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Whole-soil warming shifts species composition without affecting diversity, biomass and productivity of the plant community in an alpine meadow

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A B S T R A C T

The structure and function of plant communities in alpine meadow ecosystems are potentially susceptible to climate warming. Here, we utilized a unique field manipulation experiment in an alpine meadow on the Qinghai-Tibetan Plateau and investigated the responses of plant species diversity, composition, biomass, and net primary productivity (NPP) at both community and functional group levels to whole-soil-profile warming (3–4 °C across 0–100 cm) during 2018–2021. Plant species diversity, biomass and NPP (both above- and belowground) at the community level showed remarkable resistance to warming. However, plant community composition gradually shifted over time. Over the whole experimental warming period, aboveground biomass of legumes significantly decreased by 45%. Conversely, warming significantly stimulated aboveground biomass of forbs by 84%, likely because of better growth and competitive advantages from the warming-induced stimulation of soil water and other variables. However, warming showed minor effects on aboveground biomass of grasses and sedges. Overall, we emphasize that experimental warming may significantly affect plant community composition in a short term by triggering adjustments in plant interspecific competition or survival strategies, which may cause potential changes in plant productivity over a more extended period and lead to changes in carbon source-sink dynamics in the alpine meadow ecosystem.

1. Introduction

From 1850–1900 to 2010–2019, human-caused global surface temperature has increased approximately 1.1 °C, and will continue to rise by about 4.4 °C at the end of this century in the SSP5–8.5 scenario [1]. Plants, as the major producers in terrestrial ecosystems, have been investigated by multiple studies on their potential responses to climate warming, with both prompt reactions of physiological adaptation [2,3] and slow regulation of ecological shifts [4] being found. Ecologically, climate warming has potential to directly alter plant community diversity, composition and biomass production through shifting species proportion [5,6], triggering species invasion or loss [7,8] and/or changing species growth or allocation [9,10]. However, environmental regulators across different habitats may be uniquely associated with warming, leading to disparate responses of plant communities [11]. Among all ecosystems, climate warming impacts on alpine ecosystems have re-ceived much concern due to their high sensitivity and low resistance to environmental alteration, yet scarce and controversial experimental evidence is provided to describe alpine plant responses in a warming world.

Plant species diversity is generally recognized as a key regulator of ecosystem functions. For example, greater plant species diversity and complex community composition has potential to resist environmental disturbance via complementarily using limited resources [12], while species diversity loss may amplify the negative influence of climate change such as enhancing interspecific competition [13]. A recent meta-analysis reported that experimental warming significantly and negatively affected species richness, but did not affect Shannon-Wiener index and species evenness among global grasslands [14]. Shi et al. [15] proposed that significant changes in plant species diversity and community composition (e.g. species reordering) are likely to be slow processes [16], as they are often affected by chronically altered resource

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availability over a long time. However, the biota of alpine habitats may have inconsistent responses, since specialist cold-tolerant species may not be able to adapt to increasing temperature in abiotic and biotic conditions such as the range extension of species from warmer areas [17], and hence lead to fast and unpredictable changes in plant species diversity or community composition. For instance, Klein et al. [7] reported a rapid and dramatic decline of plant species richness on the Qinghai-Tibetan Plateau in an open-top chamber (OTC) warming experiment, which can be explained by changes in various factors induced by warming, such as altered soil nutrient supply and reduced plant reproductive success. However, recent studies also found inconsistent responses of plant species diversity and community composition to experimental warming in different cold regions [18–20]. Taken together, how plant species diversity and composition in alpine ecosystems respond to warming remains unclear.

Evaluating changes of above- and belowground plant biomass (AGB and BGB) as well as net primary productivity (ANPP and BNPP) under climate warming is vital because of their direct influence on the C feedback between the biosphere and the atmosphere. Once the balance between C sequestration and C release breaks in these ecosystems, a positive feedback may occur, exacerbating climate warming and causing severe consequences to the whole planet. Many studies showed positive responses of biomass and NPP [21,22] to warming, while neutral [23] and negative responses [24] were also reported. The inconsistent results are mainly due to different trade-offs of both positive and negative effects of warming on plants at the community level. Warming not only directly stimulates plant growth in temperature-limited ecosystems, but also alters soil water and nutrient supply to plants, which are recognized as key regulators of plant biomass and NPP (especially belowground) in response to climate change [25,26]. Moreover, differences of initial plant community diversity and composition, as well as species shifts due to rising temperature, may also determine whether plant biomass and NPP show response or resistance to experimental warming. For example, Shao et al. [27] found that warming increased plant productivity when species richness in grasslands was lower than 10, whereas warming decreased plant productivity when it was greater than 10. As a consequence, the responses of single species or functional groups (especially temperature-sensitive species/groups) to temperature rising and warming-induced environmental filtering may potentially explain the disparate responses of plant biomass and NPP to warming at the community level.

The paucity of information at the species/functional group level is likely to result in misleading conclusions on the stability of the whole plant community in response to experimental warming, since changes of single species/functional groups may not be consistent with changes at the community level [28]. Particularly, the decrease in density, biomass or richness of temperature-sensitive species or functional groups may be masked and compensated by the increase of other species or functional groups. Previous studies have revealed significant changes in species or functional groups in response to warming, especially in alpine ecosystems. For example, experimental warming is reported to increase the relative abundance of grasses at the expense of sedges and/or forbs in alpine meadows [23,24,29], while Ma et al. [30] found that warming significantly stimulated legume biomass but reduced forb and sedge biomass, and grasses remained stable over the 5-year experimental period. However, how experimental warming affects plant biomass at the species/functional group level is incompletely understood, which is mainly due to different physiological and phenological strategies of specific species used to adapt to environmental changes. For example, warming-induced soil water loss may consequently enhance the survival advantage of grasses and lead to higher biomass (especially belowground) compared to shallow-rooted plants [23]. At the same time, warming would advance the date with above-freezing soil temperatures, and cause snow to melt with ample water supply, leading to earlier germination and growth of some species in forbs compared to grasses [31,32]. Therefore, due to the diverse and inconsistent survival strate-

gies of different species, investigating potential mechanisms of how plant biomass of different species/functional groups respond to experimental warming is still challenging.

The ubiquitous alpine meadows on the Qinghai-Tibetan Plateau are important for the livelihood of native nomads and potentially susceptible to climate warming. Moreover, in the past 50 years, the warming rate on the Qinghai-Tibetan Plateau is two times faster than the global average warming rate over the same period [33]. Consequently, several studies and approaches have been taken to investigate the impact of climate warming on this high-altitude, alpine ecosystem. However, previous studies often paid attention to the response of one aspect of the plant community to experimental warming, rather than comprehensively assessing the potential warming-induced impacts on alpine plant species diversity, community composition, biomass, and productivity. Here, based on a whole-soil-profile experimental warming platform, we investigated changes in plant species diversity, composition, biomass, and NPP (both above- and belowground) to warming from 2018 to 2021. We hypothesized that: 1) experimental warming would cause significant changes in plant species diversity as well as community composition because of the shifts of temperature-sensitive species; 2) Plant biomass and NPP at the community level would have a positive response to warming as a result of environmental changes, such as warming-induced increases in soil nutrient availability and growing season length; and 3) aboveground biomass of different plant functional groups may inconsistently respond to experimental warming due to species-specific survival strategies.

2. Materials and methods

2.1. Site description

The study site is located at the Haibei National Field Research Station of Alpine Grassland Ecosystem (37°37′ N, 101°12′ E, altitude of 3200 m) on the northeastern Qinghai-Tibetan Plateau in Qinghai Province, China (Fig. S1a, b). The station is in a large valley nearby the Qilian Mountains, experiencing a continental monsoon climate with a 5-month growing season (May to September). From 2017 to 2021, the mean annual temperature of this area is −0.6 °C, with a maximum temperature of 22.0 °C, and a minimum temperature of −17.6 °C (Fig. S4a). The mean annual precipitation is 460 mm, with > 80% of precipitation occurring in growing seasons (Fig. S4a). Vegetation at this site is a typical alpine meadow dominated by *Stipa aliena, Helictotrichon tibeticum, Elymus nutans, Festuca rubra, Poa annua*, and *Aster tataricus*, which together account for ~75% of ANPP. The soil in this area is classified as Mat-Gryic Cambisol, which has an average thickness of 100 cm [34]. The mean soil pH value of topsoil (0−10 cm), subsoil (10−40 cm) and deep soil (40−100 cm) were 7.9, 8.3 and 8.5, respectively.

2.2. Experimental design

In June 2018, a whole-soil-profile warming experiment platform was established within an area of 16 m × 28 m in the study site (Figs. S1c, S2a). The platform consists of 8 circular plots (4 paired plots with or without warming). Each plot measures 350 cm diameter, with 2.5 m intervals between each pair of control (CT) and warming (W) plots and a minimum interval of 2.5 m between different pairs (Fig. S2a). In each warming plot, a total of 20 equidistant stainless-steel rods with a length of 120 cm (100 cm belowground) were vertically embedded into the edge of the heating square (Fig. S3). Totally, we threaded 20.5 m of heating cable (BriskHeat, Ohio, USA) and filled the remaining space of the rods with quartz sand, selected for its high thermal conductivity (Fig. S3). Between the adjacent two rods, the heating cables were connected with a normal cable. To compensate for heat loss caused by frequent heat exchange between the topsoil and the atmosphere, approximately 3.1 m and 6.3 m of heating cables were buried at the concentric positions (1 m and 2 m in diameter, respectively) in each warming plot, with the top

of the flexible conduit 5 cm belowground (Figs. S2c, S3). Generally, the plot design and heating methodology basically follow previous studies [35–37]. Dummy heating rods were used in control plots, but were not electrified (Fig. S2c).

In each plot, the temperature sensors and the moisture sensors (Delta-T, UK) at different soil depths were both 0.75 m away from the center of the plot, and the distance between them was 0.20 m (Fig. S2b, c). Temperature sensors were set at 5 cm, 10 cm, 20 cm, 30 cm, 40 cm, 60 cm, 80 cm and 100 cm depths, and moisture sensors were set at 10 cm, 20 cm, 30 cm, 40 cm, 60 cm and 100 cm depths. The soil moisture sensors can maintain high-precision detection when the ambient temperature is during 0 °C–40 °C, and can still ensure the quality and reliability of the collected data if the ambient temperature exceeds this range within 20 °C (delta-t.co.uk). The CR1000 dataloggers would collect soil temperature and moisture at different soil depths every 10 min. Besides, the electronic supply of the heating cable was also controlled by CR1000 via converting the real-time voltage of each paired plots by Silicon Variable Rectifier (SCRs, Watlow, Missouri, USA), which kept the temperature difference between each paired plots around 4 °C. Surface heating and vertical heating are controlled separately. The operation of 2 loops of heating cable on the soil surface was controlled by the temperature difference detected by thermistors set at 5, 10 and 20 cm depth, while the operation of 20 heating rods was controlled by the temperature difference detected by thermistors set at 30–100 cm depth.

2.3. Plant community monitoring and sampling

Prior to treatment (August 2017), the initial plant species diversity (represented by species richness, dominance, evenness, and Shannon-Wiener index) and biomass (AGB and BGB) in areas prepared to set as control or warming plots were investigated, and no significant differences of any variable between two groups were found (Figs. 1 and 3a, b).

From 2018 to 2021, plant community monitoring and sampling were conducted in late August (the peak of the growing season) each year [23]. In each plot, two 50 cm × 50 cm quadrats were randomly chosen to estimate the density and biomass of individual species (Fig. S2b, c). After counting the number of individuals of each species, all living plants were harvested from the two diagonal 25 cm × 25 cm subquadrats from each quadrat, and the litter on the ground was also collected. The living plants from the same plot were then pooled together, sorted into species (2018–2021), and oven-dried at 65 °C for 48 h. Plants were classified into four functional groups (grasses, sedges, legumes, and forbs) based on their functional forms [30]. The measured peak biomass (living plants and litters) served as a proxy for AGB (g m^{-2}), and the measured peak living biomass served as a proxy for ANPP (g m^{-2}). At the end of December, all aboveground litters within all plots and buffer zones (areas 20 cm outside the plot boundary) was removed from 2018 to 2021.

In late August 2018, 2019, and 2021, four soil cores (5 cm in diameter) were randomly collected at the site of surface litter removal and were divided into different soil depths. After removing all soils, all dead roots were separated taking the shape and color into consideration, and the living root samples were weighed after oven-drying at 65 °C for 48 h. The BGB (g m^{-2}) in each plot was calculated as the sum of living root samples across soil depths. BNPP (g m^{-2}) was estimated using an ingrowth-core method [23]. Specifically, in August 2018, a soil core (5 cm in diameter) was collected in each plot and divided into four soil layers: 0–10, 10–20, 20–30, and 30–40 cm. Within each soil core, the pre-existed roots were removed. Then, sieved soils from the same depth outside the plots with polyester mesh bags (1 mm in mesh size) which allowed roots to pass through were refilled back to the sampling holes. In August 2019, the polyester mesh bags were re-collected and divided into four depths same as before, and all living roots at each depth were collected, cleaned, oven-dried, and weighed to represent BNPP. The same processes were conducted in later years.
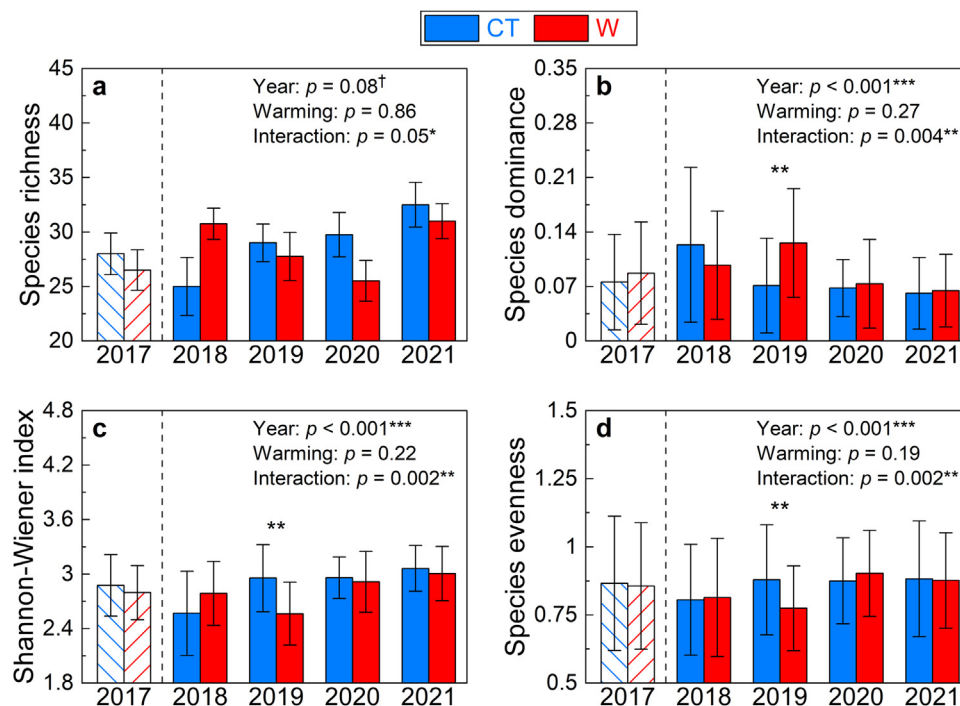
Fig. 1. The initial plant diversity in 2017 and the response of plant diversity to warming over 3.5 years (2018–2021). (a) Species richness; (b) Species dominance; (c) Shannon-Wiener index; (d) Species evenness. The linear mixed-effects model was used to assess the effects of warming, year and their interactions on these variables during 2018 to 2021. In each year, paired t-test was used to detect differences of these variables between control and warming plots. Each group of dots and lines indicates different treatments: CT (control, blue dots and lines) and W (warming, red dots and lines). Vertical bars represent standard errors (SE, $n = 4$). †, *, ** and *** represents $p < 0.10$, $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively.

2.4. Calculations of plant community properties

In each plot, species richness was defined as the number of species found in two quadrats. Species dominance, represented by Simpson's dominance index [38], was calculated as:

$$D = \sum_{i=1}^{S} p_i^2 \tag{1}$$

where D is Simpson's dominance index, p_i is the relative density of species i, and S is the number of species in two quadrants. We also calculated the Shannon-Wiener index (H′) and Pielou's evenness (J') based on the relative density of each species [38]:

$$H' = -\sum_{i=1}^{S} p_i \ln(p_i) \tag{2}$$

$$J' = \frac{H'}{\ln S} \tag{3}$$

Principal coordinates analysis (PCoA) was used to clarify the compositional changes of community/functional groups [39].

After dividing plants into four functional groups, the relative biomass (RB) and density (RD) of each functional group to the whole community was calculated as:

$$RB\ (\%) = \frac{\sum_{i=1}^{S'} b_i'}{ANPP} \tag{4}$$

$$RD(\%) = \frac{\sum_{i=1}^{S'} p_i'}{TI} \tag{5}$$

where b_i' is the aboveground biomass of species i in the functional group with S′ species, p_i' is the number of individuals of species i in the functional group with S′ species, and TI is the total number of individuals in the whole community. We also calculated ΔRB and ΔRD to represent the difference of RB and RD in the paired plots with or without warming, respectively.

Similar calculation was used to define relative value of BNPP at specific soil depths:

$$\text{Relative BNPP}\ (\%) = \frac{BNPP'}{BNPP} \tag{6}$$

where BNPP′ was the values of BNPP at specific soil depths. Similarly, Δrelative BNPP was calculated as the difference of relative BNPP in the paired plots with or without warming.

2.5. Statistical analyses

Before analyzing, the normality and homogeneity of variances were confirmed for all variables using Shapiro-Wilk and Levene's tests, respectively. Linear mixed-effects models (function *lme* in package *nlme*) were used to assess the effects of warming, year, and their interactions on soil temperature and moisture at different soil depths, plant community/functional group properties, in which warming and year were treated as fixed factors, and plot nested within block was treated as a random factor. In each year, paired t-test (function *t.test*) was used to detect differences in variables mentioned above between control and warming treatments. Besides, PCoA analyses (function *vegdist* and *dudi.pco* in package *vegan*) based on Bray-Curtis distance were conducted with species relative aboveground biomass in whole community or functional groups, and the axis 1 and 2 were used as the axis of principal co-ordination plots with treatments (CT or W) set as the grouping factors. Permutational multivariate analysis of variance (PERMANOVA, function *adonis2* in package *vegan*) with 999 permutations [28] was used to evaluate the effects of warming on plant community/functional group composition in specific years (2018, 2019, 2020, and 2021). Univariate linear regression (function *lm*) and Pearson correlation analyses (function *corrplot* in package *corrplot*) were used to examine the relationships of plant community properties to soil temperature and moisture. All statistical analy-

ses were performed using R (version 4.1.2, R Development Core Team, 2021).

3. Results

3.1. Interannual variation in climate and experimental warming effects on plot microclimate

At the field site, from 2018 to 2021, the mean annual air temperature was −0.7 °C, with the highest (−0.2 °C) and lowest (−1.4 °C) value appeared in 2018 and 2020, respectively (Fig. S4). Besides, the mean annual precipitation over four years was 436 mm, while the highest (547 mm) and lowest precipitation (361 mm) appeared in 2021 and 2019, respectively (Fig. S4).

Over the 3.5-year experimental period, whole-soil-profile warming significantly increased mean annual soil temperature (AST) across all soil depths (Table S1), with 3.03 °C, 3.66 °C and 3.47 °C higher than the control treatment at 0–10 cm, 10–40 cm and 40–100 cm soil depths, respectively (all $p < 0.01$; Fig. S5d–f). Similar significant changes were also found in mean growing season soil temperature (GST) and non-growing season soil temperature (NGST) across all soil depths (Tables S2, S3; Fig. S5g–l). However, mean annual soil moisture (ASM) as well as mean growing season soil moisture (GSM) across all soil depths did not significantly respond to warming (Tables S1, S2; Fig. S6d–i). Mean non-growing season soil moisture (NGSM) at 0–10 cm and 10–40 cm depth in warming plots was significantly or marginally significantly higher than that in control plots, respectively (Fig. S6j, k).

3.2. Responses of the diversity, composition, biomass and NPP of whole plant community to experimental warming

Over the whole experimental period (2018–2021), warming did not significantly affect plant species richness, dominance, evenness and Shannon-Wiener index (Fig. 1a−d). However, in 2019, species dominance in warming plots was significantly higher than that in control plots (Fig. 1b), and Shannon-Wiener index as well as species evenness significantly decreased in warming plots compared with control treatment (Fig. 1c, d). Yet, PCoA and PERMANOVA demonstrated that with the extension of the warming period, initial similar plant community composition in control and warming plots gradually changed into two significantly different groups: in 2018 and 2019, no significant differences were found between control and warming plots (Fig. 2a, b), while marginally significant ($p < 0.10$; Fig. 2c) and significant ($p < 0.05$; Fig. 2d) differences between control and warming plots were found in 2020 and 2021, respectively.

From 2018 to 2021, neither biomass (AGB and BGB) nor productivity (ANPP and BNPP) significantly responded to whole-soil-profile warming (Fig. 3a−d), but AGB and ANPP in warming plots were significantly higher than those in control plots in 2018 (Fig. 3a, c).

3.3. Responses of the composition, density and aboveground biomass of four plant functional groups to experimental warming

After dividing the whole plant community into four functional groups, similar to compositional shifts of the whole community between warming and control plots, the interannual variations were also found in grasses and forbs by PCoA and PERMANOVA (Fig. 2e−h, q−t).

Warming caused significant decrease of the relative density of legumes (Fig. S8c), but did not affect the relative density of other functional groups (Fig. S8a, b, d). From 2018 to 2021, no significant difference of aboveground biomass of grasses or sedges between control and warming plots was found (Fig. 4a, b). The aboveground biomass of legumes significantly decreased in warming plots (Fig. 4c), while the aboveground biomass of forbs significantly increased with warming treatment (Fig. 4d).
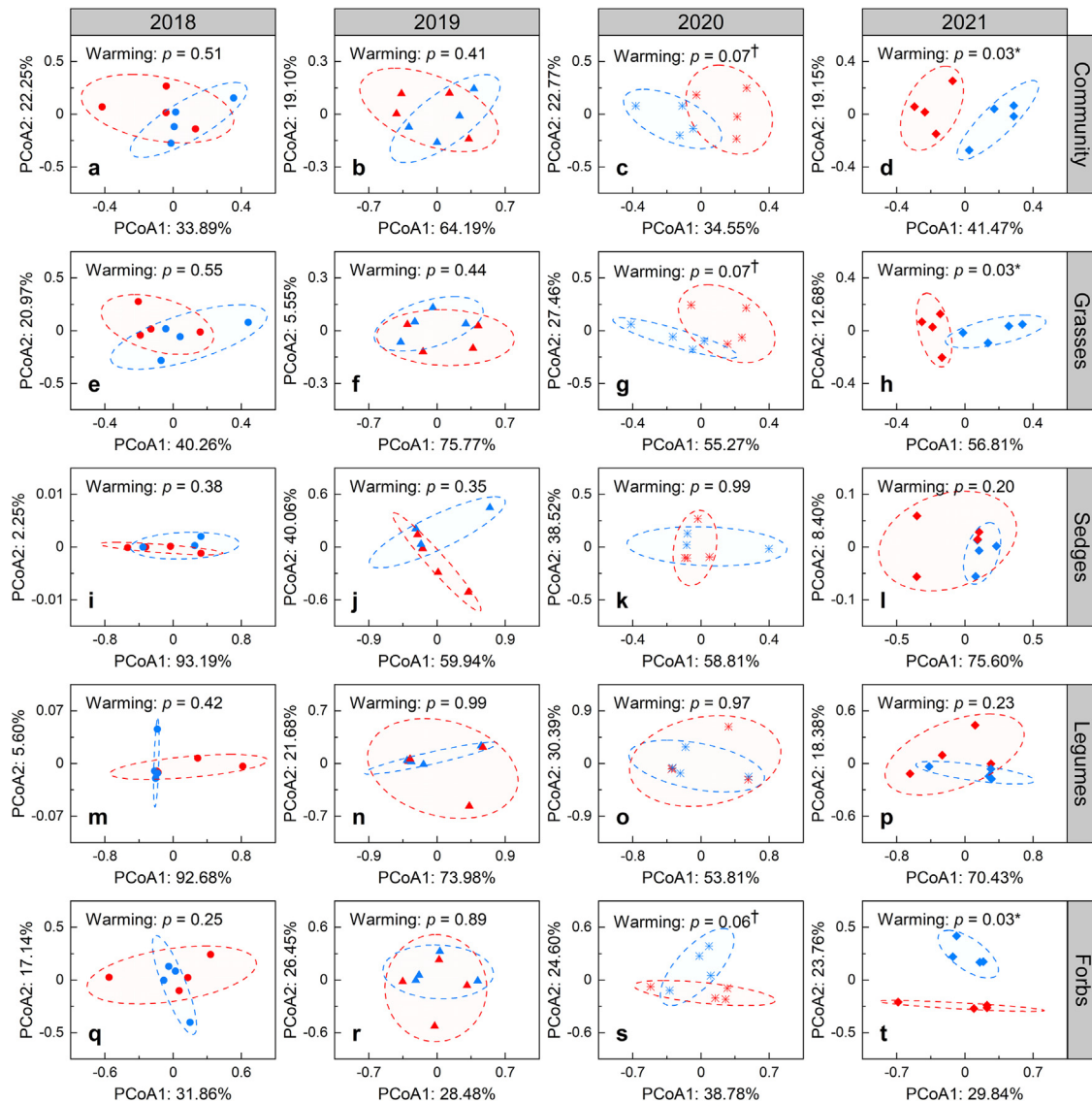
Fig. 2. Principle co-ordinations of plant community or functional groups in control or warming plots within each year from 2018 to 2021, with axes 1 and 2 scores. Each group of dots indicates different treatments or years: CT (control, blue dots), W (warming, red dots), 2018 (circles), 2019 (triangles), 2020 (asterisks) and 2021 (rhombuses). 90% confidence ellipses are shown to represent the data distribution. †, *, ** and *** represents $p < 0.10$, $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively.

4. Discussion

4.1. Warming effects on plant species diversity and community composition

Although considerable efforts have been devoted to determining responses of plant community diversity to climate warming, the results of experimental studies and meta-analyses have been controversial [30,31,40]. Among terrestrial ecosystems, experimental warming often negatively affects plant species diversity in temperature-limited areas [7,41]. However, inconsistent with our first hypothesis, plant species diversity in warming plots did not significantly change compared to the control treatment (Fig. 1a–d). There are three possible explanations for why no response of plant species diversity was found in our experiment. First, we only investigated plant responses to 3.5-year experimental warming, and significant trends in plant species diversity changes to warming tend to occur on longer time scales [4]. Second, our experimental plots are fully open, much larger (3.5 m in diameter), and more heterogeneous in microclimate and soil conditions, which may buffer changes in species occurring at smaller and more homoge-

neous scales [42], and avoid unexpected disturbance to plant migration and colonization (e.g. seed dispersal) caused by artificial blockers (e.g. OTC chambers, Klein et al. [7]). Third, the high initial plant species richness (> 20) in our study site may lead to high resistance to non-extreme climate and habitat changes [27]. Taken together, no significant response of plant species diversity to short-term soil warming was found in our experiment. The significant changes of species dominance, evenness and Shannon-Wiener index in 2019 may be results of the lowest precipitation during 2018 to 2021 (Fig. S4b, c). With the results of a 2-year climate change manipulation experiment, Volenec and Belovsky suggested that the declines of plant species diversity may be exacerbated by warming and lessened by extended supplemental precipitation [43]. Our findings indicated that less annual precipitation may magnify the negative effects of experimental warming on soil water supply, and probably restrict the dispersal, germination and growth of water-sensitive plants. Consequently, the species dominance significantly increased, and the species evenness as well as the Shannon-Wiener index decreased with warming treatment in the dry year 2019.
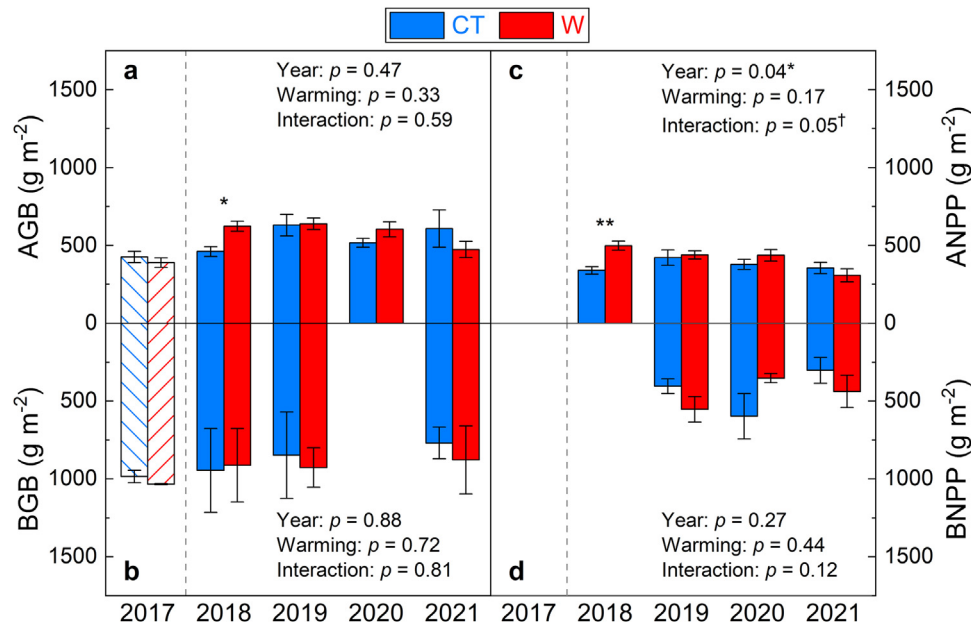
Fig. 3. The initial plant biomass in 2017 and the response of above- and belowground plant biomass and net primary productivity (NPP) to warming over 3.5 years (2018–2021). (a) AGB; (b) BGB; (c) ANPP; (d) BNPP. Linear mixed-effects model was used to assess the effects of warming, year and their interactions on these variables during 2018 to 2021. In each year, paired t-test was used to detect differences of these variables between control and warming plots. Each group of bars indicates different treatments (mean ± SE, $n = 4$): CT (control, blue bars) and W (warming, red bars). †, *, ** and *** represents $p < 0.10$, $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively. AGB, aboveground biomass; BGB, belowground biomass; ANPP, aboveground net primary productivity; BNPP, belowground net primary productivity.

Although the results of plant species diversity did not meet our first hypothesis, changes of plant community composition partly supported our hypothesis. The PCoA ordination revealed that differences in plant community composition in control or warming plots became gradually larger over time (Fig. 2a−d). Shi et al. [15] reported analogous phenomenon in a tallgrass prairie, showing that plant community composition did not show any response to experimental warming until the eighth year. Our results may be critical because a marginally significant difference between control and warming plots appeared since the third warming year (Fig. 2c), indicating that faster response of plant community composition to climate warming may occur in temperature-limited alpine ecosystems. The potential plant-climate feedback may be far more rapid than our realization, with limited changes being detected via traditional plant diversity evaluation (e.g. species richness). Therefore, more plant investigation at the community, functional group and species levels with high-precision assessment should be applied to explore plant-climate interaction in the future. According to the trend of plant community composition, we propose that with the extension of the warming period, this community composition shift may lead to changes in community diversity and productivity. However, Smith et al. [16] suggested that chronically altered environments under long-term climate change may induce nonlinear changes in plant community composition through species reordering and/or species invasion. Since the experiment had only been running for 3.5 years (2018–2021), longer-term monitoring of plant community compositional changes is still necessary for the future.

### 4.2. Warming effects on above- and belowground plant biomass and NPP

Inconsistent with our second hypothesis, the neutral effects of warming on plant biomass and NPP were quite surprising, since numerous studies reported significantly positive [22,44] or negative [24,29] responses to experimental warming. Liu et al. [23] reported a similar phenomenon in a nearby alpine meadow and posited the importance of compensatory interactions among major functional groups in stabilizing plant productivity. Our results supported their view and found that

the decrease of legume biomass could be compensated by the increasing forb biomass. In 2018 (the first year of warming), warming significantly stimulated AGB and ANPP (Fig. 3a, c). We proposed that this may be a result of the short-term growth stimulation or establishment of sensitive species in newly established experimental warming plots, with significant increase in forb biomass (Fig. 4d) as well as presence of 11 extra species (e.g. *Ligularia sagitta*) being found only in warming plots.

However, total BGB and BNPP showed no response to warming over the whole experimental period (Fig. 3b, d). Wang et al. [44] reported different results that stronger warming-stimulation of root biomass can be found under experimental warming, especially in deeper soils, and they proposed that this may be due to the stimulation of plant growth and higher requirements of water and nutrient supply in deeper soils. However, in our experimental site, warming did not affect AGB and ANPP (Fig. 3a, c) and no change of the growing season soil moisture was found from 2018 to 2021 (Fig. S6). Therefore, warming did not significantly alter aboveground or belowground plant growth at the community level in the present study, and there was no higher need for plants to devote more allocation in deeper soils for water supply under the whole-soil-profile warming.

4.3. Warming effects on the composition and aboveground biomass of different plant functional groups

After dividing the whole community into four functional groups, we found a similar pattern in principal co-ordinations of grasses and forbs (Fig. 2e−h, q−t). We propose that the similarity of the whole community and grasses may be a result of the high contribution of grasses to total biomass (∼65% of ANPP). Therefore, even marginal responses of grasses to experimental warming would be revealed in PCoA analysis. Conversely, the composition shifts of forbs may be related to temperature-sensitive species loss or re-establishment. Since this functional group comprises most rare species which may be severely affected by environmental changes, the fast responses of these rare species to experimental warming may highly contribute to the alteration of the composition of forbs [45].
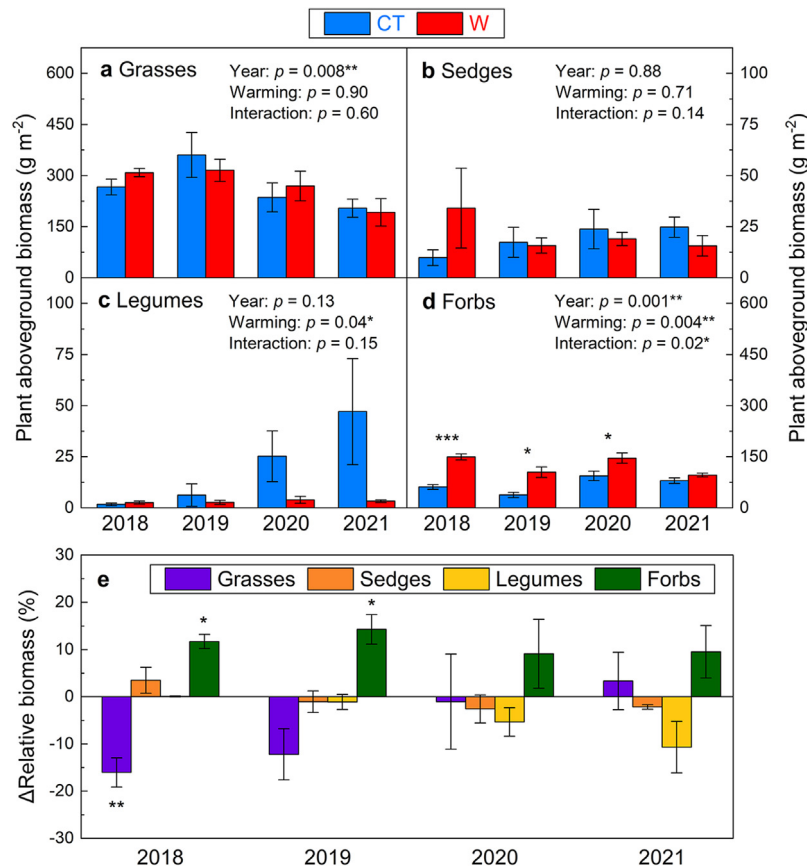
Fig. 4. The response of plant aboveground biomass of four functional groups to warming over 3.5 years (2018–2021). (a) Grasses; (b) Sedges; (c) Legumes; (d) Forbs; (e) ΔRelative biomass (warming − control) in different functional groups. (a-d) Linear mixed-effects model was used to assess the effects of warming, year and their interactions on these variables during 2018 to 2021. In each year, paired t-test was used to detect differences of these variables between control and warming plots. Each group of bars indicates different treatments (mean ± SE, $n = 4$): CT (control, blue bars) and W (warming, red bars). †, *, ** and *** represents $p < 0.10$, $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively.

From 2018 to 2021, we found an increasing trend of the aboveground biomass of legumes in control plots (Fig. 4c). We assumed that this may demonstrated that legumes in natural environments could gain higher survival advantages in intense competition with forbs or sedges in the lower canopy because of their ability of N fixation [46], especially in N-limited ecosystems such as the alpine meadows. Therefore, the aboveground biomass of legumes could rise every year. However, the aboveground biomass of legumes in the warming plots maintained at a low value, and was significantly lower than that in control plots over the whole experimental period (Fig. 4c). Two possible mechanisms are proposed to explain the lower aboveground biomass of legumes under warming. First, experimental warming may increase nutrient release from soil organic matter (SOM) via enhancing microbial decomposition [47,48], consequently weakening the competitiveness of legumes (Fig. 5b). Second, although most of the legumes in our plots (e.g. *Oxytropis ochrocephala*) are poisonous for large herbivores [49], small rodents and insects (e.g. *Ochotona curzoniae*) would forage these plants as their main dietary item [50,51] since they are nutritious [52]. Therefore, the shortening time of snow cover and the extension of herbivore activity in warming plots may lead to higher risks of being eaten or taken for storage in burrows for legumes (Figs. 5b, S11c). Therefore, the aboveground biomass of legumes in warming plots was significantly lower than that in control plots in the present study.

The increasing aboveground biomass of forbs with experimental warming in this study was interesting, since previous studies in alpine meadows mainly reported warming-induced inhibition of forbs [23,28,53]. They assumed that this may be a result of species loss of forbs in more intense competition for light and nutrients with grasses. In the present study, owing to unchanged aboveground grass biomass (Fig. 4a), our results may provide another potential perspective to explore direct responses of forbs to warming without competitive disadvantage. First, our results showed a significant positive relationship between aboveground forb biomass and soil temperature (0–30 cm, all $p < 0.01$; Fig. S9d–f). We propose that this may demonstrate that soil warming may be more effective on forb growth, since most of species in forbs are small and rosette-like. Therefore, their stems and leaves would grow more closely to the ground and could receive more extra heat from warmed soil (Fig. 5a, c). Second, a positive relationship between forb biomass and annual mean soil moisture (ASM, 0–30 cm) was found in our study ($p < 0.10$; Fig. S9g). After dividing the whole year into growing season and non-growing season, we found that the significant positive relationship between aboveground forb biomass and soil moisture only appeared in the non-growing season ($p < 0.05$; Fig. S9i). This finding may be vital since it demonstrates that an earlier date of snow melting due to soil warming may be pivotal for some species in forbs [32]. During the non-growing season, snow beds cover this alpine meadow, and at the end of April or the beginning of May, when the air temperature rises back above 0 ℃, snow beds will melt, consequently increasing soil moisture. Indeed, we found significant or marginally significant increases of soil moisture at 0–10 cm and 10–40 cm soil depths in the non-growing season (October to April of the next year; Fig. S6j, k), which demonstrated that whole-soil-profile warming may cause extra water supply after snow melting. Our results indicate that earlier snow melting with additional water supply for propagules or seeds in warm-
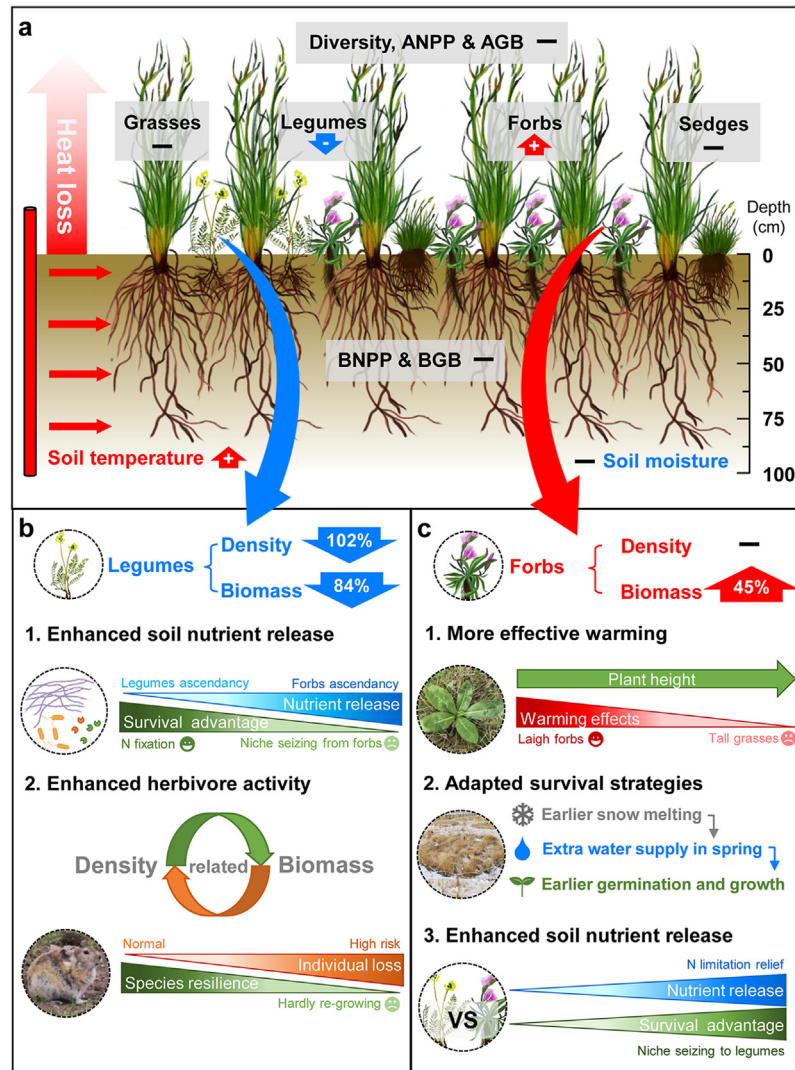
Fig. 5. A conceptual diagram of the impact of whole-soil-profile warming on plant community and functional groups in the alpine meadow on the Qinghai-Tibetan Plateau. (a) Warming did not affect plant species diversity, biomass and NPP, but induced community composition shift; (b) Warming led to decreases of aboveground biomass of legumes, likely due to soil nutrient release and enhanced herbivore activity; (c) Warming stimulated the aboveground biomass of forbs probably because of better warming effect, extra water and nutrient supply. More detailed explanation could be found in the text. The red up arrows (with "+" or numbers) represent increase, the blue down arrows represent decrease, and the black dashes ("−") represent no response. The maximum root depth distribution of each functional group is based on the results of an adjacent experiment at the same study site from Liu et al. [23]. The diagram of plant does not fully represent all of the morphological and functional variation within species in each functional group.

ing plots may contribute to earlier germination, longer growing period, and consequently more biomass accumulation of forbs relative to other functional groups (Fig. 5c). Third, previous studies have demonstrated that sufficient nutrient (especially N) supply is more critical for forbs, since forbs contain most of the dicotyledonous plants and have higher N requirement (e.g. *Ajania tenuifolia*, Zhang et al. [54]) to produce photosynthesis related enzymes (e.g. Rubisco) for compensating low light intensity in the lower canopy [55]. Experimental warming may stimulate nutrient release from SOM decomposition, and the relief of nutrient limitation may not only stimulate growth of forbs, but also give them more competitive advantage (e.g. niche occupation, light competition) compared with legumes (Fig. 5b, c).

The significant changes of aboveground biomass of legumes and forbs partly supported our third hypothesis, but warming did not significantly affect aboveground biomass of grasses and sedges in our experiment (Fig. 4a, b). Previous studies reported inconsistent responses of aboveground biomass of grasses to experimental warming in alpine meadows or grasslands [18,56], and highlighted the dominant role of

soil moisture for determining the response of grasses to warming [23–25]. Grasses are more affected by drought than other functional groups in alpine ecosystems, since they have a lower relative reduction in stomatal conductance in response to drought [57]. In our study, however, the unchanged aboveground biomass of grasses may be partly explained by the stability of soil moisture (annual mean and growing-season, ASM and GSM, 0−100 cm) under warming (Fig. S6). In addition, though a high soil warming magnitude (4 °C) was chosen in our design, the warming effect may diminish rapidly with increasing plant height due to substantial heat dissipation in cold air and consequential decay of aboveground temperature increase (Fig. 5a). Therefore, the temperature limitation on growth of tall-stature grasses was only slightly alleviated by the minor warming of air in this experiment. For sedges, like grasses, soil water supply is also considered a key factor of plant growth [24]. Moreover, though small stature may allow sedges to be better exposed to the heat from soil in warming plots, they would allocate more biomass belowground than grasses [58]. Accordingly, no significant change was found in aboveground biomass of sedges in this study.

4.4. A new perspective in exploring plant-climate interactions with whole-soil warming experiments in grassland ecosystems

Grassland ecosystems cover approximately 40% of the terrestrial land and provide important ecosystem services to our planet [59]. In recent years, numerous field experimental warming studies were conducted in grasslands all over the world [21], with dozens of different warming methods being applied. However, most warming methods only cause an elevation of air temperatures [7], ground surface temperatures [60], near-surface soil temperatures [61] or both, while the belowground biotic and abiotic responses to global temperature rising were out of consideration or cannot be explored due to technology restrictions. However, the reality often overlooked in experimental warming studies is that deep soil temperatures will also become elevated as they equilibrate with new mean annual temperatures [35]. In fact, roots, soils and soil microbes are widely considered to be closely linked and all of them are often sensitive to environmental temperature, especially in deep soils. Besides, traditional warming methods applied in grasslands have specific performance issues, which restrict further exploration of plant-climate interactions in the context of climate warming. For instance, the widely-used OTCs may become incapable of sustaining efficient warming during the night and winter periods [7], and may cause unexpected and extreme leaf temperature rising [62]. Infrared heaters provide more stable and realistic warming simulation to aboveground plants and top soils, but have a minor effect on deep soils and roots distributed there [63]. In addition, these facilities are often established in small experimental plots (e.g. ~1 m^2 for most OTCs), which may inadvertently increase results' bias because of the heterogeneity of plant distribution and soil properties. Whole-soil warming may be such a compromise solution, which can simultaneously provide controllable and stable warming treatment, less disturbance to soil, chances to figure out deep soil responses to temperature rising, etc. However, it also has some limitations, such as minor warming effects on aboveground air and plants, and higher installation or maintenance costs. A better plan is the whole-ecosystem warming method used in the SPRUCE experiment [64].

To our knowledge, this study is the first to report the effects of whole-soil-profile warming on plants in grassland ecosystems. Based on this new technology, we detected inconsistent responses of different plant groups to experimental warming. We also provided preliminary insights about how the plants of different groups whose roots distributed in different soil layers may respond to warming-induced alteration of soil properties (Fig. 5). However, more precise mechanisms would be found in the future if the roots were identified and analyzed at the species level while combined with depth-specific data of soil and microbial properties. Overall, whole-soil-profile warming may be helpful in linking above- and belowground responses of the whole grassland ecosystem and thoroughly evaluating the plant-climate interactions with detailed mechanisms in a new era.

5. Conclusion

Based on a whole-soil-profile warming (3–4 °C across 0–100 cm) experimental platform in an alpine meadow on the Qinghai-Tibetan Plateau, we investigated the responses of plant species diversity, community composition, biomass, and NPP to warming from 2018 to 2021. We showed that plant species diversity, above- and belowground biomass or NPP in this alpine meadow showed remarkable resistance to soil warming, but plant species composition significantly shifted at the community level. At the functional group level, soil warming significantly stimulated aboveground biomass of forbs, decreased that of legumes, and had minor effects on that of grasses and sedges over the 3.5-year warming period. Complementary interactions between legumes and forbs may stabilize plant biomass and NPP at the community level, and the unique experimental design, combined with the relatively short-term investigation, may together explain the neutral response of plant species diversity to warming. Moreover, warming may stimulate soil nutrient release and enhance herbivore activities (although we have no data to directly prove these assumptions), thus leading to a competitive disadvantage and biomass loss of legumes. However, warming-induced extra water supply (non-growing season) and other potential alterations (e.g. nutrient supply) may also stimulate forb growth, resulting in a significant aboveground biomass increase of forbs. Generally, we emphasize the potential risk of significant and fast plant community composition changes in a warming world, which may significantly affect the carbon source-sink dynamics in alpine ecosystems. Longer-term monitoring and investigating are still required in the future, and more efforts should also be devoted to exploring the reproduction, germination and growth strategies of specific plant species above- and belowground in response to climate warming in the whole plant community.

Declaration of competing interest

The authors declare that they have no conflicts of interest in this work.

Author contributions

B.Z. conceived the idea and secured the funding; W.K.Q., Y.C., H.Y.Z., Y.H.H., X.D.W., and Q.F.Z. conducted the experiment and collected the data; W.K.Q., Y.C. and B.Z. analyzed the data and wrote the manuscript with input from all authors.

Data availability statement

All data that support the findings of this study can be found in the article and/or Supporting Information.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.fmre.2022.09.025.

References

[1] IPCC, Summary for PolicymakersClimate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel On Climate Change, Cambridge University Press, Cambridge, UK, 2021 Masson-Delmotte, V., P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu and B. Zhou (eds.) in press.

[2] Z. Wu, P. Dijkstra, G.W. Koch, et al., Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation, Glob Chang Biol 17 (2011) 927–942.

[3] N.G. Smith, J.S. Dukes, Short-term acclimation to warmer temperatures accelerates leaf carbon exchange processes across plant types, Glob Chang Biol 23 (2017) 4840–4853.

[4] Y. Luo, J. Melillo, S. Niu, et al., Coordinated approaches to quantify long-term ecosystem dynamics in response to global change, Glob Chang Biol 17 (2011) 843–854.

[5] C.M. Dieleman, B.A. Branfireun, J.W. McLaughlin, et al., Climate change drives a shift in peatland ecosystem plant community: implications for ecosystem function and stability, Glob Chang Biol 21 (2015) 388–395.

[6] C. Li, C. Lai, F. Peng, et al., Dominant plant functional group determine the response of the temporal stability of plant community biomass to 9-year warming on the qinghai–tibetan plateau, Front Plant Sci 12 (2021) 704138.

[7] J.A. Klein, J. Harte, X. Zhao, Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau, Ecol. Lett. 7 (2004) 1170–1179.

[8] C.S. Sheppard, B.R. Burns, M.C. Stanley, Predicting plant invasions under climate change: are species distribution models validated by field trials? Glob Chang Biol 20 (2014) 2800–2814.

[9] M. Xu, M. Liu, X. Xue, et al., Warming effects on plant biomass allocation and correlations with the soil environment in an alpine meadow, China, J Arid Land 8 (2016) 773–786.

[10] Q. Quan, F. Zhang, C. Meng, et al., Shifting biomass allocation determines community water use efficiency under climate warming, Environ Res Lett 15 (2020) 094041.

[11] L. Zhou, Y. Hong, C. Li, et al., Responses of biomass allocation to multi-factor global change: a global synthesis, Agric Ecosyst Environ 304 (2020) 107115.

[12] D. Tilman, F. Isbell, J.M. Cowles, Biodiversity and ecosystem functioning, Annu Rev Ecol Evol Syst 45 (2014) 471–493.

[13] H. Ganjurjav, E.S. Gornish, G. Hu, et al., Temperature leads to annual changes of plant community composition in alpine grasslands on the Qinghai-Tibetan Plateau, Environ Monit Assess 190 (2018) 585.

[14] K. Yue, S. Jarvie, A.M. Senior, et al., Changes in plant diversity and its relationship with productivity in response to nitrogen addition, warming and increased rainfall, Oikos 129 (2020) 939–952.

[15] Z. Shi, R. Sherry, X. Xu, et al., Evidence for long-term shift in plant community composition under decadal experimental warming, J Ecol 103 (2015) 1131–1140.

[16] M.D. Smith, A.K. Knapp, S.L. Collins, A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change, Ecology 90 (2009) 3279–3289.

[17] J.M. Alexander, J.M. Diez, J.M. Levine, Novel competitors shape species' responses to climate change, Nature 525 (2015) 515–518.

[18] S. Wang, J. Duan, G. Xu, et al., Effects of warming and grazing on soil N availability, species composition, and ANPP in an alpine meadow, Ecology 93 (2012) 2365–2376.

[19] Q. Wang, Z. Zhang, R. Du, et al., Richness of plant communities plays a larger role than climate in determining responses of species richness to climate change, J Ecol 107 (2019) 1944–1955.

[20] T.G. Britton, M.J. Hovenden, M. Porter, et al., Plant communities, populations and individuals have distinct responses to short-term warming and neighbour biomass removal in two montane grasslands, Appl Veg Sci 24 (2021) e12557.

[21] N. Wang, B. Quesada, L. Xia, et al., Effects of climate warming on carbon fluxes in grasslands—A global meta-analysis, Glob Chang Biol 25 (2019) 1839–1851.

[22] Y. Chen, J. Feng, X. Yuan, et al., Effects of warming on carbon and nitrogen cycling in alpine grassland ecosystems on the Tibetan Plateau: a meta-analysis, Geoderma 370 (2020) 114363.

[23] H. Liu, Z. Mi, L. Lin, et al., Shifting plant species composition in response to climate change stabilizes grassland primary production, Proc Natl Acad Sci 115 (2018) 4051–4056.

[24] H. Ganjurjav, Q. Gao, E.S. Gornish, et al., Differential response of alpine steppe and alpine meadow to climate warming in the central Qinghai-Tibetan Plateau, Agric For Meteorol 223 (2016) 233–240.

[25] C. Li, F. Peng, X. Xue, et al., Productivity and quality of alpine grassland vary with soil water availability under experimental warming, Front Plant Sci 9 (2018) 01790.

[26] J. Li, C. Yang, X. Liu, et al., Inconsistent stoichiometry response of grasses and forbs to nitrogen and water additions in an alpine meadow of the Qinghai-Tibet Plateau, Agric Ecosyst Environ 279 (2019) 178–186.

[27] J. Shao, X. Zhou, K.J. van Groenigen, et al., Warming effects on grassland productivity depend on plant diversity, Global Ecol Biogeogr 31 (2022) 588–598.

[28] X. Hu, W. Zhou, X. Li, et al., Changes in community composition induced by experimental warming in an alpine meadow: beyond plant functional type, Front Ecol Evol 9 (2021) 569422.

[29] X. Liu, Q. Ma, H. Yu, et al., Climate warming-induced drought constrains vegetation productivity by weakening the temporal stability of the plant community in an arid grassland ecosystem, Agric For Meteorol 307 (2021) 108526.

[30] Z. Ma, H. Liu, Z. Mi, et al., Climate warming reduces the temporal stability of plant community biomass production, Nat Commun 8 (2010) 15378.

[31] G.L. Hoyle, S.E. Venn, K.J. Steadman, et al., Soil warming increases plant species richness but decreases germination from the alpine soil seed bank, Glob Chang Biol 19 (2013) 1549–1561.

[32] B. Fernández-Marín, A. Sáenz-Ceniceros, T. Solanki, et al., Alpine forbs rely on different photoprotective strategies during spring snowmelt, Physiol Plant 172 (2021) 1506–1517.

[33] J. Hansen, R. Ruedy, M. Sato, et al., Global surface temperature change, Rev Geophys 48 (2010) RG4004.

[34] X. Yuan, W. Qin, H. Xu, et al., Sensitivity of soil carbon dynamics to nitrogen and phosphorus enrichment in an alpine meadow, Soil Biol Biochem 150 (2020) 107984.

[35] P.J. Hanson, K.W. Childs, S.D. Wullschleger, et al., A method for experimental heating of intact soil profiles for application to climate change experiments, Glob Chang Biol 17 (2011) 1083–1096.

[36] P.C.E. Hicks, C. Castanha, R.C. Porras, et al., The whole-soil carbon flux in response to warming, Science 355 (2017) 1420–1423.

[37] A.T. Nottingham, P. Meir, E. Velasquez, et al., Soil carbon loss by experimental warming in a tropical forest, Nature 584 (2020) 234–237.

[38] B. Smith, J.B. Wilson, A Consumer's Guide to Evenness Indices, Oikos 76 (1996) 70–82.

[39] Y. Tsuzuki, T.F. Koyanagi, T. Miyashita, Plant community assembly in suburban vacant lots depends on earthmoving legacy, habitat connectivity, and current mowing frequency, Ecol Evol 10 (2020) 1311–1323.

[40] J.M. Alatalo, A.K. Jägerbrand, U. Molau, Impacts of different climate change regimes and extreme climatic events on an alpine meadow community, Sci Rep 6 (2016) 21720.

[41] M.D. Walker, C.H. Wahren, R.D. Hollister, et al., Plant community responses to experimental warming across the tundra biome, Proc Nat Acad Sci 103 (2006) 1342–1346.

[42] A.J. Suggitt, R.J. Wilson, N.J.B. Isaac, et al., Extinction risk from climate change is reduced by microclimatic buffering, Nat Clim Chang 8 (2018) 713–717.

[43] Z.M. Volenec, G.E. Belovsky, The interaction of temperature and precipitation determines productivity and diversity in a bunchgrass prairie ecosystem, Oecologia 188 (2018) 913–920.

[44] J. Wang, C. Defrenne, M.L. McCormack, et al., Fine-root functional trait responses to experimental warming: a global meta-analysis, New Phytol 230 (2021) 1856–1867.

[45] J.I. Sprent, J. Ardley, E.K. James, Biogeography of nodulated legumes and their nitrogen-fixing symbionts, New Phytol 215 (2017) 40–56.

[46] V.E. Crisfield, J.M. Dennett, C.K. Denny, et al., Species richness is a surrogate for rare plant occurrence, but not conservation value, in boreal plant communities, Biodivers. Conserv. 29 (2020) 99–114.

[47] E. Bai, S. Li, W. Xu, et al., A meta-analysis of experimental warming effects on terrestrial nitrogen pools and dynamics, New Phytol 199 (2013) 441–451.

[48] W. Liu, Y. Jiang, Y. Su, et al., Warming affects soil nitrogen mineralization via changes in root exudation and associated soil microbial communities in a subalpine tree species Abies fabri, J Soil Sci Plant Nutrition 22 (2022) 406–415.

[49] H. Lu, S. Wang, W. Wang, et al., Effect of swainsonine in *Oxytropis kansuensis* on golgi α-mannosidase II expression in the brain tissues of sprague–dawley rats, J. Agric. Food Chem. 62 (2014) 7407–7412.

[50] D. Ge, Z. Zhang, L. Xia, et al., Did the expansion of C4 plants drive extinction and massive range contraction of micromammals? Inferences from food preference and historical biogeography of pikas, Palaeogeogr Palaeoclimatol Palaeoecol 326-328 (2012) 160–171.

[51] S. Ren, C. Fan, L. Zhang, et al., The plant secondary compound swainsonine reshapes gut microbiota in plateau pikas (*Ochotona curzoniae*), Appl. Microbiol. Biotechnol. 105 (2021) 6419–6433.

[52] P.E. Hulme, Herbivores and the performance of grassland plants: a comparison of arthropod, mollusc and rodent herbivory, J Ecol 84 (1996) 43–51.

[53] D.E. Winkler, K.J. Chapin, L.M. Kueppers, Soil moisture mediates alpine life form and community productivity responses to warming, Ecology 97 (2016) 1553–1563.

[54] R. Zhang, A.A. Degen, Y. Bai, et al., The forb, *Ajania tenuifolia*, uses soil nitrogen efficiently, allowing it to be dominant over sedges and Graminae in extremely degraded grasslands: implications for grassland restoration and development on the Tibetan Plateau, Land Degrad, Develop 31 (2020) 1265–1276.

[55] L. Jiang, S. Wang, P. Zhe, et al., Plant organic N uptake maintains species dominance under long-term warming, Plant Soil 433 (2018) 243–255.

[56] J.A. Klein, J. Harte, X. Zhao, Decline in medicinal and forage species with warming is mediated by plant traits on the tibetan plateau, Ecosystems 11 (2008) 775–789.

[57] C. Wellstein, P. Poschlod, A. Gohlke, et al., Effects of extreme drought on specific leaf area of grassland species: a meta-analysis of experimental studies in temperate and sub-Mediterranean systems, Glob Chang Biol 23 (2017) 2473–2481.

[58] X.M. Mou, X.G. Li, N. Zhao, et al., Tibetan sedges sequester more carbon belowground than grasses: a ^{13}C labeling study, Plant Soil 426 (2018) 287–298.

[59] W. Wang, J. Fang, Soil respiration and human effects on global grasslands, Glob Planet Change 67 (2009) 20–28.

[60] X. Xu, Z. Shi, D. Li, et al., Plant community structure regulates responses of prairie soil respiration to decadal experimental warming, Glob Chang Biol 21 (2015) 3846–3853.

[61] J.M. Melillo, S.D. Frey, K.M. DeAngelis, et al., Long-term pattern and magnitude of soil carbon feedback to the climate system in a warming world, Science 358 (2017) 101–105.

[62] H.J. De Boeck, T. De Groote, I. Nijs, Leaf temperatures in glasshouses and open-top chambers, New Phytol 194 (2012) 1155–1164.

[63] B.A. Kimball, Theory and performance of an infrared heater for ecosystem warming, Glob Chang Biol 11 (2005) 2041–2056.

[64] A.D. Richardson, K. Hufkens, T. Milliman, et al., Ecosystem warming extends vegetation activity but heightens vulnerability to cold temperatures, Nature 560 (2018) 368–371.
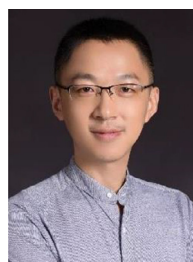
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