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Changes in plant species richness distribution in Tibetan alpine grasslands under different precipitation scenarios

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ABSTRACT

Species richness is the core of biodiversity-ecosystem functioning (BEF) research. Nevertheless, it is difficult to accurately predict changes in plant species richness under different climate scenarios, especially in alpine biomes. In this study, we surveyed plant species richness from 2009 to 2017 in 75 alpine meadows (AM), 199 alpine steppes (AS), and 71 desert steppes (DS) in the Tibetan Autonomous Region, China. Along with 20 environmental factors relevant to species settlement, development, and survival, we first simulated the spatial pattern of plant species richness under current climate conditions using random forest modelling. Our results showed that simulated species richness matched well with observed values in the field, showing an evident decrease from meadows to steppes and then to deserts. Summer precipitation, which ranked first among the 20 environmental factors, was further confirmed to be the most critical driver of species richness distribution. Next, we simulated and compared species richness patterns under four different precipitation scenarios, increasing and decreasing summer precipitation by 20% and 10%, relative to the current species richness pattern. Our findings showed that species richness in response to altered precipitation was grassland-type specific, with meadows being sensitive to decreasing precipitation, steppes being sensitive to increasing precipitation, and deserts remaining resistant. In addition, species richness at low elevations was more sensitive to decreasing precipitation than to increasing precipitation, implying that droughts might have stronger influences than wetting on species composition. In contrast, species richness at high elevations (also in deserts) changed slightly under different precipitation scenarios, likely due to harsh physical conditions and small species pools for plant recruitment and survival. Finally, we suggest that policymakers and herdsman pay more attention to alpine grasslands in central Tibet and at low elevations where species richness is sensitive to precipitation changes.

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1. Introduction

Biodiversity is the key to maintaining ecosystem service and functionality (Le Bagousse-Pinguet et al., 2019; Pires et al., 2018). Ecosystems structured with more species are thought to be more resistant and stable than those with fewer species in response to external disturbances that are caused by nature or humans, and this is always attributed to niche differentiation and functional compensation among species (Conti et al., 2018; Kohler et al., 2017). Climate change and irrational human activity are primarily responsible for the losses of ecosystem biodiversity and functioning, and this topic is now receiving close attention, from both scientists and the public (De Boeck et al., 2018; Pires et al., 2018; Titeux et al., 2016). However, it remains a significant challenge to accurately predict biodiversity change under different climate change scenarios (Fordham et al., 2016; Fournier et al., 2017).

In biodiversity research, species richness is one of the most critical indices for quantifying ecosystem responses to changes in climatic and anthropogenic drivers (Maestre et al., 2012; Sandau et al., 2017). Previously, scientists conducted manipulative greenhouse experiments and *in situ* field observations to examine the influences of climate change and land-use shifts on species richness change, either over time at a small scale or across space for a short duration (Kreyling et al., 2017; Lü et al., 2019). Such studies have greatly improved our understanding of ecosystem sensitivity to global environmental change and have highlighted the importance of biodiversity conservation for sustainable use of ecosystems with ongoing climate warming. Limited by either the local scales or short time periods, such findings are rarely applicable to large-scale biodiversity scenarios, although these are essential in policy denominations and practical solutions (Bellard et al., 2012; Fleishman et al., 2000; Thuiller et al., 2008).

Environmental filtering theory recently provided a comprehensive view to better untangle these environmental controls over species richness and assembly in natural ecosystems under global change (Castellanos et al., 2019; Le Bagousse-Pinguet et al., 2017; Lozada-Gobilard et al., 2019). As predicted, environmental heterogeneity is the main reason for variations in species composition across taxa and biomes (Stein et al., 2014). With remote sensing data and environmental variables together, Leutner et al. (2012) simulated both species richness and floristic composition in a temperate montane forest in Germany. However, it is still difficult to assess the relative importance of climatic, edaphic, and topographical factors for spatial species distribution, especially in alpine biomes where plants survive various physical stresses, i.e., droughts (Leitinger et al., 2015; Rosbakh et al., 2017), freezing (Neuner, 2014), intense UV radiation (Salter et al., 2017), and poor soils (Körner, 2003b; Monson et al., 2006; Xu et al., 2014). Such a global scientific question can be solved well with deep learning algorithms. For example, random forest algorithms are recommended in machine learning due to their excellent capability in dealing with collinearity and nonlinearity problems between response and effect variables (Li et al., 2017; Schmitt et al., 2017; Shiferaw et al., 2019).

The Hindu-Kush-Himalayan area is one of the global hotspots of biodiversity conservation (Myers et al., 2000), where alpine ecosystems are critical for the livelihoods of residents and wildlife (Xu et al., 2019). The Tibetan alpine grasslands are sensitive and fragile to climate change and human disturbance, but they play a vital role in safeguarding environments downstream of both mainland China and South Asia (Miehe et al., 2019; Wang and Wesche, 2016). Unfortunately, approximately 20% of alpine grasslands have degraded due to warming, population expansion, and overgrazing on this plateau (Harris, 2010). To protect alpine grasslands on the Tibetan Plateau, the government has implemented a number of policies and programmes in the past decade (Dong et al., 2020). In many studies, precipitation is confirmed to be the principal driver of both species richness and grassland productivity on the Tibetan Plateau (Ma et al., 2010; Niu et al., 2015; Wang et al., 2013). Zhao et al. (2011) predicted that alpine meadows and steppes will shrink due to the expansion of alpine shrubs with ongoing climate warming on the Tibetan Plateau. However, we know little about changes in species richness under climate changes, especially shifted precipitation, at a broad scale over different alpine grassland types on this plateau.

Therefore, with this study we aim to determine the following: (1) the plant species richness pattern across typical grassland communities under current climatic conditions; (2) the relative contributions of climatic, edaphic, and geographic factors in driving such a spatial pattern of plant species richness and ascertain whether precipitation overrides other environmental factors to be the most critical driver as reported in previous studies; (3) the change in the spatial pattern of plant species richness when seasonal or annual precipitation decreases or increases, compared to current species richness distribution. Using relevant analyses, we also hope to examine (1) whether there is an evident difference in the sensitivity of species richness distribution to precipitation among different typical grasslands, meadows, steppes, and deserts and (2) whether species richness response to precipitation change is elevation specific and different between high- and low-elevations. Finally, we hope these findings will contribute to the theory and practice of biodiversity conservation, not only in Tibet, but also in other alpine biomes globally.

2. Materials and methods

2.1. Study region

Our study sites for simulation and validation are in the northern area of the Tibetan Autonomous Region, China (Fig. 1a), which covers approximately 1.23 million km² with an average elevation of above 4000 m a.s.l. There are three most widely distributed grassland communities, *Kobresia* dominant alpine meadows (AM), *Stipa* dominant alpine steppes (AS), and desert steppes (DS), which are co-dominated by *Ceratoides* and *Stipa* species. Vegetation distribution coincides with zonal climate

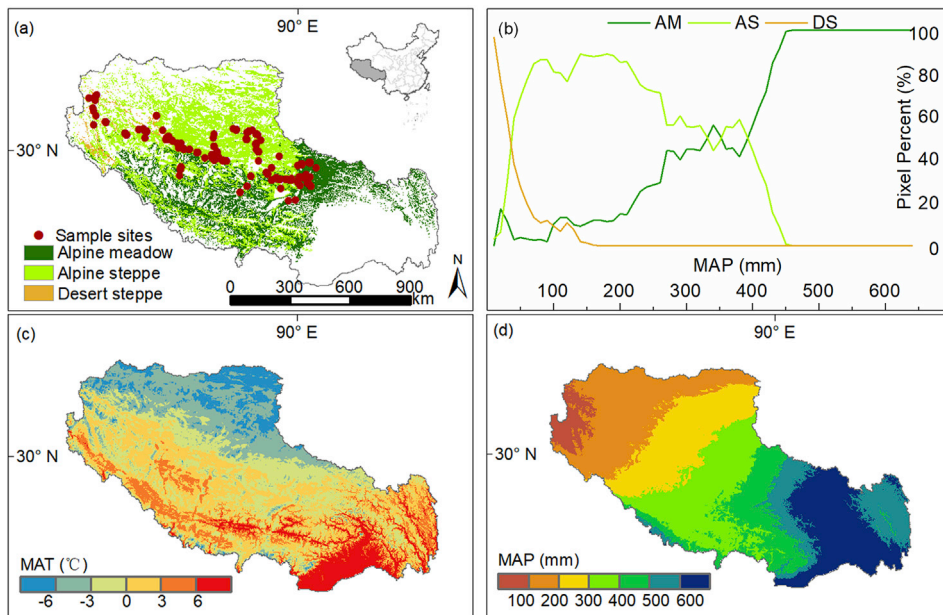


Fig. 1. Vegetation and climate of the Tibetan Autonomous Region, China. Panels, (a) sampling sites and vegetation map; (b) grassland composition (percent, %) along a precipitation gradient at the pixel scale; (c) mean annual temperature (MAT) from 2000 to 2017; and (d) mean annual precipitation (MAP) from 2000 to 2017. AM, alpine meadows; AS, alpine steppes; DS, desert steppes.

across space (Fig. 1 b–d), especially with precipitation decreasing westwards (Fig. 1 b & d). Specifically, meadows dominate where mean annual precipitation (MAP) is higher than 450 mm, both steppes and meadows mosaic in places with MAP ranging from 150 mm to 450 mm, and desert-steppes are mainly scattered in the most northwestern area where MAP is less than 100 mm (Fig. 1 a & b). Grazing is the main human disturbance to alpine grasslands on the Tibetan Plateau, which has resulted in the degradation of 17.2% alpine grasslands there in the 1990s (Yu et al., 2012). With the implementation of the ecological restoration projects by fencing in degraded pastures and economic compensatory payment policies to local pastoralists, livestock grazing was found to have little influence on species richness and composition between fenced and grazed alpine grasslands on this plateau (Wu et al., 2014b, 2016). For more detailed information on climate, vegetation, and soil in this study area, please refer to our previous publications (Li et al., 2011; Wu et al., 2014a, 2019).

2.2. Data collection and preprocessing

We carried out field campaigns annually from 2009 to 2017 at sites that covered 75 meadows, 199 steppes, and 71 desert-steppes (Fig. 1 and Table 1). Species richness was measured at each site from late July to mid-August each year when most plants were flowering or fruiting. Thus, we could identify the rare tiny species besides dominant tall ones and avoid underestimating species richness. For species identification, we had five 1 m × 1 m quadrats, which were laid out at 20-m or 50-m intervals within a relatively homogeneous area of 200 m × 200 m at each site. However, at a few sites, the weather was so harsh that we had to use a smaller quadrat of 0.5 m × 0.5 m for measurements to avoid getting sick at high elevations. Species richness at these sites was finally standardized to one square metre using the species-area relationship specified for each grassland type (Wu et al., 2014a; Zhou et al., 2016). Therefore, species richness refers to the number of species identified per square metre (no. m⁻²) for both sampling and simulation in this study.

In this study, we collected climate data for simulating species richness distribution across typical alpine grasslands in the Tibetan Autonomous Region, China. We first downloaded daily values of temperature, precipitation, and radiation for the

Table 1
Location, climate, and vegetation information for sites sampled from 2009 to 2017 across the Tibetan Autonomous Region, China. MAP, mean annual precipitation; ANPP, aboveground net primary productivity; SR, plant species richness.

Type	Sites	Longitude (°E)	Latitude (°N)	Altitude (m)	MAP (mm)	MAT (°C)	ANPP (g m ⁻²)	SR (no. m ⁻²)
All	345	81.8–92.3	31.4–33.2	4448–4995	32.8–656.3	−5.0 – +4.2	3.0–176.3	2–28
AM	75	91.5–92.3	31.6–32.3	4618–4715	361.7–656.3	−2.5 – +4.2	25.8–176.3	4–26
AS	199	86.7–91.0	31.4–33.2	4542–4995	153.5–567.8	−5.0 – +3.9	3.1–101.5	2–28
DS	71	81.8–85.1	32.0–32.3	4448–4607	32.8–352.8	−3.5 – +3.6	3.0–32.1	2–11

2000–2017 period from the China Meteorological Data Service Centre (CMDC) (<http://data.cma.cn/en>) for all stations in both Qinghai Province and the Tibetan Autonomous Region of China. Then, we calculated the weather data as monthly averages for temperature and monthly sums for precipitation and radiation. Next, we followed the instruction of Chen et al. (2014) and interpolated the monthly weather data into raster surfaces with a spatial resolution of 1 km × 1 km with ANUSPLIN 4.3 (Hutchinson, 2004). Such interpolated climate data agreed well with weather records autonomously logged by micro-weather stations in the field (Chen et al., 2014; Li et al., 2019). Seasonal weather conditions have specific influences on different stages of the plant's life cycle, sprouting, growth, reproduction, and survival. For example, freezing temperatures in late spring might be harmful to seeding. Finally, we calculated the averages of temperature and sums of both precipitation and radiation by season for the next simulation and allocated them to winter (December–next February), spring (March–May), summer (June–August), and autumn (September–November).

Topographic factors, including elevation, aspect, and slope, are also seriously considered in species distribution modelling because they can affect the combination of available water, light, and heat and indirectly limit plant settlement, growth, reproduction, and survival in the mountains. In alpine communities, altitude and topography affect not only the species richness of vascular plants but also that of bryophytes and lichens (Bruun et al., 2006). For alpine grasslands on the Qinghai-Tibetan Plateau, species richness and community productivity are highly dependent on elevations in response to climate change (Qiong et al., 2010; Sa et al., 2012; Tao et al., 2015). In this study, we calculated the slope and aspect information in ArcGIS10.0 (Environmental Systems Research Institute, Inc., ESRI) with the digital elevation model (DEM) data with a 90-m spatial resolution obtained from the USGS website (<http://earthexplorer.usgs.gov/>). In addition, we downloaded spatial data of soil texture and the sand, clay, and silt contents (%) from the Resource and Environment Data Cloud Platform (<http://www.resdc.cn/data.aspx>). Soil organic matter (SOM) and pH were available from the Land-Atmosphere Interaction Research Group (<http://globalchange.bnu.edu.cn/research/soil2>). Before topographical analyses, both DEM and edaphic data were resampled to the same spatial resolution of 1 km × 1 km as for seasonal climate variables.

Thus, we finally prepared raster surfaces of 20 environmental variables for simulating species richness distribution under different climate scenarios. Climatic variables were seasonal temperature (°C), precipitation (mm), and radiation (MJ/m²). Topographic regimes included elevation (m), slope (°), and aspect (°). Edaphic data were soil texture (sand, silt, and clay contents), pH values, and SOM content (g/kg). Before modelling, we extracted all environmental variables to each site according to its coordinates with grassland type referring to the 1:1 000 000 vegetation map of the whole Qinghai-Tibetan Plateau, Chinese Academy of Sciences, 2001. Detailed information on the response and effect variables at each site is available online (Site data in [Supplementary file](#)).

2.3. Model selection and validation

A pre-analysis for model selection and comparison was first conducted because generalized linear models (GLM) (Wood, 2012), partial least square (PLS) regressions (Carrascal et al., 2009; Feilhauer and Schmidtlein, 2009), and random forest modelling (RF) (Schmitt et al., 2017) have been used for simulating species richness change under different climate scenarios. In this step, we randomly selected the data of 80% of sites for model building and training while the data of the remaining 20% sites were used for validation. This procedure was iterated 300 times. After each iteration, we extracted simulated species richness and plotted this against the corresponding values measured in the field (see details in [Table S1](#) for model performance comparison and [Fig. S1](#) for the relationships between simulated and observed species richness). This pre-analysis finally confirmed that random forest modelling was capable of processing datasets with mutually correlated variables as recommended by Breiman (2001).

2.4. Scenario simulation and analysis

In the following simulations, we used the R package *randomForest* in R 3.5.2 (<http://www.r-project.org/>), which requires two parameters for model optimization: (1) *mtry*, the number of splits per node in each tree, and (2) *ntree*, the number of decision trees or the number of bootstrap samples. Random forest modelling uses a given number of bootstraps repeatedly and randomly to extract subsamples from the original dataset, constructs a multitude of decision trees at the training time, and outputs the classification or mean prediction of individual trees (Lopatin et al., 2016). Here, *ntree* was fixed to 500, and the optimized *mtry* value was set to five, as recommended in previous studies (Lopatin et al., 2016). After 300 iterations as described above, the importance of each predictor, which was defined as the total decrease in node impurity average over that of all trees of the ensembles, was calculated with the Gini importance function in the package (Louppe et al., 2013).

By the end of the 21st century, summer precipitation over the Tibetan Plateau will change by 0–10% relative to current conditions, with 80% probability, and by 10%–20%, with 40%–60% probability (Chen et al., 2011). Under such climate changes, Zhao et al. (2011) predicted that alpine meadows and steppes would shrink due to alpine shrub-meadow expansion. Based on our pre-analysis in the first step, we also confirmed that summer precipitation overrode the other 19 predictors to be the most critical driver for the current species richness distribution (see details in the Result and Discussion section). Therefore, we set up four different scenarios of summer precipitation, increasing and decreasing by 10% and 20%, compared to the current summer precipitation. Thus, the plant species richness pattern under each precipitation scenario was simulated with a random forest model that was structured in the same way as that in the pre-analysis.

We calculated and mapped the difference in species richness between current and changed precipitation scenarios for alpine grasslands in the whole Tibetan Autonomous Region, China. Here, we calculated the areas of alpine grasslands with species richness increased or decreased slightly by 0–0.5 species, moderately by 0.5–1.0 species, and evidently by more than one species, compared to the current species richness distribution (Table 2). Next, we examined changes in species richness under each scenario, compared to that under current summer precipitation, at the alpine grassland type level, by referring to the vegetation map (Fig. 1a). With these analyses, we could determine (1) where alpine grasslands are sensitive to summer precipitation change and what type communities they are and (2) how many alpine grasslands would have evident variation in species richness when responding to different scenarios of summer precipitation.

In this study, we also aimed to test the hypothesis that the species richness of alpine grasslands at low elevations is more sensitive than that at high elevations. Here, we divided the area of alpine grasslands mainly distributed from 3400 m to higher than 5600 m into 22 100-m elevation belts. For each belt, we calculated the means of the species richness difference between current and changed summer precipitation scenarios and plotted them along an increasing elevation gradient. Finally, the *segmented* package (Mugge, 2008) was used for searching elevation breakpoints. Segmented regressions were performed to examine the trends of species richness change with increasing elevations above and below the breakpoint for each summer precipitation scenario. All scatter/bar graphs were plotted in R3.5.2 (<http://www.r-project.org/>), and all maps were produced in ArcGIS 10.2 (<http://www.esri.com/>).

3. Results

3.1. Importance of environmental variables in simulating spatial species richness distribution

Species richness simulated with random forest modelling matched well with the data measured in the fields ($R^2 = 0.72$, $P < 0.001$) (Fig. 2a). Climate factors dominantly controlled the species richness of alpine grasslands on the Tibetan Plateau, with a sum of climatic importance of approximately 73%. As expected, summer precipitation was the most critical driver, with an importance value of about 10%, followed by summer radiation (7.5%) and spring temperature (6.4%) (Fig. 2b). The importance of temperature over all seasons summed to be 23.7%, being lower than that of precipitation (25.7%) in controlling the species richness of the Tibetan alpine grasslands (Fig. 2b). Soil texture, in terms of the sand, clay, and silt contents, ranked lowest in species richness modelling, with their importance values being around 2% (Fig. 2b).

3.2. Current species richness distribution across alpine grasslands in the Tibetan Autonomous Region

Species richness of alpine grasslands on the Tibetan Plateau decreases from alpine meadows in the east to desert steppes in the northwest (Fig. 3a), with the observed vs. simulated means being highest in meadows (15.9 vs. 15.5), moderate in steppes (10.6 vs. 10.5), and lowest in deserts (5.3 vs. 5.6) (Fig. 3b). Overall, the species richness pattern simulated with random forest modelling was reliable for all three grassland types, which showed slight changes, less than one species per square metre, compared to field measurements (Fig. 3b).

3.3. Species richness change under different summer precipitation scenarios at the grassland type level

Species richness will remain stable in 56%–82% of alpine grasslands with changing summer precipitation (Table 2), mostly in alpine steppes and deserts in the northwest area (Fig. 4, and vegetation referring to Fig. 1a). When summer precipitation declines by 20%, species richness will decrease by more than one species per square metre in 29.5% of alpine grasslands (Table 2), mainly in alpine meadows or in the ecozone between meadows and steppes in central Tibet (Fig. 4a). When summer precipitation declines by 10%, species richness will decrease by more than one species per square metre in 9.6% of alpine grasslands in the central area (Table 2, Fig. 4b). In contrast, when summer precipitation increases by 10% and 20%, species richness will increase by more than one species per square metres in 7.4% and 20.4% of alpine grasslands in the central area (Table 2, Fig. 4c&d).

Decreasing summer precipitation will decrease species richness moderately, by 0.6–0.8 species per square meters, while increasing precipitation by 10–20% will increase species richness slightly, by 0.2–0.4 species per square meters for all three

Table 2

The area percentage (%) of alpine grasslands with changes in species richness under the four scenarios of changed summer precipitation on the Tibetan Plateau.

Changes in species richness (no. m ⁻²)	Scenarios of precipitation _{summer} changed by			
	–20%	–10%	+10%	+20%
< –1	29.51	9.64	0.22	0.46
–1––0.5	8.52	10.04	0.80	1.68
–0.5–0.5	56.41	78.42	82.04	69.90
0.5–1	4.26	1.72	9.58	7.57
>1	1.30	0.18	7.35	20.38

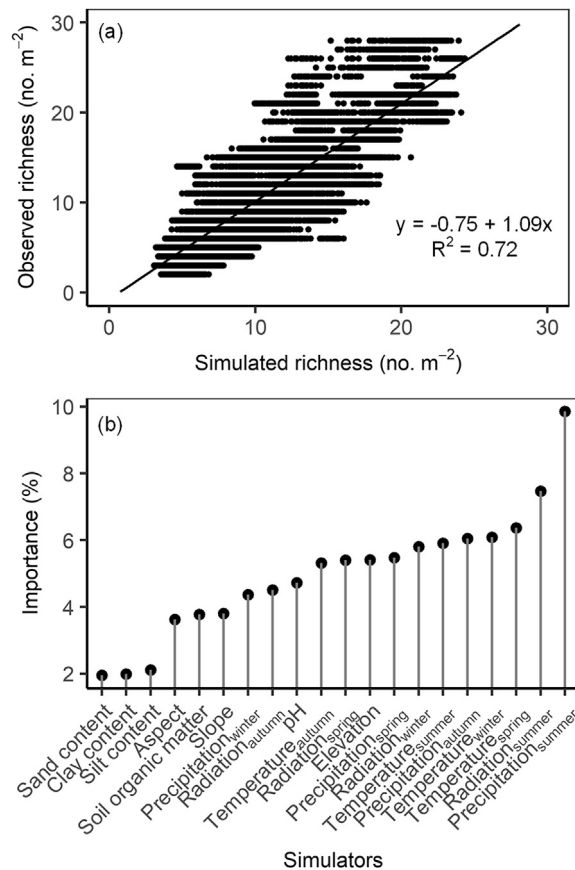


Fig. 2. Model performance and predictor importance in simulating species richness across the Tibetan alpine grasslands under current climate conditions. Panel (a), the relationship between observed and simulated values; Panel (b), the relative importance ranking of climatic, edaphic, and topologic variables used for random forest modelling.

grassland types in the study area (Fig. 5a). However, the species richness response to changing summer precipitation is grassland-type specific. In particular, alpine deserts are resistant to changes in summer precipitation, with species richness being unchanged (Fig. 5b). Species richness of alpine meadows and steppes will decline under decreasing summer precipitation and will increase under increasing summer precipitation. However, alpine steppes might be more sensitive than meadows in response to increasing summer precipitation by 10–20% and decreasing summer precipitation by 10%, with considerable changes in species richness (Fig. 5b). Alpine meadows will experience a higher reduction in species than steppes under changes in summer precipitation of 20% (Fig. 5b).

3.4. Species richness at low-vs. high elevations in response to changes in summer precipitation

The species richness response to changes in summer precipitation differs between low- and high-elevation grasslands (Fig. 6 and Table S2). The elevation breakpoints are also different under different precipitation scenarios. There was no evident trend in species richness change along the elevation gradient where the elevation was above the breakpoint. Notably, species richness will decrease by 0.5–2.0 species per square meters in alpine grasslands with elevations lower than 5500 m under a summer precipitation decrease of 20%. Species richness will decrease by 0.4–0.8 species per square metres in alpine grasslands with elevations lower than 3700 m, where precipitation decreases by 10%. Under summer precipitation increases of 10 and 20%, the species richness of alpine grasslands with elevations lower than 4200 m and 4700 m will increase by 0–0.4 species per square metres.

4. Discussion

In this study, based on multi-year observations in the field, we first simulated the current spatial pattern of plant species richness for alpine grasslands in Tibet with random forest modelling. Summer precipitation was further confirmed as the primary driver of species richness change across space. Next, we simulated species richness patterns under different summer

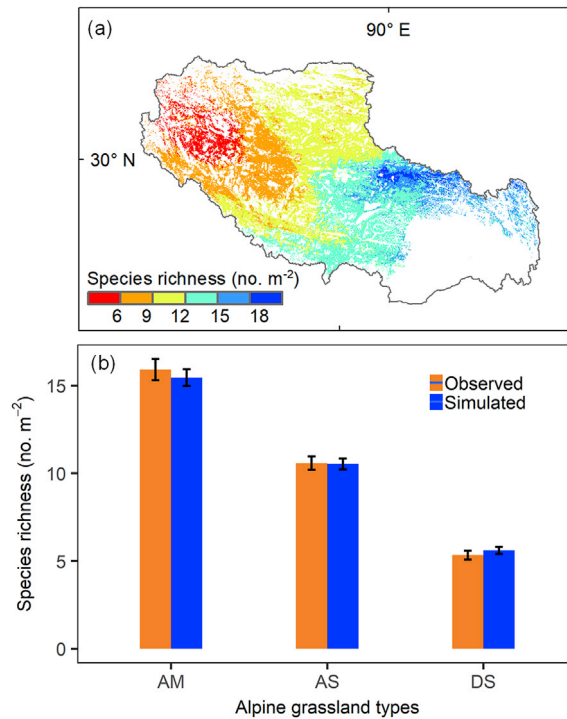


Fig. 3. Species richness of alpine grasslands on the Tibetan Plateau under current climatic conditions. Panel (a), simulated species richness distribution; Panel (b), comparison between simulated and observed species richness (mean with standard error bar) at the grassland type level.

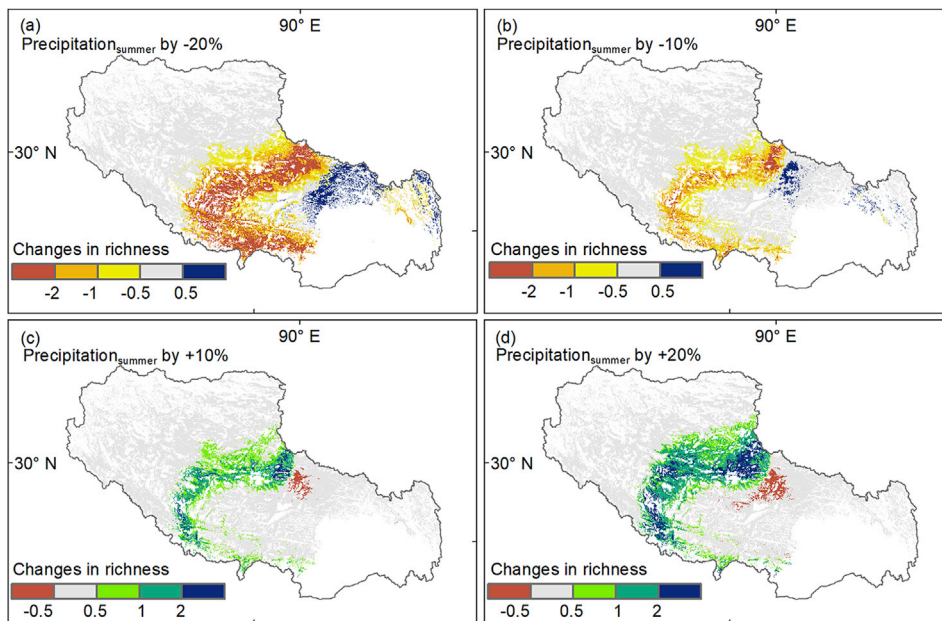


Fig. 4. Mapping species richness changes under different summer precipitation scenarios compared to current climatic conditions (see Fig. 3a) in the Tibetan Autonomous Region, China. Non-grassland areas (see Fig. 1a) were masked out during modelling and are shown in white.

precipitation scenarios, with current precipitation increasing and decreasing by 10% and 20%. We calculated and mapped the difference in simulated species richness patterns from that under current precipitation conditions. Finally, the sensitivity of species richness response to summer precipitation was specified at the grassland type level and from an elevation gradient perspective. More details on the relative importance of the environmental drivers and potential mechanisms will be discussed below.

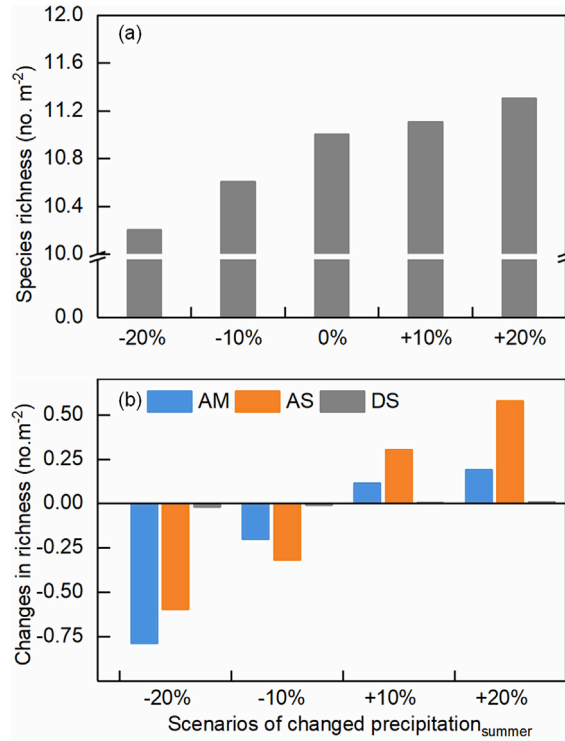


Fig. 5. Changes in species richness under different summer precipitation scenarios compared to current climatic conditions. Panel (a), mean species richness of all alpine grassland types; Panel (b), the difference in species richness between current and changed summer precipitation scenarios at the grassland type level. AM, alpine meadows; AS, alpine steppes; DS, desert steppes.

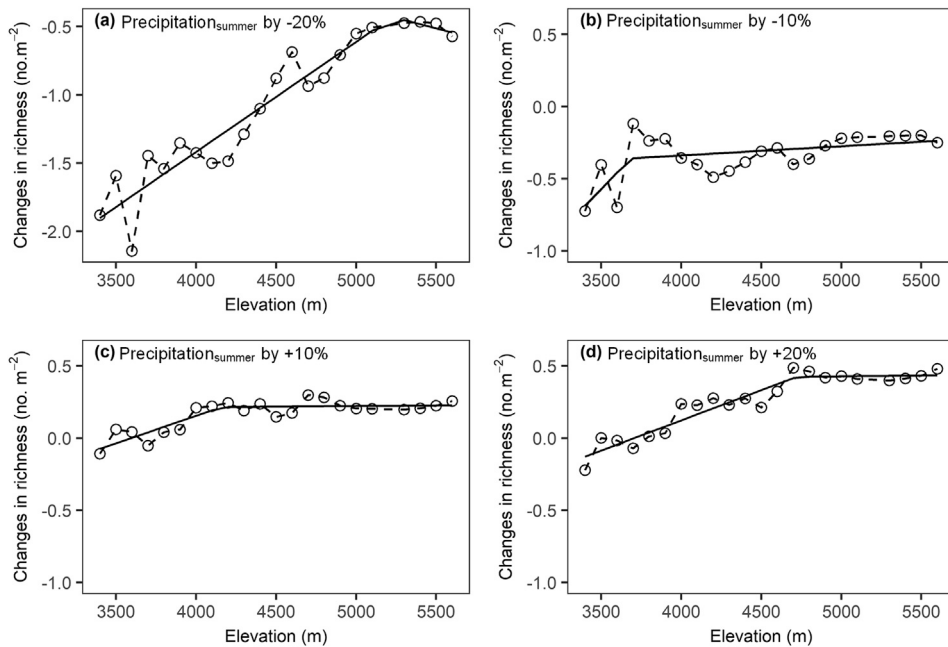


Fig. 6. Breakpoint analysis of species richness changes along the elevation gradient under different scenarios of changed summer precipitation compared to current climate conditions.

4.1. Importance of environmental variables in driving current species richness patterns

First, summer precipitation was most critical driver of the current species richness pattern compared with the other 19 environmental variables used in random forest modelling (Fig. 2b). This is consistent with studies in semi-arid grasslands at regional and global scales (Duffy et al., 2017; Grossiord et al., 2017; Siepielski et al., 2017), agrees with studies in temperate grasslands on the Inner Mongolian Plateau (Bai et al., 2008; Hu et al., 2010), and coincides with previous findings in alpine grasslands on the Qinghai-Tibetan Plateau (Shi et al., 2014; Yang et al., 2010). A potential explanation is that plants in such semi-arid habitats have been environmentally selected (Griffin-Nolan et al., 2018; Pérez-Camacho et al., 2012) to evolve specific functional traits to adapt to limited precipitation and soil moisture. For example, Wu et al. (2016) found that plant functional trait diversity indices and the community-weighted mean and divergence of water-use related traits were as reliable as precipitation in regulating the spatial variation of community productivity across diverse alpine grassland types in northern Tibet.

Second, our finding partly agrees with Körner (2003a) that low temperature is a critical limiting factor for plants in high-elevation ecosystems. In this study, we found that temperature was less critical than precipitation in summer in simulating species richness distribution with random forest modelling (Fig. 2b). This might be caused by the distance from the oceans. The Alps in Europe are relatively close to the Mediterranean, and thus abundant precipitation might be less critical than temperature for alpine plants at high elevations (Körner, 2003a). However, surrounded by the Himalayan Ranges in the south and Hengduan Mountains in the east, the South Asian Monsoon from the Indian and Pacific Oceans is blocked and weakened. Consequently, precipitation decreases from southeast to northwest across the Tibetan Plateau (Fig. 1d) and becomes the most critical factor limiting alpine grassland plant survival in this region (Tada et al., 2016). This might be the reason why precipitation overrides temperature and other environmental factors with respect to both the spatial pattern of species richness and alpine plants' physiological process and function within this plateau. For example, Fu et al. (2018) found that increasing precipitation had much stronger influences than experimental warming on alpine meadow productivity in the central Tibetan Autonomous Region where alpine plants are able to capture the arrival signal of summer monsoon precipitation to prepare for leaf unfolding (Li et al., 2016).

Third, we found that the effects of soil properties and topographical regimes were not as crucial as expected in simulating species richness distribution (Fig. 2b). One explanation is that soil texture and nutrient availability are controlled by both climate and vegetation, especially under such a robust control of precipitation over space. For example, Ji et al. (2014) found that soil pH correlated negatively with soil moisture and the silt content decreased with increasing temperature and decreasing precipitation westwards on the Tibetan Plateau. Foliar nitrogen and carbon isotopic compositions ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) are functional traits that represent plants' water-use efficiency and nitrogen up-take preference (Peri et al., 2012; Wang and Schjoerring, 2012). However, across alpine grasslands in northern Tibet, Wu et al. (2019) found that due to the robust control of precipitation, soil nitrogen and phosphorus contents had no significant influences on the $\delta^{15}\text{N}$ differentiation among alpine grassland plants. Moreover, the weak importance of topographical regimes can be attributed to spatial scales. In a mountain valley, species richness distributes differently along different slopes, aspects, and elevations (Hofer et al., 2008; Moeslund et al., 2013). However, at a broader scale, such topographic effects might be less critical than climatic and edaphic factors, although biotic and abiotic factors together regulate plant species richness and distribution (López-Angulo et al., 2018; Moura et al., 2016).

4.2. The sensitivity of species richness in alpine grasslands to changed summer precipitation

Species richness is the key to predicting ecosystem service and function responses to future climate change (Koerner et al., 2018). With respect to this topic in alpine grasslands on the Tibetan Plateau, scientists have addressed the importance of species richness (Ma et al., 2010; Wang et al., 2013; Wu et al., 2014a) and other diversity indices (Niu et al., 2015; Wu et al., 2016) derived from species composition in regulating ecosystem multifunctionality to climate change along environmental or spatial gradients. Climate is forecasted to be warmer and wetter with shifting precipitation spatiotemporally in the near future on the Qinghai-Tibetan Plateau (Li et al., 2010; Yang et al., 2014; Zhang, 2015). Therefore, it becomes urgent to analyse the sensitivity of species richness response to precipitation change and thereby formulate sustainable and adaptive policies on ecosystem management (Weltzin et al., 2003).

Our study confirmed that such a sensitivity of species richness response to precipitation change is grassland specific. Species richness of desert steppes where annual precipitation is generally less than 100 mm (Fig. 1a & d) is resistant under different scenarios of changed summer precipitation (Figs. 4 and 5b). This is consistent with Wu et al. (2017), i.e., that no significant change in vegetation coverage was found in alpine deserts after ten years of fencing. Species pool size and soil nutrient availability might be the reasons for the stability of species richness in desert steppes. Only 2–11 species per square metres were found in desert steppes on the Tibetan Plateau (Table 1). Such a small species pool limits individual plant recruitment (Arvid Grytnes and Birks, 2002; Grace, 2001), and alien species can rarely survive in poor desert soils (Wu et al., 2014a).

In contrast, alpine meadows and steppes have more species than deserts (Table 1 and Fig. 3b). Considerable changes in species richness with changing precipitation will occur only in alpine meadows and steppes in the central area (Figs. 4 and 5). In addition, we also found that alpine steppes are more sensitive than meadows to precipitation changes except for the case of severe drought, with summer precipitation reduced by 20% (Fig. 5b). This might be partly due to the difference in community

composition of plant functional groups with different water-use-related traits and the role of dominant species in shaping community assembly (Gellesch et al., 2015; Mason et al., 2011; Zhu et al., 2015). For example, mesophytic plants in alpine steppes are able to grow in both semi-arid and humid habitats, while the hygrophytes dominant in alpine meadows cannot survive in semi-arid steppes and arid deserts. This is similar to Chelli et al. (2016), who reported that plant functional groups differ in response to precipitation change, with forbs benefiting more than grasses from increased water availability. On the other hand, the competitive advantages of dominant *Kobresia* species in alpine meadows might be obstacles for the settlement and survival of other less competitive species. However, in the sparsely structured alpine steppes dominated by *Stipa* species (Zhu et al., 2015), there is available niche space for other species recruited from either alpine meadows or deserts.

In addition, we found that the species richness of alpine grasslands at low elevations is sensitive to precipitation change while that at high elevations remains resistant and unchangeable, although the elevation breakpoints are different under different precipitation change scenarios (Fig. 6 and Table S2). This is similar to that observed in alpine deserts: species settlement and survival at high elevations are also limited by both harsh physical conditions and a small local species pool. Notably, under droughts with summer precipitation reduced by 20%, species richness at 3500–5000 m will decrease by 0.5–2 species per square metres (Fig. 6a and Table S2), implying that species richness will decrease less at higher elevations than at lower elevations. Overall, we found that alpine grasslands on the Tibetan Plateau are likely to be more sensitive to drought than to wetting, partly consistent with Byrne et al. (2017), who found a higher number of considerable changes in species richness under drought treatment than under water addition in a manipulative experiment at a sub-humid grassland site.

It is known that climatic, edaphic, and topographic drivers jointly control community assembly and ecosystem functioning across different scales (López-Angulo et al., 2018; Pires et al., 2018). However, there are still some uncertainties in simulating species richness change under increasing and decreasing precipitation. The interactions between changing precipitation and other predictors should be specified prior to modelling in further studies. In addition, plants adapt and respond to climate change differently among species and life-forms (Byrne et al., 2017). Limited by data availability, it is a considerable challenge to simulate plant species distribution at the species level.

5. Conclusions

Species richness of alpine grasslands in the Tibetan Autonomous Region, China, is mainly controlled by climate, especially summer precipitation, which overrode the 19 other environmental factors, and was further confirmed to play the most critical role in shaping current species richness distribution across alpine meadows, steppes, and deserts on the Tibetan Plateau. Species richness in response to changed summer precipitation is grassland-type specific, with alpine deserts being resistant and alpine meadows and steppes being sensitive. Alpine meadows are sensitive to severe droughts, with a reduction in species richness, while alpine steppes are sensitive to wetting through increased species richness. In addition, species richness at low elevations, even though the elevation breakpoints might be different under different summer precipitation scenarios, is likely to change considerably. Therefore, we suggest that policymakers and herdsmen pay closer attention to the alpine pastures in central Tibet and in areas where species richness likely experiences large changes under ongoing climate change.

Author contributions

JW conceptualized this study and led field surveys since 2009. ML joined the field campaign 2017, collected and analyzed data, and wrote the first draft. JW revised the manuscript for readability. XZ, YH, BN, and XW interpreted the results. All authors contributed to this work and approved the final submission. The authors declared no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00848>.

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