, 2013) found persistent seed banks to be the most frequent strategy in alpine meadows on the Tibetan Plateau. By persisting in the soil, species maximize their fitness by minimizing the risk of failed germination via bet-hedging against precipitation and temperature events that could trigger seed germination, but would be insufficient for seedling growth and survival to maturation (e.g., Simons and Johnston 2006). To allow species persistence in alpine meadows of the Tibetan Plateau, a high proportion of seeds in the seed bank must remain viable to buffer against failed germination in the face of extreme cold weather and short growing seasons. Future climate change that increases both temperature and precipitation in this region might break seed dormancy more often, leading to increasing local extinction risk.

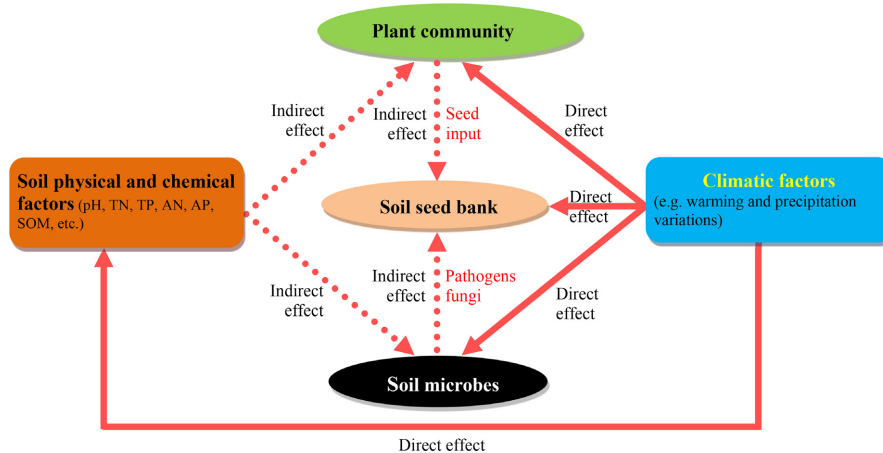
In general, the composition of soil seed banks results from the balance between seed inputs (e.g., local and long-distance dispersal) and seed output (e.g., germination, granivory, pathogens; Fenner and Thompson 2005). We developed a conceptual model of the direct and indirect effects of precipitation and temperature governing seed inputs and outputs (Fig. 1). Climatic factors including temperature and precipitation have a direct effect on plant community and soil seed bank composition, soil microbial communities, and soil physical and chemical factors. Climatic factors, plant species composition and soil microbes, including pathogens and endophytes, all influence seed production, survivorship, and germination cues. Precipitation and temperature

indirectly affect seed banks through their direct effects on plant community composition and soil microbial communities. In addition, climatic factors indirectly affect seed banks through their direct effect on soil physical and chemical factors (Fig. 1). As a consequence, soil seed bank structure and function results from complex direct and indirect effects of climatic factors on plant community, soil environmental factors, and soil microbial communities. We argue that soil seed banks are often neglected when considering how vegetation will respond to climate change. Thus, understanding how temperature and precipitation change affects seed bank processes is important for our ability to predict the impacts of climate change on these and other terrestrial ecosystems.

In this study, we used elevation gradients as surrogates for climate change (space-for-time; e.g., Alexander et al. 2015) to explore the effect of climate change on soil seed bank composition and density. Elevation gradients are a powerful “natural experiment” for addressing the potential impacts of climate change (Körner 2007). In this study, we chose 57 representative sites dominated by alpine meadow species along an elevation gradient from 2,039 to 4,002 m in the northeastern Tibetan Plateau. This elevation gradient covers the broad range of environmental conditions experienced by alpine meadow vegetation within the context of climate change. In many cases, species from lower elevations are moving up in altitude, likely in response to climate warming that has already occurred (e.g., Alexander et al. 2015). This provides an ideal opportunity to determine the effect of climate change on aboveground vegetation in conjunction with the corresponding belowground seed bank.

Temperature is the primary factor controlling seed dormancy status (Baskin and Baskin 1998) and stimulation of seed germination in many species (Hoyle et al. 2013). Increased soil temperature has been predicted to contribute to seed bank loss in arid habitats (Ooi et al. 2009) and boreal wetlands (Hogenbirk and Wein 1992) through increased seed germination and/or reduced seed viability. Moreover, Cowling et al. (2005) reported that the size of the persistent seed bank decreased as annual precipitation increased. Seed longevity is generally negatively correlated with precipitation because increased precipitation results in higher soil moisture and relative humidity, which can benefit seed pathogens (Gallagher 2013). Thus, it seems likely that higher temperature and precipitation will reduce seed bank density directly by increasing seed germination or indirectly by reducing seed viability.

Observational (Chapin et al. 1995), experimental (Klein et al. 2004, Keryn and Mark 2009), and modeling (Thuiller et al. 2005) studies have found that climate warming changes the structure and composition of high elevation plant communities. In general, higher precipitation and soil water availability in alpine grassland supports higher ANPP and nutrient availability (Yang et al.



and Zhu 2013). The Tibetan Plateau is about 2.5 million km<sup>2</sup>, 35% of which is alpine meadow at an average altitude of more than 4,000 m (Zheng 2000). In this study, we chose 57 representative sites along an elevation gradient from 2,039 to 4,002 m, which included six meadow types (Table 1; Appendix S1: Table S1 and Fig. S1): alpine meadow (AM, 27 sites, mean elevation 3,514 m), swamp meadow (SM, seven sites, 3,498 m), alpine scrub meadow (ASM, eight sites, 3,406 m), sub-alpine meadow (SAM, six sites, 2,967 m), forest edge meadow (FEM, four sites, 2,835 m), and upland meadow (UM, five sites, 2,680 m). All research sites are representative of typical vegetation at these elevations, and they have been experiencing moderate grazing for centuries (Ma et al. 2017).

### Soil seed bank sampling

Seed bank samples were collected in August 2009, after the spring germination flush but before dispersal of the current season's seeds, in order to capture the persistent subset of the soil seed bank. Three randomly selected replicate meadows ( $100 \times 100$  m) at least 1–2 km apart were established in each of the 57 elevation level/meadow types, and each replicated meadow within an elevation/meadow type was treated as a spatial replicate. We then randomly chose three plots ( $10 \times 10$  m) in each of the three replicate meadows, and 10 cylindrical soil cores (3.6 cm diameter) were taken randomly from each plot for a total sample of area of  $0.092 \text{ m}^2$ /plot. The soil cores were divided into two fractions: the shallow layer (0–5 cm depth) and lower layer (5–10 cm depth). The 10 cores from each depth were pooled for each subplot. Overall, there were 18 samples from each elevation level/meadow type, 57 elevation levels/meadow type for a total of 1,026 soil samples in all (two soil samples  $\times$  three plots  $\times$  three replicate meadows  $\times$  57 elevation levels = 1,026 samples).

This study was conducted in the northeastern part of the Tibetan Plateau, P.R. China (101°06′–103°33′ E, 33°22′–35°24′ N, about 37,000 km<sup>2</sup>, mean altitude 3,318 m above sea level; Table 1; Fig. 2. Appendix S1: Table S1). The climate of Tibetan Plateau is characterized by strong solar radiation, wet, humid summers and cool, dry winters (Ma et al. 2017). Mean daily air temperature is low, with high day–night temperature fluctuations, but little seasonal change in temperature (Xie

TABLE 1. Descriptions of the meadow types and their dominant species.

Vegetation type	Sites	Extent	Elevation (m)	Dominant species
Alpine scrub meadow	8	34°07'–35°05' N 101°06'–103°17' E	3,205–3,576	<i>Potentilla fruticosa</i> , <i>Spiraea alpina</i> , <i>Salix cupularis</i> , <i>Scirpus pumilus</i> , <i>Elymus dahuricus</i> , <i>Stipa capillata</i>
Alpine meadow	27	33°22'–35°04' N 101°23'–103°18' E	3,158–4,002	<i>Elymus dahuricus</i> , <i>Kobresia capillifolia</i> , <i>Polygonum viviparum</i> , <i>Poa poophagorum</i> , <i>Potentilla fragarioides</i> , <i>Anemone rivularis</i>
Subalpine meadow	6	34°46'–35°24' N 102°20'–103°14' E	2,039–3,219	<i>Roegneria kamoji</i> , <i>Polygonum viviparum</i> , <i>Medicago ruthenica</i> , <i>Scirpus pumilus</i> , <i>Saussurea nigrescens</i> , <i>Kobresia humilis</i>
Swamp meadow	7	33°46'–35°19' N 101°52'–103°10' E	3,488–3,612	<i>Potentilla anserina</i> , <i>Agrostis hugoniana</i> , <i>Carex zekogensis</i> , <i>Blysmus sinocompressus</i> , <i>Kobresia tibetica</i> , <i>Kobresia capillifolia</i>
Forest edge meadow	4	34°22'–35°12' N; 102°47'–103°33' E	2,631–3,032	<i>Kobresia humilis</i> , <i>Carex zekogensis</i> , <i>Medicago ruthenica</i> , <i>Bupleurum smithii</i> , <i>Kobresia capillifolia</i>
Upland meadows	5	34°15'–35°21' N; 102°48'–103°47' E	2,402–2,969	<i>Brachypodium sylvaticum</i> , <i>Stipa capillacea</i> , <i>Heteropappus hispidus</i> , <i>Bromus sinensis</i> , <i>Medicago ruthenica</i> , <i>Agropyron cristatum</i>

*Soil seed bank germination experiment*

To examine the species composition and density of the soil seed banks, a germination experiment was conducted at the Research Station of Alpine Meadow and Wetland Ecosystems of Lanzhou University (Hezuo Branch), Gansu Province, P.R China (34°55' N, 102°53' E, altitude 2,900 m above sea level), which was also located on the northeastern part of the Tibetan Plateau. The mean annual precipitation is 560 mm and the mean annual temperature is 2.0°C. We used the seedling emergence method to quantify the germinable species composition and quantity of viable seeds in the seed bank (ter Heedrt et al. 1996). Each sample was sieved to remove stones, plant fragments, and coarse debris, then sieved through a coarse (4 mm mesh), and finally a fine (0.2 mm mesh) sieve (Ma et al. 2013, 2017). Plastic germination trays (30 × 30 cm) were filled with sand previously sterilized at 140°C for 24 h. The sieved samples were carefully and evenly spread on the surface of sterile sand (15 cm). Twenty control trays only containing sterilized sand were included among the experimental trays to check for contamination from wind-dispersed seeds. Trays were watered and monitored several times a day. Emerging seedlings were noted and removed once they could be identified. The seedlings that could not be identified were grown separately until they could be identified. The soil was turned over carefully and regularly to facilitate seed germination. After five months (10 May–10 October 2010), the germination experiment was ended as no more seedlings emerged after three consecutive weeks.

*Plant community sampling*

Aboveground plant communities were surveyed in August 2009 during peak biomass production. Three 50 × 50 cm quadrats were randomly chosen within each meadow where seed bank samples were collected to record the richness, composition and cover of the aboveground plant community resulting in total of 171 quadrat samples (57 sites × three quadrats).

*Analysis of soil properties*

Three additional soil samples were collected in August 2009 from random locations within each plot where the soil seed bank and aboveground plant community were sampled. The three cores (3.6 cm diameter × 15 cm deep) were mixed to generate a single soil sample for each plot within each site, resulting in nine mixed soil samples from each site. Overall, 513 (57 elevation levels × nine samples) soil samples were used to analyze soil characteristics. After removing the litter materials by hand, each soil sample was homogenized, and stored in sealed plastic bags. All the fresh soil samples were taken to the laboratory immediately after collection. Each fresh soil sample was divided into two parts, one part for soil physical and chemical analyses, and another part was kept moist and stored for soil microbial biomass nitrogen and phosphorus analysis.

For this study, soil pH, available nitrogen (AN), available phosphorus (AP), and soil organic matter (SOM) were evaluated. After removal of roots, each composite soil sample was sieved to <2 mm and split into two subsamples. One subsample was kept at 4°C for analyses of soil NH<sub>4</sub><sup>+</sup>-N, NO<sub>3</sub><sup>-</sup>-N, and available phosphorus. The other subsample was air-dried at room temperature and ground to <0.15 mm for measurement of soil pH and soil organic matter (SOM). Soil pH was measured using a pH meter with a glass electrode (soil/KCl ratio 1:2.5). SOM was measured using the K<sub>2</sub>Cr<sub>2</sub>O<sub>7</sub> method (Soil Science Society of China 1983). For soil NH<sub>4</sub><sup>+</sup>-N and NO<sub>3</sub><sup>-</sup>-N, fresh soil (<2 mm) equivalent to 10 g oven-dried mass was extracted with 2 mol/L KCl (soil:solution ratio of 1:5) and determined using a Flow Solution IV Analyzer (OI Analytical Corporation, Round Rock, TX, USA). Soil available phosphorus was extracted by the Bray method (Bray and Kurtz 1945).

*Analysis of soil microbial biomass*

No analyses of microbial community composition have been conducted at this scale in the Tibetan Plateau.

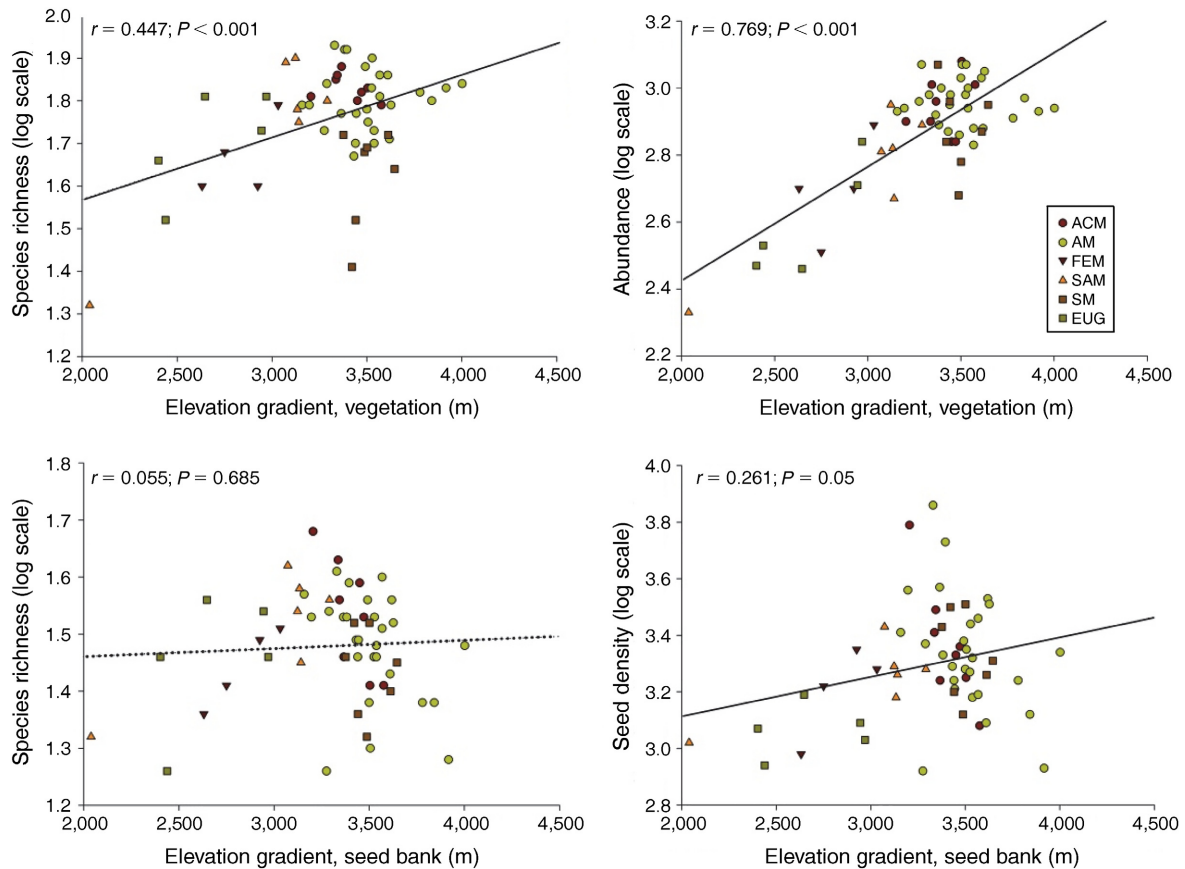


FIG. 2. The relationship between elevation (2,039–4,002 m) and species richness and abundance in aboveground vegetation (top row), and species richness and seed density in the soil seed bank (bottom row). Symbols represent different types of alpine meadow (alpine meadow, AM; swamp meadow, SM; alpine scrub meadow, ASM; subalpine meadow, SAM; forest edge meadow, FEM; and upland meadow, UM). The regression line is fitted through all points. Significant relationships are shown with solid lines ( $P < 0.05$ ).

Thus, we are using microbial biomass as a surrogate for microbial responses to precipitation and temperature, and whether or not changes in microbial biomass are correlated with changes in the soil seed bank. Admittedly, this analysis provides, at best, a very rough assessment of microbial impacts on soil seed banks, but they were included in our initial analyses because they represent the only available assessment of microbial communities at our sites. Soil microbial biomass carbon (SMBC) and nitrogen (SMBN) were determined by the chloroform fumigation–extraction method (Lu 2000). Four fresh portions equivalent to 25 g of dry soil were prepared for each soil sample. Two portions were fumigated at 25°C for 24 h prior to extraction by  $K_2SO_4$ . Then the fumigated and un-fumigated (the other two portions) samples were extracted with 100 mL of 0.5 mol/L  $K_2SO_4$  by horizontal shaking for 1 h at 200 rpm and then filtered. Dichromate oxidation was used to determine the contents of  $K_2SO_4$ -extracted carbon from the  $CHCl_3$ -treated and untreated soils. Kjeldahl digestion method was used to determine the content of  $K_2SO_4$ -extracted nitrogen from the  $CHCl_3$ -

treated and untreated soils. We calculated SMBC and SMBN by dividing the differences of total extractable carbon and nitrogen between fumigated and un-fumigated samples by the conversion factors 0.38 for biomass carbon, 0.45 for biomass nitrogen, respectively.

#### Precipitation and temperature data collection

For each of the 57 sites, we compiled mean annual temperature (MAT) and mean annual precipitation (MAP) data from the National Meteorological Bureau of China database. Data were compiled by interpolating data of monthly mean temperature and precipitation records (1951–2010) from 716 climate stations across China (data available online).<sup>4</sup> MAT across the 57 sites ranged from  $-0.86$  to  $6.74^\circ\text{C}$  (mean  $2.46^\circ\text{C}$ ), and MAP ranged from 363.1 to 912.0 mm (mean 651.6 mm; Appendix S1: Table S1).

<sup>4</sup> <http://cdc.cma.gov.cn>



### Data analysis

We examined univariate relationships between elevation (2,039–4,002 m) and species richness and abundance per site in vegetation, species richness and seed density per site in the soil seed bank by linear regressions in SPSS 23.0 (SPSS, Chicago, Illinois, USA).

The similarity of species composition between the soil seed bank and aboveground vegetation along the elevation gradient (2,039–4,002 m) was evaluated by non-metric multidimensional scaling (NMDS). NMDS is considered the best method for graphical representation of floristic relationships (Clarke 1993). The final data set consisted of 489 species present in 114 samples of 57 soil seed banks and 57 aboveground plant communities. To compare aboveground vegetation and seed bank similarity, we calculated matrices using the Bray-Curtis distance metric. Ordination was based on relative abundance data. For each species in the seed bank, relative abundance was calculated as the number of individuals in each plot divided by the total number of individuals from all species in each plot. For aboveground vegetation, relative abundance was the number of individuals of each species in each quadrat divided by the total number of individuals of all species in each quadrat.

The *envfit* function in the *vegan* package was used to determine if elevation was correlated with soil seed bank and aboveground vegetation composition along the NMDS ordination axes. Elevation was fitted as a factor to the NMDS ordination. *P* values were estimated from the comparison of correlation coefficients with those generated from 1,000 random permutations of the data. PERMANOVA (permutational multivariate analysis of variance) using a Bray-Curtis distance matrix was used to assess differences between seed banks and aboveground vegetation across the 57 sites. In addition, we used the Jaccard index to calculate dissimilarity on presence/absence data. Ordination and PERMANOVA were calculated with the *vegan* package (Oksanen et al. 2016) in R 3.4.3 (R Core Team 2018).

We fitted a piecewise structural equation model (SEM) to infer the direct and indirect effects of climatic factors (MAP and MAT), plant community structure (species richness and abundance), soil properties (soil pH, TN, TP, and SOM), and soil microbial biomass (SMBC and SMBN) on soil seed banks (species richness and seed density). SEM is a powerful tool to analyze the relationships among causally linked intercorrelated variables (Grace 2015). Each single-headed arrow in an SEM represents a hypothesized causal relationship where the variable at the tail of the arrow is a direct cause of the variable at the head.

SEM was conducted using Amos 21.0. All variables were examined for normality prior to analysis. Species richness, soil seed bank density, SMBC, and SMBN data were log-transformed to improve normality. We used  $\chi^2$ , df, CMIN/df, CFI, and RMSEA to determine if the covariance structures implied by the model adequately

fit the actual covariance structures of the data. When the initial model structure did not adequately fit the data, we used model modification indices (MI) as a tool for data exploration and hypothesis generation. Coefficients with  $P < 0.05$  were considered significant, and non-significant paths (arrows) were deleted in the final model.

## RESULTS

### Seed bank and aboveground vegetation composition

No seedlings emerged in the control trays, indicating no airborne seed contamination occurred in our seed bank samples. During the germination experiment, a total of 11,726 seeds germinated from the soil samples, belonging to 150 species and 26 families. Of these species, 19.4% were annuals, 2.3% biennials, and 78.3% perennials. Seven species could only be identified to genus level (*Arenaria*, *Cerastium*, *Draba*, *Pedicularis*, *Poa*, *Potentilla*, and *Saussurea*), three species only to family level (one Ranunculaceae and two Poaceae), and 11 seedlings were unidentifiable. Species richness showed no significant relationship with elevation, while seed density was weakly, but significantly positively, correlated with elevation (Fig. 2).

The aboveground vegetation sampled at the 57 sites across the elevation gradient consisted of 396 species, belonging to 47 families, of which 11.3% were annuals, 2.4% were biennials, and 86.3% were perennials. Three species could only be identified to genus level (*Artemisia* and two species of *Pedicularis*), seven species to family level (Caryophyllaceae, Chenopodiaceae, Asteraceae, Brassicaceae, Orchidaceae, Polygonaceae, and Ranunculaceae), and five plants were unidentifiable. Both species richness and abundance were significantly positively correlated with elevation (Fig. 2).

Both soil seed bank ( $R^2 = 0.34$ ,  $P < 0.001$ ) and aboveground vegetation ( $R^2 = 0.65$ ,  $P < 0.001$ ) changed significantly with elevation (Fig. 3). Based on PERMANOVA, the differences in species composition between the soil seed bank and aboveground vegetation were significant ( $r^2 = 0.207$ ,  $P < 0.001$ ; Fig. 3). In general, differences in species composition between aboveground vegetation and soil seed banks were >80%. However, the degree of aboveground-seed bank dissimilarity increased significantly with elevation ( $P < 0.05$ ; Fig. 4).

### Direct and indirect effects of precipitation and temperature change on soil seed banks

Overall, the initial SEM adequately fit the data ( $\chi^2 = 41.048$ , df = 20, CMIN/df = 2.052, CFI = 0.940, RMSEA = 0.137). Based on the SEM, the indirect influence of MAP and MAT on seed bank richness was mediated through soil pH, total nitrogen (TN), and aboveground plant species richness. As precipitation and

temperature increased, seed bank richness decreased, but these variables had no direct effect on seed bank density (Table. 2, Fig. 5, Appendix S1: Fig. S2). Abundance of aboveground vegetation increased as precipitation increased, while species richness of aboveground vegetation decreased as temperature increased. This decline in aboveground species richness led to decreases in seed bank richness and density. Soil pH also decreased as precipitation and temperature increased, whereas aboveground species richness increased as soil pH decreased. Conversely, soil TN increased as precipitation and temperature increased, whereas aboveground richness decreased as TN increased. Soil microbial biomass nitrogen (SMBN) increased as precipitation and temperature increased but these variables were unrelated to seed bank richness and density. TN and TP increased as precipitation and temperature increased, whereas SOM increased as precipitation increased. Further, the increase in TN was reflected in an increase in SMBC and SMBN, yet none of these variables directly or indirectly affected seed bank richness or density (Table. 2, Fig. 5).

## DISCUSSION

Overall, species richness and abundance of above- and belowground communities increased with elevation across this region of the Tibetan Plateau. We found that temperature and precipitation had strong direct effects on seed bank species richness, but indirectly affected

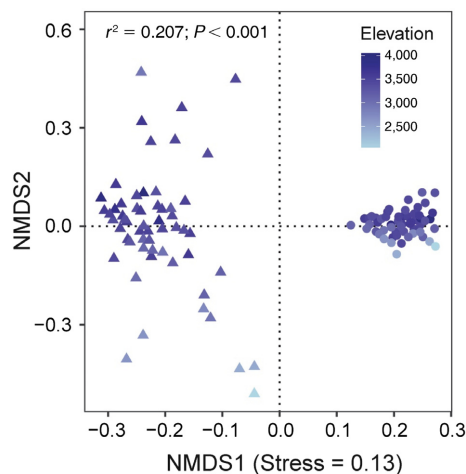


FIG. 3. Two-dimensional nonmetric multidimensional scaling (NMDS) ordination of species composition of the 57 sites based on abundance data for seed bank and aboveground vegetation (stress value = 0.13) along an elevation gradient (2,039–4,002 m) on the Tibetan Plateau. A strong separation between vegetation communities and the soil seed bank occurs along NMDS axis 1. A clear gradient in aboveground vegetation occurs along the elevation gradient (NMDS axis 2), but not for the soil seed bank. Blue triangles and circles represent aboveground vegetation and seed banks, respectively. Shades from light blue to dark blue represent increasing elevation.

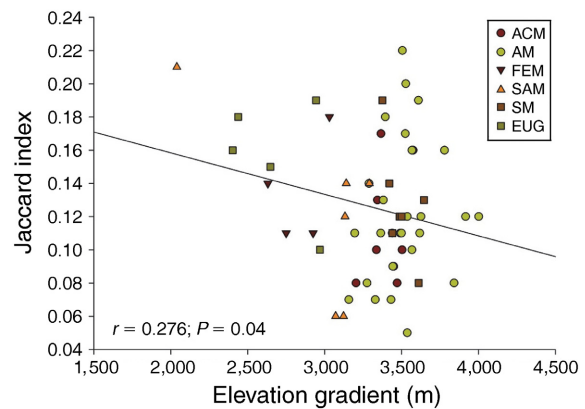


FIG. 4. Compositional similarity (based on Jaccard's index) between species in the soil seed bank and aboveground vegetation decreases along the elevation gradient on the Tibetan Plateau.

seed bank density via their effects on species richness of aboveground vegetation. We found the similarity of species composition between the soil seed bank and aboveground vegetation decreased as elevation increased, indicating that the role of the soil seed bank in aboveground plant community regeneration decreased as elevation increased. Together these results suggest that changes in temperature and precipitation under climate change will have important impacts on ecosystem resistance and resilience under climate change.

## Similarity between seed bank and aboveground vegetation along an elevation gradient

We found that the similarity between seed bank and aboveground vegetation decreased as elevation increased. Cold and harsh environments in high mountains or latitudes can contribute to the maintenance of seeds in the soil (Cavieres and Arroyo 2001) by favoring seed longevity (Murdoch and Ellis 2000) and accumulation of persistent seed banks (Ma et al. 2010). Hopfensperger (2007) also reported that extreme growing conditions drove formation of persistent seed banks. Cold climates at higher altitudes are not conducive to seed germination (Ma et al. 2010). In this study, we also found that density of the persistent seed bank increased along the elevation gradient (Fig. 2). The persistent seed bank, composed of long-lived seeds, has a lower contribution to aboveground regeneration relative to transient seed banks. Moreover, at high altitudes, plant communities are dominated by slow-growing and long-lived species with low seed production annually (Thompson 2000). Low biomass and seed production are common characteristics of species growing in high stress environments that experience unseasonably cold years and short growing seasons (Cummins and Miller 2002). In addition, the majority of sedge and grass species are clonal in alpine meadows on the Tibetan Plateau (Ma et al. 2013, 2017). The seed bank in these high elevation

TABLE 2. Bivariate correlations between variables included in the structural equation model.

Variable	MAP	MAT	pH	TN	TP	SOM	Ve-rich	Ve-abun	SMBC	SMBN
MAP	–									
MAT	–	–								
pH	<b>–0.75***</b>	<b>–0.18*</b>	–							
TN	<b>0.79***</b>	<b>0.36***</b>	–	–						
TP	<b>0.72***</b>	<b>0.58</b>	–	–	–					
SOM	<b>0.43***</b>	0.04	–	–	–	–				
Vrichness	–0.32	<b>–0.46**</b>	<b>–0.34*</b>	<b>–0.53***</b>	0.08	0.05	–			
Vabundance	<b>0.79**</b>	0.15	–0.11	–0.26	–0.22	0.14	–	–		
SMBC	0.30	0.22	–0.01	<b>0.42***</b>	0.22	<b>–0.20*</b>	–	–	–	
SMBN	<b>0.39*</b>	<b>0.30**</b>	0.02	<b>0.22**</b>	0.28	–0.01	–	–	–	–
SB-rich	<b>–0.46**</b>	<b>–0.39**</b>	–	–	–	–	<b>0.40***</b>	–0.05	0.06	0.04
SB-den	0.27	–0.20	–	–	–	–	<b>0.33*</b>	0.18	0.15	0.10

Notes: Values in boldface type and asterisks indicate the significance of the correlation coefficients (\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ). Cells with dashes means there no correlation between two same variables or the correlation between two variables were not considered in structural equation model. MAP, mean annual precipitation; MAT, mean annual temperature; SB-den, seed bank density; SB-rich, seed bank species richness; SMBC, soil microbial biomass carbon; SMBN, soil microbial biomass nitrogen; SOM, soil organic matter; TN, total nitrogen; TP, total phosphorus; Ve-abun vegetation abundance; Ve-rich, vegetation species richness.

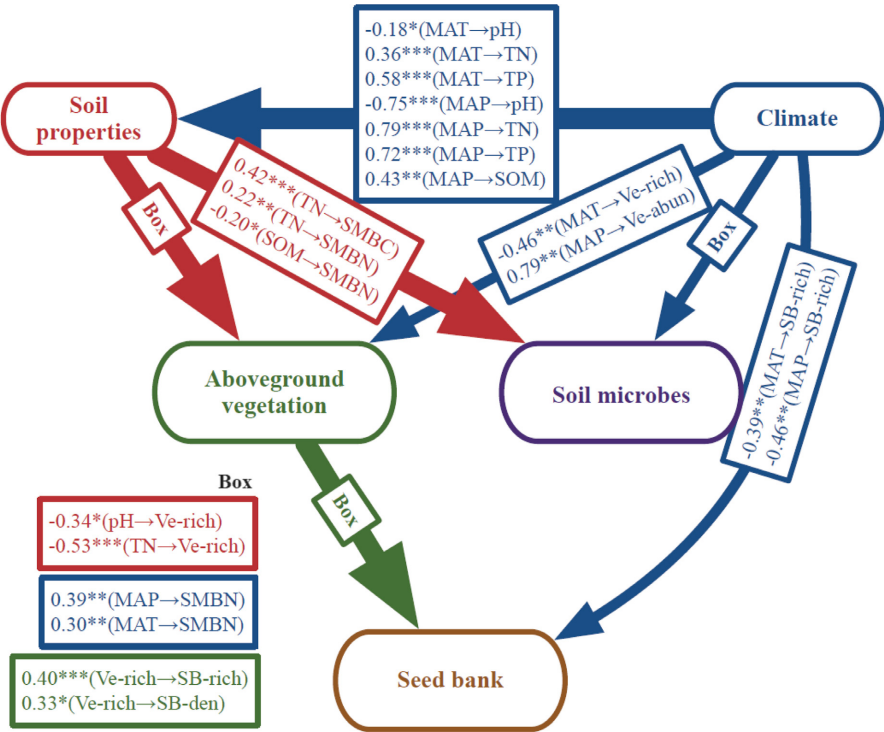


FIG. 5. Structural equation model linking climate variables (mean annual precipitation [MAP] and mean annual temperature [MAT]) to soil environmental variables (soil pH, total nitrogen [TN], total phosphorus [TP], and soil organic matter [SOM]) to aboveground vegetation variables (species richness [Ve-rich] and abundance [V-abun]), and to soil microbial variables (soil microbial biomass carbon [SMBC] and nitrogen [SMBN]) and to soil seed bank variables (seed bank species richness [SB-rich] and seed density [SB-den]). We grouped the different categories of predictors (climatic, soil properties, aboveground vegetation, soil microbes, and soil seed bank) in the same box in the model for graphical simplicity. Each arrow represents a causal relationship such that a change in the variable at the tail of the arrow is a direct cause of a change in the variable at the head. The directional arrows reflect the magnitude of the standardized SEM coefficients. Directional arrows linking two variables depict direct effects (\* $P \leq 0.05$ ; \*\* $P \leq 0.01$ ; \*\*\* $P \leq 0.001$ ). In order to make the SEM figure more concise and clear, we rebuilt the figure based on Appendix S1: Fig. S2. Only significant correlations were retained. The thickness of the solid arrows reflects the magnitude of the standardized SEM coefficients, which are listed in the box on or beside each path.



communities contributes little to aboveground vegetation because few regeneration niches occur in this system. The aboveground plant community is dominated by perennials that rely primarily on vegetative reproduction (Thompson 2000, Körner 2003), an adaptation in harsh, higher elevation environments where sexual reproduction is risky (Jia et al. 2011). Asexual reproduction reduces seed input to the soil seed bank.

#### *Direct effect of temperature and precipitation on soil seed banks*

We found a decline in seed bank richness with increasing mean annual temperature. Soil warming has been shown to facilitate seed germination in alpine and Arctic seed banks (e.g., Harte and Shaw 1995, Milbau et al. 2009). Generally, cold climates (e.g., high mountains or high latitudes) may slow embryonic metabolic rates and consumption of seed reserves, favoring seed longevity (Murdoch and Ellis 2000), seed viability and persistence in the soil (Cavieres and Arroyo 2000). However, increasing temperature could accelerate germination for many physiologically dormant seeds (Baskin and Baskin 1998), and physical dormancy is broken mainly by high temperature or high day and night fluctuations in temperature (e.g., Baskin and Baskin 2005). Mira et al. (2011) found that increased temperature facilitated dormancy release in an endangered species (*Silene diclinis*). In some alpine and Arctic systems, increases in incubation temperature increased or accelerated seed germination (e.g., Milbau et al. 2009). Moreover, Ooi et al. (2009) found temperature increase to be a critical driver for species persistence in the seed bank, and potentially for species coexistence. Hence, temperature is the main mechanism controlling dormancy for most species with dormant seeds (Baskin and Baskin 1998). In addition, increased temperature may increase predation risk. For example, Noroozi et al. (2016) found a significant positive correlation between mean air temperature and predator activity. Hence, from the perspective of bet-hedging, the effects of temperature are directly related to seed bank persistence, because increasing soil temperature may alleviate dormancy, trigger germination cues, and enhance predation rates for many plant species.

We also found that species richness declined as precipitation increased along the elevation gradient. Both seed germination and seed death are possible reasons. Precipitation plays an important role in the spatial and temporal heterogeneity of seed bank richness and density (Santos et al. 2013). Cowling et al. (2005) reported that the size of the persistent seed bank decreased as annual precipitation increased or aridity decreased. Increased precipitation could stimulate germination in seeds that are sensitive to changes in soil moisture. For example, Liu et al. (2011) found that seed hydration is the main factor for breaking seed dormancy on the Tibetan Plateau. In some cases, physiological dormancy is broken only by wet cold storage, while morphological or

morphophysiological dormancy can be broken more readily in imbibed vs. dry seeds (Baskin and Baskin 1998, Finch-Savage and Leubner-Metzger 2006). Most likely, seeds store better in dry than in wet soil environments, because more seeds degenerate or decay in wet soils under higher precipitation. Therefore, increasing temperature and precipitation directly alter and/or disrupt the bet-hedging and/or risk-spreading strategy of seeds through their effect on germination and dormancy status of seeds in the soil seed bank.

#### *Indirect effect of temperature and precipitation on soil seed banks*

We found that as temperature increased, aboveground vegetation richness declined, resulting in lower soil seed bank richness. Klein et al. (2004) found a decline in plant species richness with climate warming, which is rapidly occurring in alpine areas on the Tibetan Plateau. Moreover, Yang et al. (2015) also found species richness and diversity decreased after five years of experimental warming in the same region, which has been widely observed in alpine and Arctic tundra (Walker et al. 2006). In many Arctic regions, warming increases dominance by shrubs and graminoids, causing local extinction of some forbs and cryptogams (e.g., Walker et al. 2006, Elmendorf et al. 2012). In general, biodiversity is expected to decrease across a wide range of alpine and arctic tundra as temperature continues to rise (Walker et al. 2006, Elmendorf et al. 2012). Because soil seed banks result from the balance between seed inputs and output (Fenner and Thompson 2005), the decline in aboveground vegetation richness as temperature and precipitation increase will lead to a decline in seed bank richness, as well.

We found that soil pH decreased with increasing precipitation and temperature, whereas vegetation richness increased as soil pH decreased. Leaching intensity and soil mineral weathering are controlled by temperature and precipitation. Soil pH decreases due to high rates of leaching under warm and wet conditions. Conversely, soil pH is neutral or alkaline due to less intense leaching and weathering under dryer climates. Rengel (2011) indicated that changes in precipitation under climate change will influence soil pH. In dry environments, evapotranspiration exceeds precipitation and salts may be retained in topsoil, which increases soil pH. In contrast, leaching of Ca and Mg under high annual precipitation increases pH as salts are diluted or leached gradually to deeper soil layers, decreasing pH in upper soil layers.

In some cases, pH has been shown to be one of the most important factors controlling plant species richness in high latitude ecosystems (e.g., Van der Welle et al. 2003). Foth (1990) found low plant community richness at low soil pH due to low soil nutrient availability, whereas Peet et al. (2003) found high species richness in higher soil pH habitats. A unimodal relationship with soil pH was found in vascular species of Arctic riverine

communities (Gould and Walker 1997). We found that soil pH was negatively correlated with species richness of aboveground vegetation along our elevation gradient. Grime (1973) reported that the highest species richness in unmanaged grassland occurred at a soil pH range of 6.1–6.5, and that species richness decreased towards both acidic and alkaline pH values. To some extent, the relationship between species richness and soil pH is determined by the range of soil pH studied. In this study, mean soil pH ranged from 5.59 to 8.50 with a mean of 6.79 across all 57 meadows along the elevation gradient. Likely, the negative correlation between soil pH and species richness is a consequence of more favorable soil environments for plant growth and establishment in more acid soil conditions.

Total nitrogen (TN) increased with increasing precipitation and temperature, whereas vegetation richness decreased as TN increased, ultimately decreasing seed bank richness and density. Hooper et al. (2005) found temperature and moisture were tightly correlated with nitrogen mineralization. Soil microbial activity and decomposition were enhanced by higher soil temperature in cold climates, such as tundra (Rustad et al. 2001). Thus, temperature is considered to be one of the main factors controlling organic matter decomposition in alpine and arctic environments (e.g., Stark 2007). In alpine grasslands on the Tibetan Plateau, Klein et al. (2004) also found warming increased available nitrate and ammonium when no significant decrease in soil moisture occurred.

Nitrogen (N) is considered to be a primary factor limiting plant growth in many terrestrial ecosystems (e.g., Fay et al. 2015), and increasing N availability alters community structure and composition (Bobbink et al. 1998, Stevens et al. 2004, Simkin et al. 2016). Indeed, many experimental studies have found that species richness and diversity decreased after N addition in most terrestrial ecosystems (Stevens et al. 2004, Suding et al. 2005, LeBauer and Treseder 2008). Higher soil N availability could result in competitive exclusion by some nitrophilic species, which may dominate communities after years of N fertilization (e.g., Bobbink et al. 1998). Aboveground competition for light also increases with N fertilization resulting in the loss of subcanopy species (Hautier et al. 2009). In addition, N fertilization can cause soil acidification, which can alter nutrient availability and absorption (e.g., Maskell et al. 2010).

We found that TN increased as precipitation and temperature increased, and that soil microbial biomass (SMBC and SMBN) increased as TN increased. In the Tibetan Plateau, soil nitrogen is primarily tied up in soil organic matter because low temperatures restrict mineralization (Cao and Zhang 2001). Plant growth and soil microbial activity are limited by low soil nitrogen availability (Xu et al. 2004). Therefore, higher TN could increase soil microbial biomass. Nevertheless, we found no direct relationship between soil microbial biomass and seed bank richness or density. Seed banks are

susceptible to fungal and bacterial pathogens linked to increased soil moisture (e.g., Mordecai 2012), and their deleterious effects are favored under wetter soil conditions (Blaney and Kotanen 2001). Admittedly, SMBC and SMBN are weak correlates for abundance of pathogenic microbes; thus, without sequence data we are unable to assess the direct and indirect effects of pathogens on seed bank richness and density.

Many plants in the alpine zone of the Tibetan Plateau have highly persistent seed banks (Ma et al. 2010, 2013). To allow species persistence and to facilitate resistance to climate extremes, a high proportion of seeds in the seed bank need to remain viable to buffer this system against failed germination in the face of extreme cold weather and a short growing season. In this study, we found that species diversity of above and belowground communities decreased with increasing precipitation and temperature along an elevation gradient that serves as a template for climate change in this region where both climate variables are predicted to increase in the future. The bet-hedging and risk-spreading strategies of plants via the soil seed bank may be compromised by increased germination and subsequent loss or reduction of seed bank persistence as temperature and precipitation continue to increase.

Quantitative assessments of ecosystem degradation generally focus on aboveground conditions. However, our work demonstrates that ecosystem managers and scientists should also pay attention to the direct and indirect effects of global environmental change on belowground systems, particularly the soil seed bank, which is an important component for restoration and conservation in most ecosystems. In our case, understanding how soil seed banks are influenced by biotic and abiotic drivers provided mechanistic insights into how these alpine ecosystems will respond to changes in precipitation and temperature in the future. Specifically, we found that changes in temperature and precipitation could potentially alter soil seed bank composition, and diminish the natural restoration ability and ecosystem resilience inherent in alpine zones on the Tibetan Plateau.

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## DATA AVAILABILITY

Data are available on Figshare: <https://doi.org/10.6084/m9.figshare.11590689.v1>