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Warming alters plant phylogenetic and functional community structure

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Abstract

1. Climate change is known to affect many facets of the Earth's ecosystems. However, little is known about its impacts on phylogenetic and functional properties of ecological communities.
2. Here we studied the responses of plant communities in an alpine grassland on the Tibetan Plateau to environmental warming across taxonomic, phylogenetic and functional levels in a 6-year multiple-level warming experiment.
3. While low-level warming did not alter either plant species richness or phylogenetic/functional community structure, high-level warming significantly decreased species richness. Higher level warming more strongly reduced soil moisture and caused stronger environmental filtering, consequently changing species composition and community structure. At the plant functional trait level, high-level warming promoted species turnover through altering the effects of traits such as plant height on species extinction and SLA on species colonization. As a result, high-, but not low-level warming drove phylogenetic/functional community structure from overdispersion to randomness, by filtering out species that were functionally dissimilar and distantly related to the resident species.
4. *Synthesis.* Our study provides evidence that the responses of plant phylogenetic and functional community structure to low warming differ from those in the future scenarios of increasing temperature. Importantly, the extinction of species that was functionally dissimilar and distantly related to the resident species contributed to alterations in plant community structure under high warming. Our study underscores the need to incorporate the phylogenetic and functional perspectives to gain a more complete understanding of community responses to climate warming.

KEYWORDS

alpine grassland, climate warming, functional traits, phylogenetic community structure, species colonization, species extinction

1 | INTRODUCTION

The past two decades have witnessed a surging interest among ecologists to consider species phylogenetic background and functional traits, which have proven useful for better understanding of ecological and evolutionary processes driving community assembly (Cavender-Bares, Kozak, Fine, & Kembel, 2009; Li et al., 2016; McGill, Enquist, Weiher, & Westoby, 2006; Uchida, Hiraiwa, & Cadotte, 2019; Webb, Ackerly, McPeck, & Donoghue, 2002). This trend has been largely driven by the recognition that species functional traits, not identity, determine their performance and interactions with other species (McGill et al., 2006; Violle et al., 2007), and that species phylogenetic relationships can often serve as a reasonable proxy of similarity in their functional traits, including potentially important, but unidentified or unmeasured traits (Donoghue, 2008; Peterson, Soberon, & Sanchez-Cordero, 1999; Prinzing, Durka, Klotz, & Brandl, 2001). More recently, global change biologists have also begun to adopt the phylogenetic and functional perspectives to study the responses of ecological communities to global change stressors (Lavergne, Mouquet, Thuiller, & Ronce, 2010; Willis, Ruhfel, Primack, Miller-Rushing, & Davis, 2008; Yang et al., 2018, 2019). Nevertheless, little is known about how climate warming, an important facet of global environmental changes (IPCC, 2013), influences phylogenetic and functional properties of ecological communities (but see Li, Miller, & Harrison, 2019). On the one hand, climate warming may promote soil nutrient mineralization rates, resulting in increased soil nutrient availability (Nadelhoffer, Giblin, Shaver, & Linkins, 1992; Rolph, 2003). In nutrient-limited environments such as many terrestrial ecosystems, this alleviation of environmental stress may allow many species with various traits to coexist, thereby reducing the level of functional clustering, and in the case of traits being phylogenetically conserved, also the level of phylogenetic clustering. On the other hand, climate warming tends to reduce soil water availability (Dorji et al., 2013; Zhu, Zhang, & Wang, 2016), especially in arid and semi-arid regions. The aggravated water scarcity, coupled with physiological stress directly induced by warming, may allow only a limited number of species with similar traits (i.e. those conferring tolerance of higher temperature and lower water availability) to survive. The resultant increased level of environmental filtering would potentially lead to increased phylogenetic/functional clustering. The relative importance of these opposing mechanisms would determine how climate warming influences community phylogenetic/functional structure.

Studies of changes in community phylogenetic and functional structure have typically focused on the role of species extinction. Recent research, however, has shown that species colonization can also play an important role. For example, Li et al. (2015) reported that the observed long-term old-field succession towards phylogenetic and functional overdispersion in New Jersey, USA, was due to the colonization of species distantly related to the resident species, not the extinction of closely related resident species. Likewise, Yang et al. (2018) found that nitrogen fertilization

into a temperate grassland in Inner Mongolia, China, promoted the colonization of species distantly related to residents, resulting in community phylogenetic overdispersion. It is thus essential to examine species extinction and colonization together for a better understanding of warming-induced changes in community phylogenetic/functional structure. To our knowledge, only one study has examined climate change effects on plant community phylogenetic properties, showing that the phylogenetic diversity of a California grassland declined over a 19-year period as winter precipitation declined (Li, Zhang, et al., 2019). This finding, however, was attributed to the loss of species with high SLA that were widely distributed across families (Li, Zhang, et al., 2019), without examining species colonization. It is, therefore, worth exploring how important plant functional traits, which determine plant ecological strategies (Díaz et al., 2016; Wright et al., 2004), would influence both species extinction and colonization under climate change.

Alpine ecosystems, such as those on the Tibetan Plateau, are among the most vulnerable to climate changes (Hülber et al., 2016; Steinbauer et al., 2018), as ecological processes in alpine ecosystems are highly constrained by low temperature (Kirschbaum, 1995). Termed 'the third pole' of the earth, the Tibetan Plateau has an average altitude greater than 4,000 m. Over the past 50 years, mean annual temperature on the Tibetan Plateau has climbed by 0.4°C per decade (Dong, Jiang, Zheng, & Zhang, 2012), almost twice the rate of global average (Hansen, Ruedy, & Sato, 2010); this warming trend is projected to persist for the Tibetan Plateau during the 21st century (Piao et al., 2010). Previous studies have reported mixed results on the effects of increasing temperature on the Tibetan Plateau ecosystems. It has been shown that the Tibetan alpine meadow ecosystem productivity increased when mean air temperature (MAT) was elevated by 2.6–5.2°C (Li, Wang, Yang, Gao, & Liu, 2011), decreased when MAT increased by 0.6–2.0°C (Klein, Harte, & Zhao, 2008) and remained unchanged when MAT increased by 2.2–2.4°C (Zhu, Zhang, & Jiang, 2017), during the growing season. Likewise, both large and rapid species loss (Klein, Harte, & Zhao, 2004; Li, Zhang, et al., 2019; Li et al., 2011) and lack of change in species richness in response to warming (Ganjurjav et al., 2016; Piao et al., 2019) have been reported. These inconsistent results suggest that the magnitude of responses of the Tibetan alpine grassland, whose constituent species are adapted to low temperature, may be sensitive to warming intensity (Alatalo, Jägerbrand, & Molau, 2016; Jonasson, Michelsen, Schmidt, & Nielsen, 1999), necessitating a multi-level warming approach to better understand warming effects on the Tibetan Plateau ecosystems. Here we reported on a 6-year two-level warming experiment conducted in a Tibetan Plateau alpine grassland. Using the Tibetan alpine grassland as a model system, we aimed to understand how different levels of warming influence plant phylogenetic and functional community structure, and to identify potential mechanisms driving the observed changes in phylogenetic and functional community structure by examining species colonization and extinction.

2 | MATERIALS AND METHODS

2.1 | Study area

Our study area is located in a typical alpine meadow grassland at Naqu, northern Tibet, China (31°83'N, 92°80'E), approximately 4,600 m in elevation. The long-term mean annual temperature and precipitation are -1.2°C and 430 mm respectively. The main source of precipitation comes from summer monsoon (Dorji et al., 2013), which usually arrives in early May and ends in August. The growing season normally starts in mid-May and lasts until mid-September. The local vegetation is dominated by *Kobresia pygmaea*, accompanied by *Potentilla saundersiana*, *P. cuneata*, *Saussurea alpina*, *Carex thibetica* and *Stipa purpurea*. Plant communities usually reach their peak standing biomass in early August, when the vegetation coverage is about 60%–85%.

2.2 | Study design

We used open-top chambers (OTCs) to achieve the effects of passive warming based on the International Tundra Experiment (ITEX) design (Marion et al., 1997). Active warming via heating devices is not plausible in our study ecosystem, where plants have low height (typically lower than 5 cm) and wind is often strong. The OTCs were set up in June 2013, in a flat area covered by relatively homogeneous vegetation (Figure S1). Three treatments were included as follows: control, low-level warming and high-level warming. Each treatment comprised three replicates, resulting in a total of nine plots. The experimental plots were separated by a 2.5-m wide passage. We manipulated warming effects through changing the heights of OTCs, while keeping their uniform opening size. The transparent walls making up the hexagonal OTC in the two levels of warming treatments were measured 80 cm along the top edge, 100, 120 cm along the bottom edge and 40, 80 cm in height respectively. The transparent material was 2 mm thick clear polyvinyl chloride (PVC) sheet (the DuPont company), which allows for 95% light transmission. We measured air temperature at 10 cm above-ground using the Vaisala HMP155A sensor (Vaisala). Soil moisture 5 cm below-ground was monitored in the centre of the plots using Campbell CS655 sensors (Campbell Scientific). Two air and soil sensors were installed in each treatment, and the data were averaged over the two sensors.

2.3 | Plant community survey

Plant communities were surveyed at their peak standing biomass in early August from 2013 to 2018. For a fixed 0.5 m × 0.5 m quadrat in each plot, we placed a metal frame with 100 5 cm × 5 cm grids above the canopy. All plant species occurring in the quadrat were identified and recorded, and their coverage was estimated by counting their occurrences within the 100 grids. To avoid the edge effects,

all plant community surveys were conducted in the centre of the OTCs. Plant traits, including plant height and SLA, are known to be important traits for plant resource update and competition (Kunstler et al., 2016) and capturing plant ecological strategies (Diaz et al., 2016). Plant height and SLA were measured from the control plots during the late growing season of the last year of our experiment (2018). We measured plant height of 25 individuals for each species. Twenty-five healthy leaves per species were collected and leaf area was measured using a portable leaf area meter ADC AM-350 (ADC BioScientific Ltd.). Leaf samples were then dried at 80°C for 24 hr and weighed. SLA was calculated as leaf area per unit dry mass. The height and SLA of each species were obtained by averaging across the 25 samples. In total, we collected data on plant height for all species (27 species for the study area), and SLA for 21 common species.

2.4 | Phylogenetic and functional analyses

We constructed a phylogenetic tree for the 27 species observed in our study area at the genus level, based on the established phylogeny of vascular plants (Qian & Jin, 2016; Zanne et al., 2014). However, we found that four species, including *Potentilla saundersiana*, *P. cuneata*, *P. bifurca* and *P. multifida*, belonged to the same genus *Potentilla*. Therefore, we extracted the ITS1 and ITS2 sequences of these four species from GenBank and constructed the phylogenetic tree for the genus *Potentilla*, using *Oxytropis arctica* as an outgroup species. MEGA 7.0.26 was used for the alignment of gene sequences, selection of evolution model and the construction of the *Potentilla* tree with the maximum likelihood method. The phylogenetic tree of the four *Potentilla* species was then merged with the genus-level phylogenetic tree.

We used net relatedness index (NRI) as measures of community phylogenetic/functional structure (Webb, 2000; Webb, Ackerly, & Kembel, 2008). NRI is a measure of community phylogenetic dispersion (Webb, 2000), and defined as the differences in mean pairwise distance between the observed communities and the null communities (Webb et al., 2008). The null communities were generated by shuffling species labels across the entire phylogeny, thus randomizing phylogenetic relationships among species, with 999 iterations. The value of NRI can be positive, negative and no different from zero, which indicates phylogenetic clustering, overdispersion and randomness respectively. As for the functional community structure, we first calculated the Gower distance between each species pair based on the functional traits, plant height and SLA. Then, based on the functional trait distance, we calculated functional-NRI by using the same method as for calculating NRI.

A species was assigned as locally extinct from a plot when it was present in 1 year but absent in the following year; a species was assigned as new colonist when it was absent in the prior year but appeared in the current year. We used β NRI as a measure of the phylogenetic and functional similarities between locally colonizing/extinct species and resident species of each plot. Positive β NRI indicates that the colonizing/extinct species are more closely related to

the residents than by chance, whereas negative β NRI indicates the opposite (Webb et al., 2008). We detected the phylogenetic signal of species colonization/extinction in experimental plots through the *D* statistic (Blomberg, Garland, & Ives, 2003; Fritz & Purvis, 2010). We calculated the *D* statistic at the replicate level based on 1,000 permutations. We also examined the phylogenetic signal of each plant functional trait by using the *K* statistic (Blomberg et al., 2003). The phylogenetic signal was evaluated by comparing the variance of independent contrasts for each trait to the expected values obtained by shuffling leaf traits across the tips of the phylogenetic tree 999 times. All of the phylogenetic and functional metrics were calculated by using the *PICANTE* package (Kembel et al., 2010) in *R* (R Core Team, 2014). The *D* statistic was calculated by using the 'phylo.d' function of the *R* package *CAPER* (Orme, 2013), and *K* was calculated by using the 'multiPhylosignal' function of the *PICANTE* package (Kembel et al., 2010). The Gower distance was calculated by using Gower function from the *R* package *FD*.

2.5 | Statistical analysis

We used linear mixed-effects model of repeated measures to examine the effects of warming treatment (low warming: LW; high warming: HW), year and their interactions on species richness, NRI and functional-NRI, where we treated warming treatment and year as fixed factors, and the experimental plots as random factors. Afterwards, we conducted Tukey's HSD test to assess the difference in each of the three metrics between treatments (i.e. LW and control, HW and control and HW and LW). Structural equation modelling (SEM) was used to explore the causal pathways via which our experimental manipulation influenced different facets of plant diversity (species richness, NRI and functional-NRI). We constructed an a priori full SEM considering all possible pathways, and eliminated non-significant pathways until the final model was attained. The goodness of fit of the model was evaluated by chi-square test, the Akaike information criteria and the root mean square error of approximation. We ran logistic regressions to evaluate the effects of initial plant coverage and species traits on species extinction/colonization under each experimental treatment. For logistic regressions, species present throughout the study in a replicate plot were assigned a value of 0, while species that colonized or went extinct in the plot were assigned a value of 1. Approximately 20% of species re-appeared after extinction in the same plots, and these species were counted for both extinction and colonization. Our results remained qualitatively unchanged when these species were excluded from our analyses. We examined whether any of warming treatments altered the effects of considered plant traits on the probabilities of species extinction/colonization, by examining treatment $\times$ trait interaction terms in generalized linear models with the binomial distribution, based on the combined data from the control and a warming treatment (i.e. control and low warming, control and high warming). All statistical analyses were carried out in *R* (R Core Team, 2014), with linear

mixed-effects models and generalized linear models conducted in the *LME4* package and SEM conducted in the *LAVAN* package.

3 | RESULTS

3.1 | Microclimate response to the multi-level warming

Averaged across all years, mean daily air temperature (MAT) was 2.3 and 3.4°C higher under low-level warming (LW) and high-level warming (HW) than the controls (Figure S2). By contrast, LW and HW reduced mean daily soil moisture (SM) in the growing season by an average of 3.3% and 8.6% respectively (Figure S3).

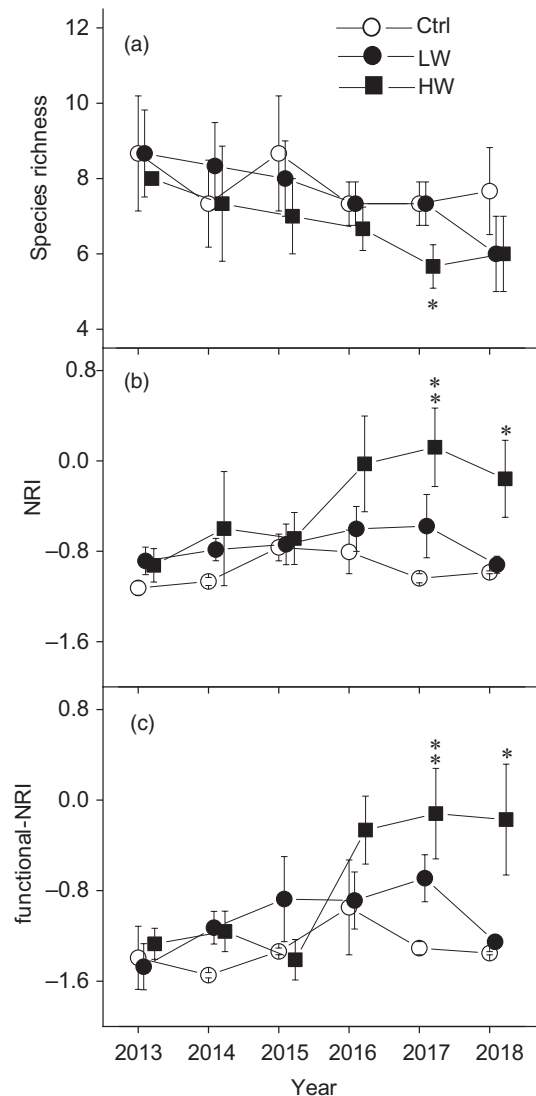


FIGURE 1 The effects of multi-level warming on species richness (a), net relatedness index (NRI, b) and functional-NRI (c) over the experimental period. The experimental treatments included control, low warming (LW) and high warming (HW). The symbols were jittered slightly in the horizontal direction to make data more visible in the figure. * and ** denote significant differences between HW and the control ($p < 0.05$ and 0.01 respectively). Error bars represent standard errors

TABLE 1 Results of linear mixed-effects models of warming treatment (low warming, LW; high warming, HW) effects on species richness, net relatedness index (NRI) and functional-NRI and of Tukey's HSD tests between treatments (LW-Ctrl, low warming-control contrast; HW-Ctrl, high warming-control contrast; HW-LW, high warming-low warming contrast). Significant p values for the difference between treatments are shown in bold ($p < 0.05$)

Source	Num. df	Den. df	Species richness		NRI		Functional-NRI	
			F	p	F	p	F	p
Warming	2	6	4.67	0.060	3.27	0.110	4.40	0.067
Year	5	30	4.07	<0.01	3.28	0.018	4.29	<0.01
Warming $\times$ year	10	30	0.62	0.782	1.57	0.164	1.97	0.074
			Z	p	Z	p	Z	p
LW-Ctrl			-0.43	0.901	0.92	0.627	1.42	0.329
HW-Ctrl			-2.75	0.016	2.53	0.031	2.97	<0.01
HW-LW			-2.32	0.054	1.60	0.244	1.54	0.271

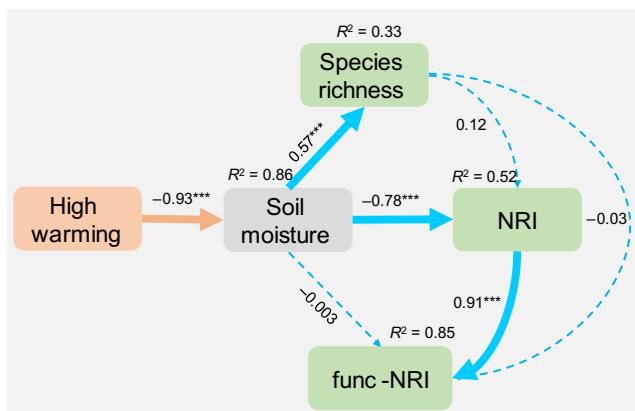


FIGURE 2 The result of structural equation modelling showing the causal effects of high warming on species richness, net relatedness index (NRI) and functional-NRI (func-NRI), via reducing soil moisture. In the figure, the arrows represent significant (solid, $p < 0.05$) and non-significant (dashed, $p > 0.05$) relationships. The width of arrows indicates the strength of the causal effect. Numbers above the arrows represent path coefficients (*, **, *** $p < 0.05$, 0.01, 0.001 respectively). R^2 values represent the proportion of variance explained for each variable. Model fit summary for species richness: $\chi^2 = 0.92$, $p = 0.820$, root mean square error of approximation (RMSEA) < 0.05 , Akaike information criteria (AIC) = 24.92

3.2 | Species richness, phylogenetic and functional community structure responses to warming

Over the 6-year experimental period, plant species richness exhibited a consistent decreasing trend in the HW treatment, but not in the control or LW treatments (Figure 1a), resulting in a significantly negative effect of HW, but not LW, on species richness (Table 1, $p < 0.05$). As the experiment progressed, the net relatedness index (NRI) and functional-NRI in HW plots increased from being significantly negative at the beginning of the experiment, indicating phylogenetic/functional overdispersion, to not being significantly different from zero at the end of the experiment, indicating phylogenetic/functional randomness (One sample t test, $p = 0.668$ and 0.726 , respectively; Figure 1b,c). This, combined with the fact that NRI and functional-NRI did not show significant trends in the control or LW plots (Figure 1b,c), resulted in significantly positive effects of HW, but not LW, on NRI

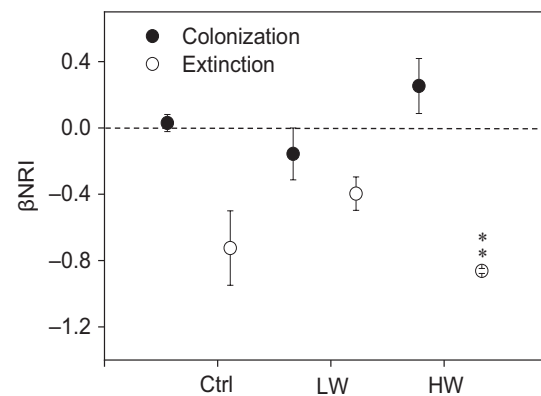


FIGURE 3 The phylogenetic dissimilarity of colonizing species (solid circles) and locally extinct species (open circles) to the resident species. The phylogenetic dissimilarity was calculated as β NRI by comparing the observed values to null models. Positive values of β NRI indicate that colonized or extinct species are more closely related to the residents than expected by chance, while negative values indicate that colonized or extinct species are more distantly related to the residents. ** denotes values that are significantly different from zero based on one-sample t test ($p < 0.01$). Error bars represent standard errors

and functional-NRI (Table 1, $p < 0.05$). Structural equation modelling (SEM) showed that the negative and positive effects of HW treatment on species richness and NRI/functional NRI were mediated through lower soil moisture (Figure 2). SEM also showed that species richness was unrelated to NRI or functional-NRI, but NRI and functional-NRI were strongly positively associated with each other (Figure 2; see similar simple regression results in Figure S4).

3.3 | Species colonization and extinction response to warming

During the experimental period, an average of 1.5 ($SE = 0.6$), 1.6 ($SE = 0.6$) and 2.4 ($SE = 0.5$) species went extinct, and an average of 0.5 ($SE = 0.4$), 0.3 ($SE = 0.3$) and 0.9 ($SE = 0.4$) species colonized in the control, LW and HW plots, respectively (Figures S5 and S6). Most of the colonized species were forbs from the genus *Potentilla* in the control and HW plots, and the extinct species were grasses

from the family Poaceae and forbs from the genus *Carex* in the LW and HW plots (Figure S5).

The phylogenetic pattern of species extinction/colonization did not deviate significantly from random expectation in all treatments ($p_{\text{random}} > 0.05$; Figure S7). βNRI between extinct species and the residents did not differ from zero in the control or LW treatment ($p > 0.05$; Figure 3). However, we found significantly negative extinction-resident βNRI in the HW treatments ($p < 0.05$), indicating that extinct species in this treatment were more distantly related to the residents than expected by chance (Figure 3). βNRI between colonized species and residents did not differ from zero in all treatments ($p > 0.05$).

We found that SLA, not plant height, exhibited a significant phylogenetic signal (Table S2). The initial species coverage and plant height were significant predictors of species extinction in all treatments,

where species with lower initial plant coverage and higher stature suffered greater risk of extinction ($p < 0.001$; Figure 4a–f). In the LW and HW plots, SLA also affected species extinction, where species with smaller SLA were more likely to go extinct ($p < 0.001$; Figure 4h,i). We also found that SLA, but not other traits, was a significant predictor of the probabilities of species colonization, where species with larger SLA were more likely to colonize in the HW plots ($p < 0.001$; Figure 4i). Finally, we found that warming altered the effects of plant traits on species extinction and colonization (Table 2). Specifically, there were significant interactive effects of HW and plant height on species extinction ($p < 0.05$), and significant interactive effects of HW and SLA on species colonization ($p < 0.001$), indicating increased probabilities of species with higher stature going extinct and species with larger SLA colonizing under high warming.

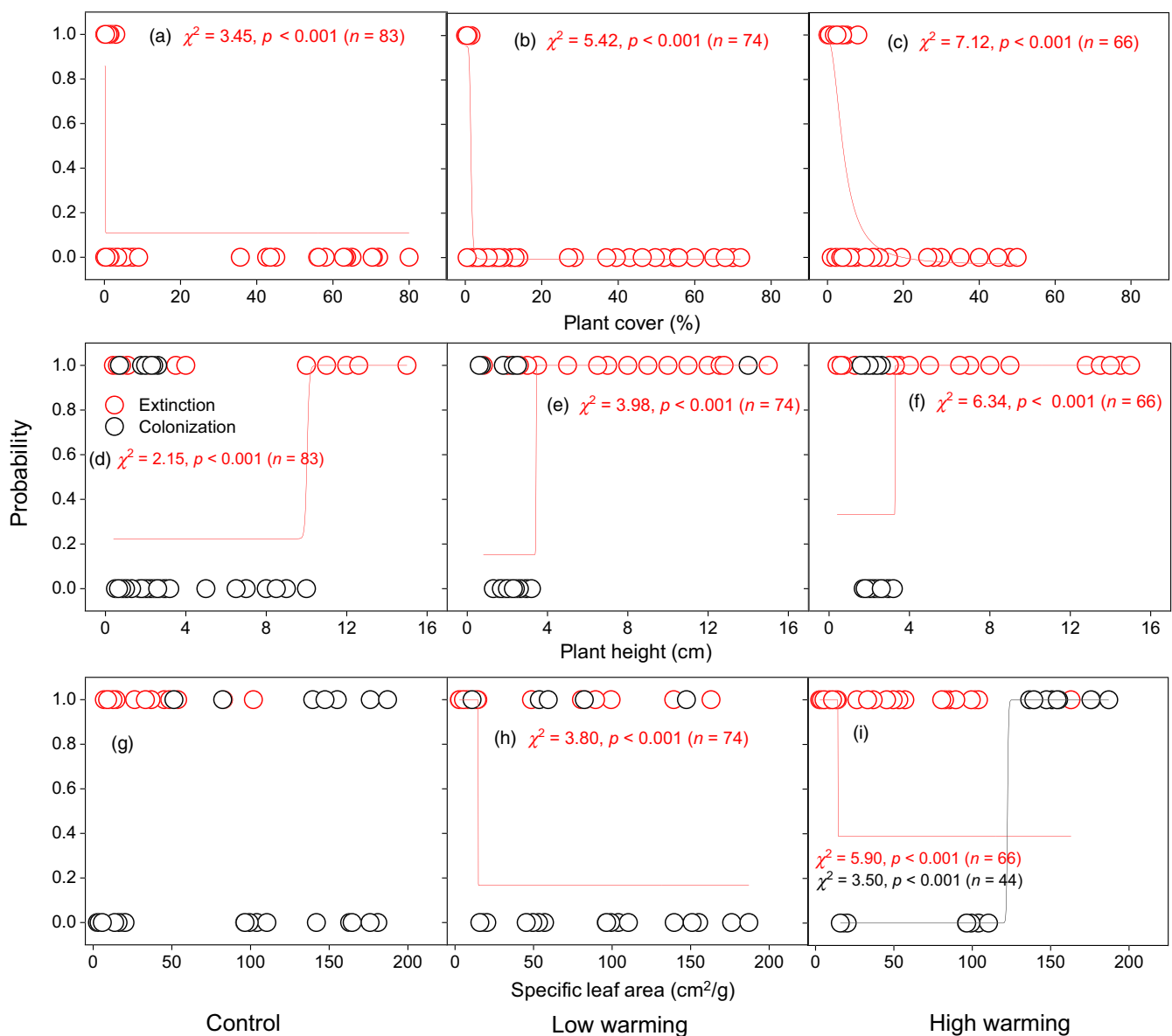


FIGURE 4 Species local extinction (red circles) and colonization (black circles) as functions of initial coverage (a–c), plant height (d–f) and SLA (g–i) under each treatment. Species were assigned a value of 0 when they did not colonize or go extinct in a replicate plot. Otherwise, species were assigned a value of 1. Significant logistic regression lines ($p < 0.05$) were shown

TABLE 2 Results of generalized linear models comparing each treatment (low warming, LW; high warming, HW) to the control to discern whether treatment altered plant trait (plant height: height; SLA) effects on the probabilities of species extinction/colonization. *p* values for significant interaction terms are shown in bold ($p < 0.05$)

Source		Height				SLA			
		LW		HW		LW		HW	
		χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>
Extinction									
Treatment	1	0.48	0.489	10.34	0.001	0.85	0.356	11.47	<0.001
Trait	1	24.24	<0.001	15.82	<0.001	3.59	0.058	5.24	0.022
Treatment × trait	1	16.43	<0.001	6.12	0.013	0.66	0.415	0.79	0.373
Colonization									
Treatment	1	0.006	0.939	5.85	0.016	0.013	0.911	11.83	<0.001
Trait	1	0.005	0.942	4.16	0.041	4.40	0.036	28.47	<0.001
Treatment × trait	1	4.48	0.034	1.82	0.177	1.33	0.249	15.86	<0.001

4 | DISCUSSION

Our study adopts phylogenetic and functional approaches to explore the impacts of environmental warming on plant community structure, and also differs from many other studies of the ecological consequences of climate change by imposing multiple levels of warming and by linking trait-based species extinction and colonization to observed changes in plant phylogenetic and functional community structure. Our results showed that only high-level warming significantly reduced plant species richness. Moreover, only high-level warming drove community phylogenetic and functional structure from overdispersion to randomness, as a result of the extinction of species distantly related to the residents. Finally, we also found that high-level warming not only directly affected species colonization and extinction, but also altered the effects of plant traits on species colonization and extinction.

4.1 | Effects of warming on species richness

Our finding of the lack of the low-level warming effects on species richness is in accordance with other studies conducted in alpine grassland ecosystems (Ganjurjav et al., 2016; Wang et al., 2012). In our experiment, low-level warming (an increase of 2.3°C) reduced soil water content, but failed to alter species extinction/colonization patterns. These results suggest that plant communities of the alpine grassland on the Tibetan Plateau are fairly resistant to modest levels of climate warming (Ganjurjav et al., 2016). On the other hand, high-level warming (an increase of 3.4°C) more strongly depleted soil water content (Figure S3), which promoted species turnover by altering the effects of species traits such as plant height on species extinction and SLA on species colonization (Table 2). Note, however, high-level warming increased species extinction more than colonization (Figure S6), thereby consequently decreasing plant species richness (Figure 2). Similar effects of warming on species richness have been reported in other alpine and montane grasslands (Berauer et al., 2019; Debouk, de Bello,

& Sebastià, 2015; Sebastià, Kirwan, & Connolly, 2008). Together, these results lend support to the significant role of soil water availability in regulating the responses of plant species and communities to climate warming (Ganjurjav et al., 2016; Klanderud & Totland, 2007).

4.2 | Effects of warming on phylogenetic and functional community structure

In our experiment, high-level warming reduced species richness and increased NRI associated with lower soil moisture, resulting in changes in plant functional community structure (Figure 2). The semi-arid nature of our study alpine grassland means that warming would aggravate the constraining effects of the limited soil water supply on plant growth (Dorji et al., 2013; Zhu et al., 2016), which promotes strong environmental filtering. These effects, however, were not random with regard to plant traits and phylogeny. In our study, species characterized by greater height and smaller SLA were more likely to experience extinction after warming, and these species also tended to be distantly related to the remaining residents, resulting in changes in community structure from phylogenetic/functional overdispersion to randomness. These results thus indicate that warming tended to homogenize our study alpine meadow grassland, reducing its functional potential and evolutionary history. A comparable result was observed for a California grassland where the decline in winter precipitation over a 19-year period led to the decline in plant phylogenetic diversity, which was, nevertheless, driven by the loss of species with high SLA (Li, Zhang, et al., 2019). Also note that although high-level warming affected both species extinction and colonization, changes in phylogenetic and functional community structure were mainly driven by species extinction in our experiment. This contrasts with a previous study reporting that altered species colonization, not extinction, was primarily responsible for the observed community change towards phylogenetic overdispersion in a semi-arid temperate grassland under nitrogen amendment (Yang et al., 2018).

We found that initial species coverage and plant height were significant predictors of species extinction in all treatments, where species with lower initial coverage and higher stature suffered greater risk of extinction. Rare species in a community tend to be more likely to go extinct because of greater demographic stochasticity associated with smaller populations (Orrock & Watling, 2010; Zhang, Pu, Li, & Han, 2016). Taller species, however, are generally considered more competitive when competing for light (Dybzinski & Tilman, 2007; Hautier, Niklaus, & Hector, 2009). Nevertheless, high-stature species were at greater risk of extinction in our experiment, suggesting that light is not a limiting factor at our study site where plant stature is low (generally <5 cm). One possibility is that higher-stature species may have greater demand for water due to their larger size, which may have made them disadvantageous in our high-elevation study grassland where water is an important limiting resource and strong irradiance enhances evaporation (Zhu et al., 2017). Another explanation for the higher extinction risk of high-stature species, such as *Stipa purpurea* and *Carex thibetica*, is that they are often simultaneously characterized by small SLA (Figure S8). Species with smaller SLA tend to exhibit lower photosynthetic rates and lower metabolism rates (Reich et al., 1999; Reich, Walters, & Ellsworth, 1992), which may make them more disadvantaged compared with larger SLA species, especially when the length of the growing season is limited as in our study system. Indeed, we found that plant species with smaller SLA tended to go extinct more frequently under both low- and high-level warming. This result contrasts with that of Li, Zhang, et al. (2019), who reported that plant species with higher SLA were more likely to go extinct in a California grassland under dryer climate (Li, Zhang, et al., 2019). This discrepancy could be potentially explained by the shorter growing season at our study site, which favours fast-growing species with large SLA over species with more conservative strategies. Consistent with this idea, we found that in our experiment, species with larger SLA were more likely to colonize high warming plots, which may be attributed to the fast growing strategy of these species (Díaz et al., 2016; Wright et al., 2004).

4.3 | Caveats

Our study has several limitations. First, environmental warming was achieved by using open-top chambers (OTCs) in our experiment. This passive warming approach was used because environmental harshness and the unavailability of electrical power at our study site prevented us from actively warming (e.g. via infrared lamps) our experimental plots. However, besides temperature, OTCs are known to alter other microclimatic and environmental variables (e.g. soil moisture content, wind velocity, light availability, plant pollination, seed dispersal; Kennedy, 1995; Marion et al., 1997). These unwanted effects almost certainly occurred in our experimental plots, despite our effort to mitigate them by constructing OTCs with highly transparent PVC and by surveying plant communities at the centre of each plot. Therefore, caution must be exercised when extrapolating our results, before they can be verified using other warming methods. Second, our

experimental treatments were replicated only three times due to logistic constraints. Although three replicates were sufficient for detecting treatment differences in our study, there were situations where one replicate deviated substantially from the other two, resulting in considerable variation among the mean responses (see Figure 1). Adding more replicates, which tends to increase the power of statistical analyses, would be desirable. Third, our functional trait analyses were based on trait values collected from the control plots, assuming that intraspecific trait variation among our experimental treatments may not overcome interspecific trait difference. Recent evidence, however, suggests that climate warming may lead to significant changes in key plant functional traits (Bjorkman et al., 2018). Future studies should explicitly consider temporal change in plant traits in response to warming, as well as interspecific and intraspecific variation in plant traits across warming treatments at our study site.

5 | CONCLUSIONS

Our study provides unique experimental evidence that warming can alter phylogenetic and functional structure of plant communities. It remains to be seen how these changes at the community level contribute to changes at the ecosystems level. Future studies should also test the applicability of our findings across other regions of the Tibetan Plateau and other high altitude ecosystems. Finally, our study highlights the responses of plant species and communities to low warming differ from those in the future scenarios of increasing temperature, and underscores the need to investigate the dynamic community structure as regulated by species colonization and extinction under global environmental change.

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AUTHORS' CONTRIBUTIONS

Y.Z., L.J. and J.Z. conceived and designed the project; J.Z. and N.C. carried out the field experiments; J.Z., X.Y., S.L. and P.W. carried out the statistical analyses; J.Z. and L.J. wrote the paper. All authors contributed to manuscript revision and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.1zcrjdfpt> (Zhu et al., 2020).

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REFERENCES

- Alatalo, J. M., Jägerbrand, A. K., & Molau, U. (2016). Impacts of different climate change regimes and extreme climatic events on an alpine meadow community. *Scientific Reports*, 6, 21720. <https://doi.org/10.1038/srep21720>
- Berauer, B. J., Wilfahrt, P. A., Arfin-Khan, M. A. S., Eibes, P., Von Heßberg, A., Ingrisch, J., ... Jentsch, A. (2019). Low resistance of montane and alpine grasslands to abrupt changes in temperature and precipitation regimes. *Arctic Antarctic and Alpine Research*, 51, 215–231. <https://doi.org/10.1080/15230430.2019.1618116>
- Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., Beck, P. S. A., ... Weiher, E. (2018). Plant functional trait change across a warming tundra biome. *Nature*, 562, 57–62. <https://doi.org/10.1038/s41586-018-0563-7>
- Blomberg, S. P., Garland, T., & Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution*, 57, 717–745. <https://doi.org/10.1111/j.0014-3820.2003.tb00285.x>
- Cavender-Bares, J., Kozak, K. H., Fine, P. V. A., & Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology. *Ecology Letters*, 12, 693–715.
- Debouk, H., de Bello, F., & Sebastià, M. T. (2015). Functional trait changes, productivity shifts and vegetation stability in mountain grasslands during a short-term warming. *PLoS ONE*, 10, e0141899. <https://doi.org/10.1371/journal.pone.0141899>
- Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., ... Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, 529, 167–171. <https://doi.org/10.1038/nature16489>
- Dong, M., Jiang, Y., Zheng, C., & Zhang, D. (2012). Trends in the thermal growing season throughout the Tibetan Plateau during 1960–2009. *Agricultural and Forest Meteorology*, 201–206. <https://doi.org/10.1016/j.agrformet.2012.07.013>
- Donoghue, M. J. (2008). A phylogenetic perspective on the distribution of plant diversity. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 11549–11555. <https://doi.org/10.1073/pnas.0801962105>
- Dorji, T., Totland, O., Moe, S. R., Hopping, K. A., Pan, J., & Klein, J. A. (2013). Plant functional traits mediate reproductive phenology and success in response to experimental warming and snow addition in Tibet. *Global Change Biology*, 19, 459–472. <https://doi.org/10.1111/gcb.12059>
- Dybzinski, R., & Tilman, D. (2007). Resource use patterns predict long-term outcomes of plant competition for nutrients and light. *The American Naturalist*, 170, 305–318. <https://doi.org/10.1086/519857>
- Fritz, S. A., & Purvis, A. (2010). Selectivity in mammalian extinction risk and threat types: A new measure of phylogenetic signal strength in binary traits. *Conservation Biology*, 24, 1042–1051. <https://doi.org/10.1111/j.1523-1739.2010.01455.x>
- Ganjurjav, H., Gao, Q., Gornish, E. S., Schwartz, M. W., Liang, Y., Cao, X., ... Lin, E. (2016). Differential response of alpine steppe and alpine meadow to climate warming in the central Qinghai-Tibetan Plateau. *Agricultural and Forest Meteorology*, 223, 233–240. <https://doi.org/10.1016/j.agrformet.2016.03.017>
- Hansen, J., Ruedy, R., Sato, M., & Lo, K. (2010). Global surface temperature change. *Reviews of Geophysics*, 48, RG4004. <https://doi.org/10.1029/2010RG000345>
- Hautier, Y., Niklaus, P. A., & Hector, A. (2009). Competition for light causes plant biodiversity loss after eutrophication. *Science*, 324, 636–638. <https://doi.org/10.1126/science.1169640>
- Hülber, K., Wessely, J., Gatteringer, A., Moser, D., Kuttner, M., Essl, F., ... Dullinger, S. (2016). Uncertainty in predicting range dynamics of endemic alpine plants under climate warming. *Global Change Biology*, 22, 2608–2619. <https://doi.org/10.1111/gcb.13232>
- IPCC. (2013). Summary for policymakers. In T. F. Stocker, D. Qin, M. Plattner, S. K. Tignor, J. Allen, A. Boschung, ... P. M. Midgley (Eds.), *Climate change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 1–30). Cambridge, UK; New York, NY: Cambridge University Press.
- Jonasson, S., Michelsen, A., Schmidt, I., & Nielsen, E. (1999). Responses in microbes and plants to changed temperature, nutrient, and light regimes in the arctic. *Ecology*, 80, 1828–1843. [https://doi.org/10.1890/0012-9658\(1999\)080\[1828:RIMAPT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[1828:RIMAPT]2.0.CO;2)
- Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., ... Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463–1464. <https://doi.org/10.1093/bioinformatics/btq166>
- Kennedy, A. D. (1995). Temperature effects of passive greenhouse apparatus in high-latitude climate change experiments. *Functional Ecology*, 9, 340–350. <https://doi.org/10.12307/2390583>
- Kirschbaum, M. U. F. (1995). The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. *Soil Biology & Biochemistry*, 27. [https://doi.org/10.1016/0038-0717\(94\)00242-S](https://doi.org/10.1016/0038-0717(94)00242-S)
- Klanderud, K., & Totland, Å. (2007). The relative role of dispersal and local interactions for alpine plant community diversity under simulated climate warming. *Oikos*, 116, 1279–1288. <https://doi.org/10.1111/j.0030-1299.2007.15906.x>
- Klein, J. A., Harte, J., & Zhao, X. Q. (2004). Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau. *Ecology Letters*, 7, 1170–1179. <https://doi.org/10.1111/j.1461-0248.2004.00677.x>
- Klein, J. A., Harte, J., & Zhao, X. Q. (2008). Decline in medicinal and forage species with warming is mediated by plant traits on the Tibetan Plateau. *Ecosystems*, 11, 775–789. <https://doi.org/10.1007/s10021-008-9160-1>
- Kunstler, G., Falster, D., Coomes, D. A., Hui, F., Kooyman, R. M., Laughlin, D. C., ... Westoby, M. (2016). Plant functional traits have globally consistent effects on competition. *Nature*, 529, 204–207. <https://doi.org/10.1038/nature16476>
- Lavergne, S., Mouquet, N., Thuiller, W., & Ronce, O. (2010). Biodiversity and climate change: Integrating evolutionary and ecological responses of species and communities. *Annual Review of Ecology and Systematics*, 41, 321–350. <https://doi.org/10.1146/annurev-ecolsys-102209-144628>
- Li, D. J., Miller, J. E. D., & Harrison, S. (2019). Climate drives loss of phylogenetic diversity in a grassland community. *Proceedings of the National Academy of Sciences of the United States of America*, 116(40), 19989–19994. <https://doi.org/10.1073/pnas.1912247116>
- Li, J. X., Zhang, Y. J., Zhu, J. T., Zeng, H., Chang, W. J., Cong, N., ... Chen, N. (2019). Responses of community characteristics and productivity to a warming gradient in a *Kobresia pygmaea* meadow of the Tibetan Plateau. *Acta Ecologica Sinica*, 39, 79–90.
- Li, N., Wang, G. X., Yang, Y., Gao, Y. H., & Liu, G. S. (2011). Plant production, and carbon and nitrogen source pools: Are strongly intensified by experimental warming in alpine ecosystems in the Qinghai-Tibet Plateau. *Soil Biology & Biochemistry*, 43, 942–953. <https://doi.org/10.1016/j.soilbio.2011.01.009>
- Li, S. P., Cadotte, M. W., Meiners, S. J., Hua, Z. S., Jiang, L., & Shu, W. S. (2015). Species colonisation, not competitive exclusion, drives community overdispersion over long-term succession. *Ecology Letters*, 18, 964–973. <https://doi.org/10.1111/ele.12476>
- Li, S. P., Cadotte, M. W., Meiners, S. J., Pu, Z., Fukami, T., & Jiang, L. (2016). Convergence and divergence in a long-term old-field succession: The

- importance of spatial scale and species abundance. *Ecology Letters*, 19, 1101–1109. <https://doi.org/10.1111/ele.12647>
- Marion, G. M., Henry, G., Freckman, D. W., Johnstone, J., Jones, G., Jones, M. H., ... Virginia, R. A. (1997). Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology*, 3, 20–32. <https://doi.org/10.1111/j.1365-2486.1997.gcb136.x>
- McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21, 178–185. <https://doi.org/10.1016/j.tree.2006.02.002>
- Nadelhoffer, K. J., Giblin, A. E., Shaver, G. R., & Linkins, A. E. (1992). Microbial processes and plant nutrient availability in arctic soils. In F. S. Chapin, R. Jefferies, J. Reynolds, G. Shaver, & J. Svoboda (Eds.), *Arctic ecosystems in a changing climate: An ecophysiological perspective* (pp. 281–300). San Diego, CA: Academic Press.
- Orme, D. (2013). *The Caper package: Comparative analysis of phylogenetics and evolution in R*. R package version 0.5, 2, 1–36.
- Orrock, J. L., & Watling, J. I. (2010). Local community size mediates ecological drift and competition in metacommunities. *Proceedings of the Royal Society B: Biological Sciences*, 277(1691), 2185–2191. <https://doi.org/10.1098/rspb.2009.2344>
- Peterson, A. T., Soberon, J., & Sanchez-Cordero, V. (1999). Conservatism of ecological niches in evolutionary time. *Science*, 285, 1265–1267. <https://doi.org/10.1126/science.285.5431.1265>
- Piao, S., Ciais, P., Huang, Y., Shen, Z., Peng, S., Li, J., ... Fang, J. (2010). The impacts of climate change on water resources and agriculture in China. *Nature*, 467, 43–51. <https://doi.org/10.1038/nature09364>
- Piao, S. L., Zhang, X. Z., Wang, T., Liang, E. Y., Wang, S. P., Zhu, J. T., & Niu, B. (2019). Responses and feedback of the Tibetan Plateau's alpine ecosystem to climate change. *Chinese Science Bulletin*. <https://doi.org/10.1360/TB-2019-0074>
- Prinzing, A., Durka, W., Klotz, S., & Brandl, R. (2001). The niche of higher plants: evidence for phylogenetic conservatism. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 268(1483), 2383–2389. <https://doi.org/10.1098/rspb.2001.1801>
- Qian, H., & Jin, Y. (2016). An updated megaphylogeny of plants, a tool for generating plant phylogenies and an analysis of phylogenetic community structure. *Journal of Plant Ecology*, 9, 233–239. <https://doi.org/10.1093/jpe/rtv047>
- R Core Team. (2014). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing 1, 409. Retrieved from www.R-project.org
- Reich, P. B., Ellsworth, D. S., Walters, M. B., Vose, J. M., Gresham, C., Volin, J. C., & Bowman, V. W. D. (1999). Generality of leaf trait relationships: A test across six biomes. *Ecology*, 80, 1955–1969. [https://doi.org/10.1890/0012-9658\(1999\)080\[1955:GOLTRA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[1955:GOLTRA]2.0.CO;2)
- Reich, P. B., Walters, M. B., & Ellsworth, D. S. (1992). Leaf lifespan in relation to leaf, plant and stand characteristics among diverse ecosystems. *Ecological Monographs*, 62, 365–392. <https://doi.org/10.2307/2937116>
- Rolph, S. (2003). *Effects of a 10-year climate warming experiment on nitrogen cycling in High Arctic Tundra* (MS thesis). Columbia, Canada: Department of Geography, University of British.
- Sebastià, M. T., Kirwan, L., & Connolly, J. (2008). Strong shifts in plant diversity and vegetation composition in grassland shortly after climatic change. *Journal of Vegetation Science*, 19, 299–306. <https://doi.org/10.3170/2008-8-18356>
- Steinbauer, M. J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., ... Wipf, S. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, 556, 231. <https://doi.org/10.1038/s41586-018-0005-6>
- Uchida, K., Hiraiwa, M. K., & Cadotte, M. W. (2019). Non-random loss of phylogenetically distinct rare species degrades phylogenetic diversity in semi-natural grasslands. *Journal of Applied Ecology*, 56(6), 1419–1428. <https://doi.org/10.1111/1365-2664.13386>
- Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, 116, 882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>
- Wang, S., Duan, J., Xu, G., Wang, Y., Zhang, Z., Rui, Y., ... Wang, W. (2012). Effects of warming and grazing on soil N availability, species composition, and ANPP in an alpine meadow. *Ecology*, 93, 2365–2376. <https://doi.org/10.1890/11-1408.1>
- Webb, C. O. (2000). Exploring the phylogenetic structure of ecological communities: An example for rain forest trees. *The American Naturalist*, 156, 145–155. <https://doi.org/10.1086/303378>
- Webb, C. O., Ackerly, D. D., & Kembel, S. W. (2008). Phylocom: Software for the analysis of phylogenetic community structure and character evolution. *Bioinformatics*, 24, 2098–2100.
- Webb, C. O., Ackerly, D. D., McPeck, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 33, 475–505. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150448>
- Willis, C. G., Ruhfel, B., Primack, R. B., Miller-Rushing, A. J., & Davis, C. C. (2008). Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 17029–17033. <https://doi.org/10.1073/pnas.0806446105>
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., ... Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821–827. <https://doi.org/10.1038/nature02403>
- Yang, X., Li, G. Y., Li, S. P., Xu, Q. N., Wang, P. D., Song, H. H., ... Jiang, L. (2019). Resource addition drives taxonomic divergence and phylogenetic convergence of plant communities. *Journal of Ecology*, 107, 2121–2132. <https://doi.org/10.1111/1365-2745.13253>
- Yang, X., Yang, Z., Tan, J., Li, G., Wan, S., & Jiang, L. (2018). Nitrogen fertilization, not water addition, alters plant phylogenetic community structure in a semi-arid steppe. *Journal of Ecology*, 106, 991–1000. <https://doi.org/10.1111/1365-2745.12893>
- Zanne, A. E., Tank, D. C., Cornwell, W. K., Eastman, J. M., Smith, S. A., Fitzjohn, R. G., ... Beaulieu, D. M. (2014). Three keys to the radiation of angiosperms into freezing environments. *Nature*, 514, 394.
- Zhang, X. M., Pu, Z. C., Li, Y. H., & Han, X. G. (2016). Stochastic processes play more important roles in driving the dynamics of rarer species. *Journal of Plant Ecology*, 9, 328–332. <https://doi.org/10.1093/jpe/rtv058>
- Zhu, J. T., Zhang, Y. J., & Jiang, L. (2017). Experimental warming drives a seasonal shift of ecosystem carbon exchange in Tibetan alpine meadow. *Agricultural and Forest Meteorology*, 233, 242–249. <https://doi.org/10.1016/j.agrformet.2016.12.005>
- Zhu, J. T., Zhang, Y. J., & Wang, W. F. (2016). Interactions between warming and soil moisture increase overlap in reproductive phenology among species in an alpine meadow. *Biology Letters*, 12, 20150749. <https://doi.org/10.1098/rsbl.2015.0749>
- Zhu, J., Zhang, Y., Yang, X., Chen, N., Li, S., Wang, P., & Jiang, L. (2020). Data from: Warming alters plant phylogenetic and functional community structure. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.1zcrjdfpt>

SUPPORTING INFORMATION

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