Permafrost and drought regulate vulnerability of Tibetan Plateau grasslands to warming

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Abstract.   The Tibetan Plateau has the largest expanse of high-elevation permafrost in the world, and it is experiencing climate warming that may jeopardize the functioning of its alpine ecosystems. Many studies have focused on the effects of climate warming on vegetation production and diversity on the Plateau, but their disparate results have hindered a comprehensive, regional understanding. From a synthesis of twelve warming experiments across the Plateau, we found that warming increased aboveground net primary production (ANPP) and vegetation height at sites with permafrost, but ANPP decreased with warming at non-permafrost sites. Aboveground net primary production responded more negatively to warming under drier conditions, due to both annual drought conditions and warming-induced soil moisture loss. Decreases in species diversity with warming were also larger at sites with permafrost. These results support the emerging understanding that water plays a central role in the functioning of cold environments and suggest that as ecosystems cross a threshold from permafrost to non-permafrost systems, ANPP will decrease across a greater proportion of the Tibetan Plateau. This study also highlights the future convergence of challenges from permafrost degradation and grassland desertification, requiring new collaborations among these currently distinct research and stakeholder groups.

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INTRODUCTION

Permafrost on the Tibetan Plateau covers 1.5 million km^2, approximately half the area of the Plateau. It accounts for 70.5% of the permafrost area in high Asia and 75% of the permafrost in Northern Hemisphere mountains (Yang et al. 2010). The presence or absence of permafrost determines the structure and nutrient status of the soil and strongly affects plant community structure, production (Yi et al. 2011), and soil carbon dynamics (Natali et al. 2014). The Tibetan Plateau's alpine grasslands, which consist primarily of alpine meadow and alpine steppe vegetation, cover more than two-thirds of the area of the Tibetan Plateau (Xue et al. 2017) and are important for regional energy balance, climate, and carbon storage (Wang et al. 2002).

Moreover, these alpine grasslands support a diverse assemblage of wildlife and pastoralism as a primary livelihood activity.

Surface temperatures on the Tibetan Plateau have increased by 1.8°C with a warming rate of 0.35°C per decade over the past 50 yr (Xu et al. 2017), and the projected rate of future warming is faster than the global average (Stocker et al. 2014). Observational data from monitoring stations on the Plateau indicate that the mean annual permafrost temperature at a depth of 6.0 m increased by 0.43°C from 1996 to 2006, at an average annual rate of 0.04°C (Wu and Zhang 2008), and it continued to increase by 0.1°C from 2006 to 2010 at an average annual rate of 0.02°C (Wu et al. 2012). These warming trends have caused the lower elevational limit of permafrost to move upward by 25–100 m since the 1980s (Cheng and Wu 2007). Within the Yellow River source region of the Tibetan Plateau, Qin et al. (2017) found a 1.1% decrease in the permafrost area ratio over the past 35 yr; permafrost area decreased sharply after 2000, a decline that correlated with strong temperature increases. In a review of permafrost dynamics on the Tibetan Plateau since the 1950s, Zhang et al. (2016) note the loss of 99,000 km^2 of permafrost per decade, increases in active layer thickness of 4–8 cm/yr, and increases in thawing days of about 10–16 d/decade. Understanding how climate warming affects ecosystem processes in permafrost and non-permafrost areas across Tibet remains a critical but poorly studied question (Xue et al. 2009). Addressing this knowledge gap is necessary to assess future ecosystem, climate, and livelihood implications in this expansive and significant region (Harris 2010, Klein et al. 2014).

Aboveground net primary production (ANPP) is commonly used as an indicator of grassland health and an ecosystem's potential for storage of nutrients and energy, and is crucial to the carbon cycling of terrestrial ecosystems (Oberbauer et al. 2007, An et al. 2013, Zha et al. 2013, Babel et al. 2014, Rodriguez et al. 2018). At regional to global scales, ANPP is positively correlated with mean annual precipitation (MAP), particularly in water-limited ecosystems (Hsu et al. 2012). The response of net primary production (NPP) worldwide to increasing temperature over time is mediated by moisture status (Zhao and Running 2010). Studies of arctic and alpine responses to climate change have frequently used experimental methods and syntheses that have demonstrated that the response of ANPP to temperature enhancement is highly variable across arctic and alpine regions (Elmendorf et al. 2012a). Increased temperatures may stimulate plant production directly by providing a warmer environment for plant growth or indirectly by stimulating microbial decomposition of organic matter and releasing more nutrients for plant uptake and growth. Conversely, soil water deficit due to warming may also induce more allocation to belowground biomass, thereby decreasing ANPP (Hollister et al. 2005) and contributing to degradation processes (Hopping 2015).

Observational studies that correlate climate data with vegetation across the Tibetan Plateau grasslands highlight the important role that climate plays in affecting plant production. Satellite data show increases in the normalized difference vegetation index (NDVI, a proxy for ANPP) with increasing precipitation over a 40-yr period (1969–2008) across the Tibetan Plateau (Ye et al. 2013). Change detection studies using satellite imagery also demonstrate that the area of alpine meadows has decreased from 1967 to 2013 (Wang et al. 2011, Du et al. 2015). This grassland degradation is attributed to the combined effects of climate change and permafrost decline, which explain 82–86% of grassland degradation (Wang et al. 2009). However, these studies rely on observational data, in which correlations may lead to spurious causal relationships (Klein et al. 2014). Factors such as grazing and soil disturbance from small mammals—and their interactions with climate—can also affect vegetative properties (Wu et al. 2009, 2017, Harris 2010). Furthermore, there may be erroneous correlations between space-borne and ground-based measurements (Jackson and Huete 1991), and commonly used remotely sensed metrics, such as NDVI, may be unable to detect finer-scale changes in vegetation species composition, which, in addition to ANPP, are an important consideration for understanding ecosystem change (Hopping et al. 2018).

Controlled experiments can help overcome limitations to observational studies by identifying causal relationships. Climate manipulation experiments on the Tibetan Plateau have revealed dramatic changes in plant production

and diversity with warming (Klein et al. 2004, 2007, Li et al. 2011, Wang et al. 2012, Yang et al. 2015). However, experimental warming in Tibet has led to increases, decreases and no effect on ANPP (Klein et al. 2007, Wang et al. 2012, Fu et al. 2013, Yang et al. 2015, Chen et al. 2016). Thus, single-site experiments can be highly site- and context-dependent, hindering broader understanding of drivers, mechanisms, and implications.

Given the disparate findings of these individual studies, and the potentially confounding factors that emerge with correlational studies, an overarching understanding of the direction of future alpine grassland structure and function across the Tibetan Plateau remains elusive. Furthermore, a clear understanding of the role of temperature, precipitation, permafrost, and their interaction in regulating plant production and diversity, and their contribution to rangeland degradation, remains uncertain across the different environmental conditions of the Tibetan Plateau. While there are important synthesis efforts across tundra sites worldwide (Elmendorf et al. 2012*a*, *b*), none has occurred across the Tibetan Plateau, and none has specifically compared the critical difference between permafrost and non-permafrost sites within a single region.

Here, we use data from 12 warming experiments across the Tibetan Plateau to examine changes in ANPP and community composition under extant and future climate conditions, with and without permafrost. We address the following questions: (1) How do climatic factors and their interactions, including presence or absence of permafrost, affect ANPP, diversity, and vegetation height under ambient climate on the alpine grasslands of the Tibetan Plateau? (2) How does experimental warming affect ANPP, diversity, and vegetation height across sites on the alpine grasslands of the Tibetan Plateau, and how do climatic factors, including presence or absence of permafrost, mediate these warming effects? A better understanding of the impacts of climate warming on ANPP and diversity in high-elevation regions will increase our ability to predict future productivity and carbon budgets of terrestrial ecosystems with direct implications for energy balance, regional climate, livelihoods, and biodiversity conservation.

MATERIALS AND METHODS

Site descriptions

We use data from experiments that simulated climate warming using open top chambers (OTCs) in nine alpine meadow and three alpine steppe sites on the Tibetan Plateau (Fig. 1, Appendix S1: Tables S1, S2). The twelve sites span 30° to 38° N, a region in which alpine grasslands ecosystems cover approximately 65% of the Plateau area, and 69% of which are alpine meadow and steppe ecosystems (Wang et al. 2002). Together, these vegetation types represent the majority of the land cover on the Tibetan Plateau. Three of the experimental warming sites were located in regions with ice-rich permafrost, and nine were located in areas with seasonally frozen ground (Zhou et al. 2000).

Open top chambers are commonly employed to simulate warming in alpine and arctic ecosystems (Marion et al. 1997). Across the 12 sites, simulated warming increased air temperature by 1.1°–3.7°C. At eleven of the sites, the increase in air temperature ranged from 1° to 2°C; at one site, Xainzha, the OTC air warming effect was 3.7°C. Open top chamber warming of soil temperature ranged from 0.23°C (Hongyuan) to 3.46°C (Xainzha). We omitted OTC warming studies that focused on forest seedlings and or shrubs, to make the studies more comparable. Large grazers (including livestock and wildlife) were also excluded from all of the study plots in our analysis to avoid the added complexity of grazing effects across sites.

Vegetation sampling, data acquisition, and statistical analyses

We obtained raw data from seven of the sites. For sites where we obtained data from published literature (Hongyuan, Damxung, Songpan, Qinghaihu, Maqu), we used GetData Graph Digitizer (v. 2.26.0.20) to extract data from figures. We use one year of data from each site due to limited data access. At Fenghuoshan, Beiluohe, Guoluo, Xainzha, Maqu, Songpan, and Damxung, Qinghaihu (Shi et al. 2008, Zong et al. 2013, Zhang 2014, Chen et al. 2016), the community composition surveys and aboveground harvest methods were conducted as follows. At peak biomass in August, the percent cover and height of all vascular plant species in a 50 × 50 cm quadrat
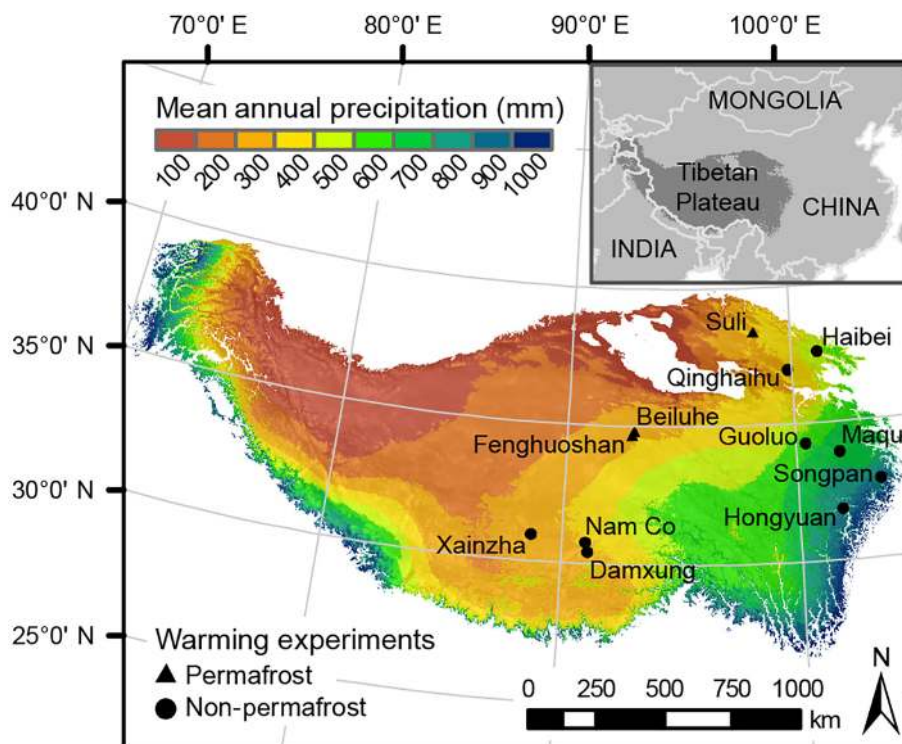
Fig. 1. Location of the 12 warming experiment sites on the Tibetan Plateau that are included in this analysis.

centered in each plot were recorded. At Maqu and Songpan, all of the aboveground live plant biomass was harvested, while at Fenghuoshan, Beiluhe, Guoluo, and Xainzha only half of the quadrat was harvested. At Damxung and Qinghaihu, investigators used a non-destructive measure to estimate ANPP. At the Suli site, vegetation cover and species composition in a 100×100 cm area were estimated by taking digital images (Fujifilm J35, Fujifilm Corporation, Tokyo, Japan) every 5–15 d during the growing season and calculating cover according to Yi et al. (2011). Live plant biomass was then harvested from a 25×25 cm quadrat in each plot at peak biomass. At the Haibei and Nam Co sites, species composition, cover, and height were estimated in 75×75 cm plots. Investigators used non-destructive sampling methods to estimate ANPP based on cover and height (Klein et al. 2007). At the Hongyuan site, plant species composition, vegetation height, and cover were recorded in a 100×100 cm quadrat, and live aboveground vegetation was harvested in September (Li et al. 2011). For sites with non-destructive biomass methods, R^2 values for the

relationships between aboveground biomass, cover, and height at Haibei, Nam Co, Damxung, and Qinghaihu were 0.98, >0.90, 0.66, and 0.95, respectively (Klein et al. 2007, Zong et al. 2013, Hopping 2015, Chen et al. 2016). From the community composition data, we calculate plant diversity using the Shannon-Wiener (H') diversity index (Ludwig and Reynolds 1988).

We used mean annual temperature (MAT) and precipitation and approximate average growing season length (June–August), soil moisture (SM) and drought index data as explanatory variables in our models. For SM, hourly soil moisture during the growing season was measured at 10 cm depth at all sites except Damxung (5 cm) and Songpan (15 cm). These measurements represent SM in the upper soil layer, where most of the plant roots are located (Zhou et al. 1986, Hu et al. 2013). The drought index at each site was extracted from the Global Standardized Precipitation-Evapotranspiration Index Database (Beguería et al. 2014). The drought index data represent the balance between growing season precipitation and potential evapotranspiration for each site in the analysis, with negative values

indicating relatively dry years and positive values representing wet years relative to long-term site averages. We selected the SPEI 3-month data product for June–August, corresponding to the approximately average growing season length across sites when vegetation sampling was conducted. The drought index thus allows us to assess moisture status in the year in which data were collected, as compared to the longer-term mean. Mean annual temperature and MAP values are from meteorological station data averaged across all available years (Appendix S1: Table S1).

We calculated log response ratios for the relative change in ANPP with warming relative to paired control plots (rel.ANPP) as: ln[(warming ANPP)/(control ANPP)] (Tilman et al. 2012). We calculated the same relative change metric for diversity (rel.Diversity), vegetation height (rel.Height), and soil moisture (rel.SM). We also report absolute changes in ANPP, diversity, and height by taking the difference between paired control and warmed plots in each experiment.

We used linear mixed effects models (LMEs) to determine the importance of the measured environmental variables in regulating ANPP, diversity, and height across all 12 sites under un-warmed conditions, using only data from control plots in each experiment, followed by LMEs testing the association of environmental variables with rel.ANPP, rel.Diversity, and rel.Height under warming. LMEs tested the significance of MAT, MAP, permafrost presence, SM (for control plots) or rel.SM (for warming effects), drought index in the year of sampling, change in air temperature with OTC warming, and all two-way interactions as fixed effects. We used site as a random effect to help account for differences in experimental and sampling protocols across sites. In the models for vegetation under un-warmed conditions, we decided a priori to only retain drought in the model if it was interacting with another predictor (MAT, MAP, or SM), since site-specific drought conditions in any given year are unlikely to explain regional patterns in vegetation communities across a vast portion of the Tibetan Plateau. For the models assessing relative changes with warming, however, we allowed drought to stay in the model as an independent effect.

We checked for collinearity and correlations among predictor variables by assessing their Variance Inflation Factors (VIF) and Pearson correlations, and we removed those with VIF > 10 or a correlation >0.80. This usually precluded MAP, MAT, and permafrost from being included in the same model, in which case we ran separate models for each of them.

We used backward selection to remove variables based on their effect on the models' Akaike Information Criteria (AIC) scores. For this, we employed log-likelihood tests to compare the full model with models in which each term was removed, and we dropped variables if they were not significant at a threshold of $P < 0.05$. For the LMEs of vegetation height under ambient climate, we used a log link function to improve model fit. In the rel.Diversity model, we removed five outliers from the data: Four were plots from Haibei known to have a different grazing history from the others, and the fifth was a very low outlier from Nam Co. We validated the final models graphically with Q-Q plots, plots of the model-fitted values against standardized residuals, and plots of the standardized residuals against each explanatory variable. We report marginal and conditional R^2, along with the change in AIC for the final model relative to the null, intercept-only model. We used the lme4 package in R (R Development Core Team) for our LMEs and ggplot2 (Wickham 2009) to make figures.

RESULTS

ANPP, diversity, and vegetation height across sites

Aboveground net primary production ranges from 77 to 352 g/m^2 (Table 1) across the twelve sites, with MAP driving ANPP under ambient climate conditions (in control plots), regardless of permafrost status (Fig. 2; Appendix S1: Tables S3, S4). No abiotic variables in our models were significant predictors for vegetation diversity or height under ambient climate (Appendix S1: Table S4).

ANPP, diversity, and vegetation height response to warming

Changes in ANPP with warming relative to control plots (rel.ANPP, calculated as log response ratios) were significantly affected by permafrost presence and by the interaction between relative change in soil moisture with warming (rel.SM) and ambient drought conditions (Appendix S1: Tables S3, S5). Rel.ANPP

Table 1. Descriptive statistics for measurements of aboveground net primary production (ANPP), vegetation diversity, and height in control plots at each site.

Site	SM (%) Mean	ANPP (g/m^2)			Shannon diversity			Height (cm)		
		n	Mean	SD	n	Mean	SD	n	Mean	SD
Fenghuoshan	53.18	6	84.11	7.81	6	2.32	0.15	6	1.62	0.34
Suli	34.63	3	202.19	29.07	0	–	–	0	–	–
Beiluhe	51.38	6	77.41	19.45	6	1.52	0.05	6	6.30	0.73
Haibei	45.16	8	291.44	36.31	8	2.77	0.23	4	8.03	1.81
Qinghaihu	8.67	3	149.17	40.29	1	1.82	–	3	2.96	1.59
Nam Co	17.79	8	87.72	15.15	8	1.18	0.26	8	1.86	0.49
Guoluo	35.04	6	200.56	20.30	1	4.17	–	6	3.09	0.25
Xainzha	17.14	3	99.71	7.84	0	–	–	0	–	–
Hongyuan	46.67	3	351.73	14.92	1	1.34	–	3	2.76	0.21
Maqu	49.00	1	251.48	–	1	1.36	–	0	–	–
Damxung	11.97	3	194.22	27.33	0	–	–	0	–	–
Songpan	54.03	3	272.00	70.86	1	2.93	–	0	–	–

Notes: There was one mean value for soil moisture (SM) in control plots at each site except for Haibei, which had two mean values for two sets of plots (SD = 0.57). En dash represents no data.
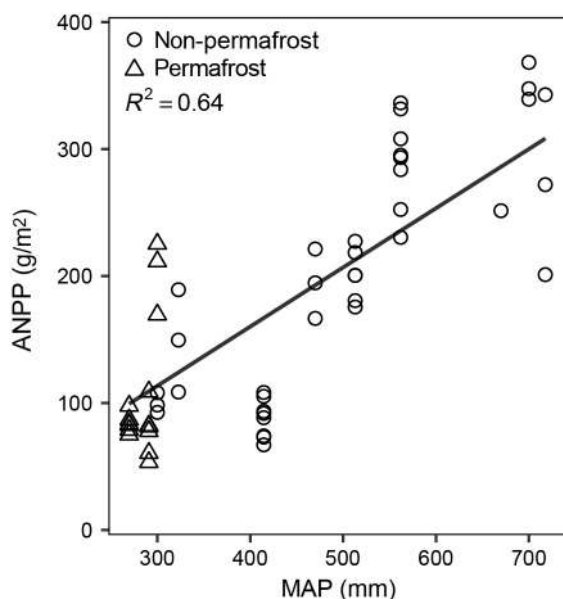

Fig. 2. General linear mixed effect model of aboveground net primary production (ANPP) in control plots regressed against mean annual precipitation (MAP), with site included as a random effect. Points represent plots at sites with and without permafrost, and the marginal R^2 for the model is shown.

increased with warming where permafrost was present but decreased at nearly all non-permafrost sites (Fig. 3a, b). Rel.SM and ambient drought further mediated ANPP responses to warming, with larger relative decreases in production in drier than average years and with greater decreases in rel.SM with warming.

Permafrost presence or absence explained much of the variation in relative changes in diversity under warming (rel.Diversity). Rel.Diversity decreased with warming at permafrost sites and exhibited little change across all of the non-permafrost sites (Fig. 4; Appendix S1: Tables S3, S5). Yet, the four sites with the lowest MAT values (and for which there are diversity measurements, which include non-permafrost sites at Haibei and Qinghaihu) all experienced declines in rel.Diversity (Appendix S1: Table S7). However, since sites with permafrost were also the coldest sites, MAT and permafrost could not be included in the same model.

Vegetation height, which ranged from 1.6 to 8.0 cm in control plots across sites (Table 1), increased in response to warming at all sites where data were available ($n = 7$; Appendix S1: Tables S6, S7), but relative changes in height (rel.Height) were significantly mediated by drought, relative changes in soil moisture with warming, changes in air temperature with warming, and site MAP and MAT (Appendix S1: Tables S3, S5). Relative increases in height were significantly larger at sites with less warming-induced SM loss and at sites with lower MAP (Fig. 5a). Moreover, under warming, rel.Height increased more at sites not experiencing drought (Fig. 5b). Temperature also mediated height responses, with rel.Height increasing more at
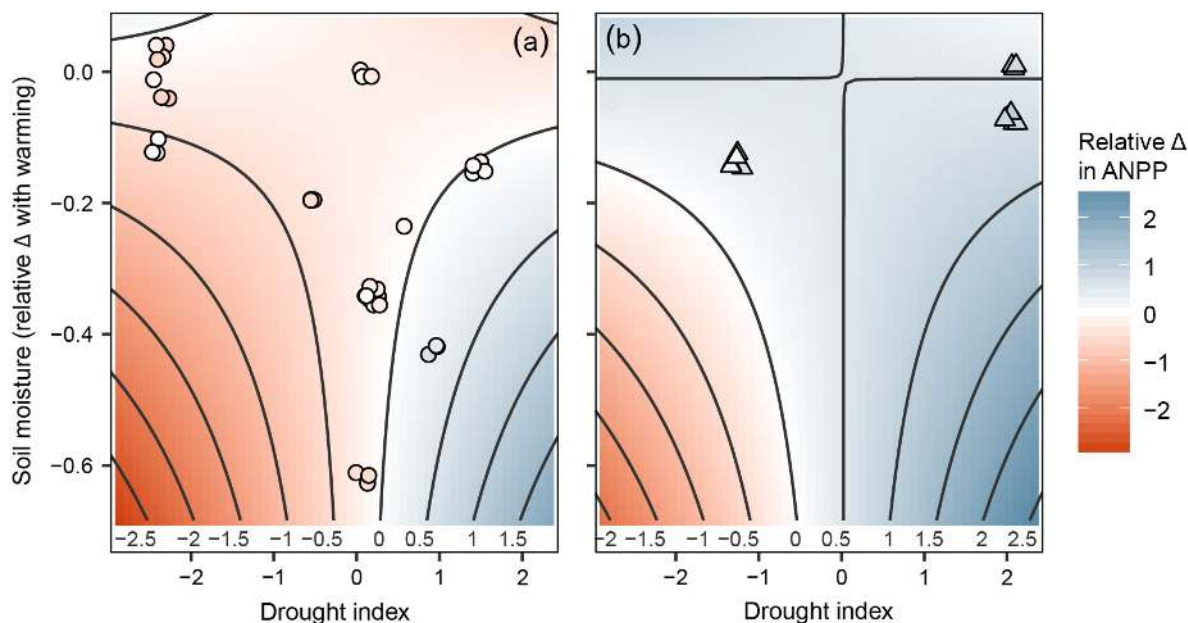
Fig. 3. (a, b) Warming-induced changes in aboveground net primary production relative to controls (rel.ANPP) are explained by the interaction of change in soil moisture with warming (rel.SM) and ambient drought conditions. Permafrost is also significant as a fixed effect, so the relationship between rel.ANPP and rel.SM × drought is displayed separately for non-permafrost (a) and permafrost (b) sites. Contour lines show rel.ANPP values predicted by the model, and points show measured rel.ANPP values in each plot. Points are jittered so that within-site rel.ANPP variation is visible. Site was a random effect in the linear mixed effects model; marginal $R^2 = 0.57$.

sites with lower MAT and with less experimental warming (Appendix S1: Table S3).

Discussion

Aboveground net primary production (ANPP) in Tibet has previously been found to be limited either by low air temperature (Wang et al. 2012) or by precipitation (Shi et al. 2014). We found that across diverse alpine grassland sites on the Tibetan Plateau, ANPP accumulated with increased precipitation, regardless of permafrost presence and other environmental variables. This suggests that across the region, precipitation, more than temperature, drives ANPP on the alpine grasslands of the Tibetan Plateau. These results are consistent with findings that NDVI increases with precipitation across the central and eastern Tibetan Plateau (Ding et al. 2007, Ye et al. 2013), and at the global scale (Wu et al. 2011).

Wang et al. (2012) reported a negative relationship between total summer precipitation and ANPP from 2006 to 2010 at the Haibei site (one

of our more mesic sites in our analysis on the northeastern region of the Tibetan Plateau). However, during this timeframe of analysis, the drought index at that site ranged from 0.68 to 2.79, indicating those observations occurred during wetter than average years. Thus, it is possible that under these wetter years, increased summer precipitation at the relatively mesic site may have negatively impacted ANPP (due to higher cloud cover, soil water saturation, and other factors). The fact that the results here are contradicted by Wang et al.'s (2012) findings is consistent with the assertion that factors that control inter-annual production within a single site differ from those that control differences in ANPP across the landscape (Lauenroth and Sala 1992).

Time lag effects between precipitation and ANPP (or NDVI) have been observed in a few studies on the Tibetan Plateau. Zhong et al. (2010) found a time lag of one month between NDVI and climate variables. Consistent with our findings, Guo et al. (2006) found a strong positive correlation between ANPP and MAP across
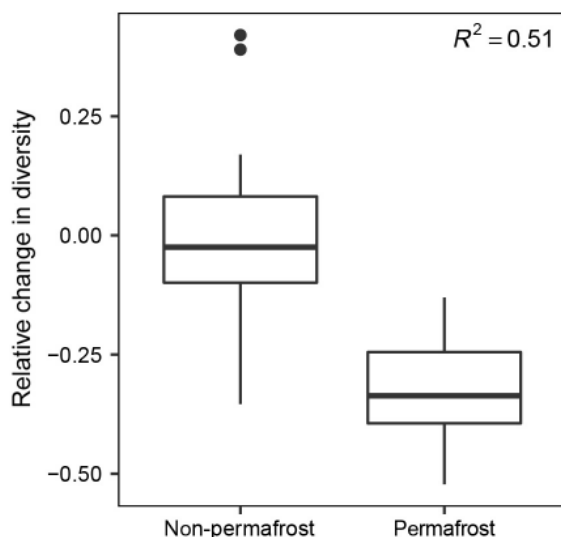
Fig. 4. Warming-induced changes in vegetation species diversity are explained by presence of permafrost, with marginal R^2 presented. Results are derived from a linear mixed effects model with mean annual temperature as a fixed effect and site as a random effect.

48 sites on the Tibetan Plateau; however, they also found a time lag between changes in inter-annual ANPP and precipitation, with cumulative precipitation over months in the previous year a strong explanatory factor. Conversely, at our Nam Co site, isotopic analyses revealed that monsoon rainfall during the growing season was a stronger driver of vegetation growth than pre-growing-season snowmelt (Hu et al. 2013). Although analysis of lag effects between ANPP and precipitation is beyond the scope of this project, the possibility that lags exist and were not captured in this synthesis is a minor caveat to our study.

Our results highlight that SM availability is an important regulator of ecosystem response to climate warming on the alpine grasslands of the Tibetan Plateau. The larger decreases in rel.ANPP occurred both in drier than average years (more negative drought index) and at sites with larger decreases in rel.SM with warming (Fig. 3). This interaction between drought and rel.SM suggests that years with favorable precipitation could buffer some of the negative effects of warming-induced SM loss on ANPP. Drier conditions inhibit plants' ability to access nutrients, expand cells during growth, and suppress photosynthesis (Liu

et al. 2009), thus reducing ANPP. Increased permafrost thaw with warming that provides additional SM may therefore be able to support increased ANPP (Yang et al. 2015) by allowing plants to more effectively exploit nutrients released from frozen soil (Schuur et al. 2007). Our findings also support results from a synthesis of warming experiments across the tundra biome reported by Elmendorf et al. (2012a), which was dominated by permafrost sites, and which found that graminoid production increased in response to warming primarily in the coldest study sites. However, our results suggest that this could be a transient effect as warming drives permafrost loss (Jin et al. 2000), whereby current permafrost sites transition to non-permafrost sites with limited SM available to support ANPP under warming.

Plant species diversity decreased with warming at all but three sites in our synthesis, providing the first evidence that climate warming can cause species loss in alpine ecosystems across diverse sites on the Tibetan Plateau. Although we cannot definitively separate the effects of MAT and permafrost with our data set, we found that non-permafrost sites also experienced relatively larger losses in diversity at sites with lower MAT. The four coldest sites (including two permafrost and two non-permafrost sites) all experienced declines in rel.Diversity with warming, suggesting that warming causes a greater disruption to community structure at colder sites.

Decreased diversity under experimental warming has been attributed to the increased advantage of dominant species, loss of forbs or cryptogams (Klanderud and Totland 2005, Yang et al. 2015), heat stress, and litter accumulation (Klein et al. 2004). Warming can also alter phenological cues, such as those that induce cold hardening or trigger shifts in the allocation of carbohydrates and resources within plants, thereby leading to freezing damage and rapid species loss (Ernakovich et al. 2014). While these mechanisms may be responsible for the warming-induced loss of diversity we observed at most sites, evidence from Nam Co, the least diverse site in this study, suggests that the inverse may also be possible if a dominant species is less competitive under warming (Hopping 2015). Conversely, Yang et al. (2015) found that production of the dominant species, *Kobresia pygmaea*, increased in response to warming at permafrost sites colder than −4°C MAT,
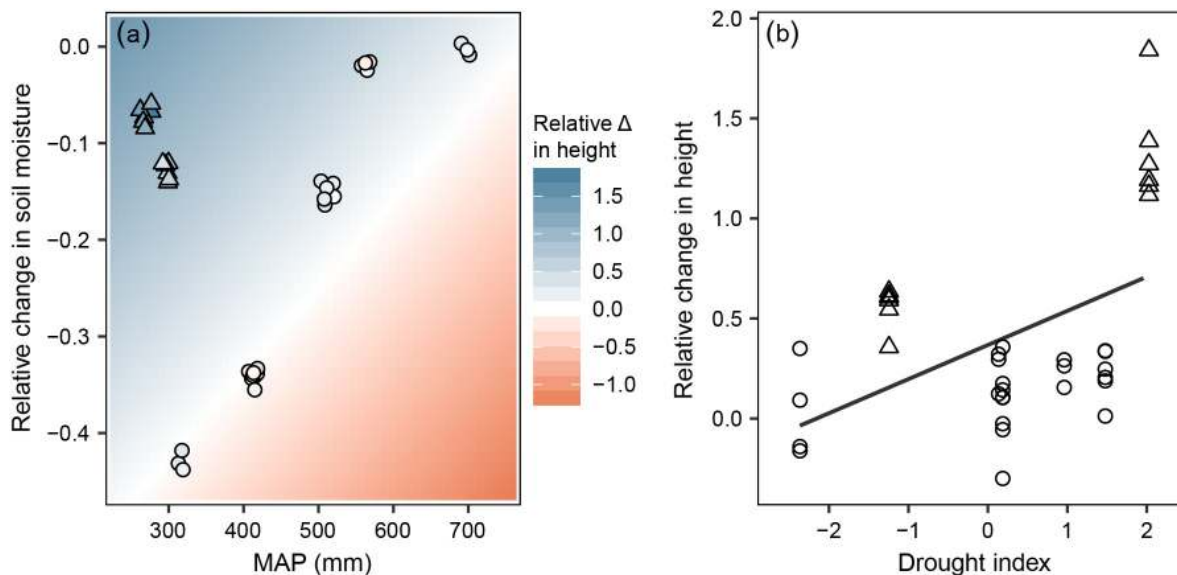
Fig. 5. (a) Warming-induced changes in plant height relative to controls (rel.Height) are explained by warming-induced changes in soil moisture and site mean annual precipitation (MAP). Shading indicates rel.Height values predicted by the model, and points show measured rel.Height values in each plot. (b) Drought is also a significant predictor, with rel.Height increasing less under stronger drought conditions. Points are jittered so that within-site rel.Height variation is visible; circles represent non-permafrost sites, and triangles represent permafrost sites. Site was a random effect in the linear mixed effects model; marginal $R^2 = 0.88$.

highlighting the role of environmental conditions in determining the response of dominant species under warming and the consequences for community diversity.

Increases in rel.Height appeared to be responsible for much of the increase in rel.ANPP across sites (Appendix S1: Fig. S1). However, plots that experienced increases in rel.Height and rel.ANPP with warming tended to have greater reductions in rel.Diversity (Appendix S1: Fig. S2), which support findings from other tundra systems, in which taller canopy heights cause species loss by altering the energy balance and increasing competition for light and space (Hollister et al. 2005, Klanderud and Totland 2005, Klein et al. 2007). The fact that lower MAP was associated with greater increases in rel.Height with warming also points to the role that aboveground competition for light and space plays in controlling plant height; across our sites, MAP was positively associated with ANPP in control plots, with less standing biomass at sites with lower MAP. Yet, belowground resources (e.g., SM status) also mediated rel.Height responses to warming. We found that both drought conditions and larger decreases in SM

with warming had a negative effect on rel.Height. Thus, lower SM due to drought conditions or warming-induced changes in SM may constrain plants from growing taller in response to climate warming. Adequate SM is necessary for plants to effectively exploit the nutrients in soil to accelerate growth that contributes to increases in plant height (Veihmeyer and Hendrickson 1950, Yang et al. 2011). However, height increases with warming on the Tibetan Plateau may only represent short-term responses. A synthesis of 61 tundra sites found an initial increase in vegetation height under short-term warming, but not a continued increase under longer-term warming (Elmendorf et al. 2012a), which suggests that increases in vegetation height on the Tibetan Plateau may be transient.

In summary, we found that water-related variables, including MAP, SM, drought conditions, and permafrost presence, regulated vegetation production under ambient climate and mediated the effects of warming on vegetation, adding to our understanding of the role that water plays in these systems. Our results align well with regional, correlative studies that found precipitation

to be a significant driver of changes in vegetation cover and desertification on the Plateau since 2000 (Lehnert et al. 2016, Li et al. 2016), as well as an eco-hydrological modeling study from the eastern Plateau that predicted decreases in SM and leaf area index with rapid, warming-induced permafrost degradation (Qin et al. 2017). These findings from the Tibetan Plateau also fit into a broader view of the importance of precipitation in driving ecosystem dynamics and mediating degradation in rangeland systems globally (Ellis and Swift 1988, von Wehrden et al. 2012, Engler and von Wehrden 2018), and the essential role of SM for vegetation growth throughout alpine and tundra regions (Berdanier and Klein 2011, Elmendorf et al. 2012b, Winkler et al. 2016). Mean annual temperature, on the other hand, significantly affected relative changes in height under warming, and colder sites also experienced larger decreases in diversity. We may therefore expect to see that regions of the Tibetan Plateau with lower MAP and MAT are likely to experience faster changes in production and diversity with warming. Other variables affecting water availability that we did not test here, such as snowmelt date, vapor pressure deficit, water-holding capacity of soil, and the timing of the start of the summer monsoon, may also play an important role in regulating plant diversity and production, and thus deserve further study. Moreover, as climate interacts with grazing (Klein et al. 2007, Wu et al. 2009, Harris 2010), synthesis work that also accounts for grazing is an important next step. We also need to monitor long-term responses (Zhang et al. 2017).

CONCLUSIONS

This is the first synthesis of its kind across diverse regions of the Tibetan Plateau, as collaborative efforts across this region are still developing. We recognize the limitations of our data and acknowledge that data from more sites that represent longer-term warming manipulations are needed to further increase our understanding. Our results suggest that a greater focus on the relationships among climate warming, permafrost, and desertification should be considered in future climate warming studies and model simulations. Our critical finding that vegetation production and diversity responses to warming diverge under permafrost presence or absence explains previous contradictory findings of both decreased and increased warming-induced shifts in ANPP across single-site studies on the Tibetan Plateau (Klein et al. 2007, Wang et al. 2012, Yang et al. 2015). Given the dramatic loss of permafrost predicted for the Tibetan Plateau (Guo et al. 2012) and its crucial role in regulating vegetation responses to warming, current estimates of ecosystem change in Tibet may be underestimating the magnitude of production and diversity losses that will occur in Tibet in a warmer future. Our work points to the need for additional collaborations across climate change scientists working on the Tibetan Plateau and highlights the novel linkage between the challenges from permafrost degradation and grassland desertification, which will require new collaborations among these currently distinct research and stakeholder groups (Xue et al. 2009, Harris 2010).

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