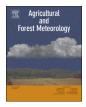


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Grazing and spring snow counteract the effects of warming on an alpine plant community in Tibet through effects on the dominant species

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ABSTRACT

Although studies have investigated the independent effects of warming, snow, and grazing on alpine plant community properties - including plant species richness, evenness, and diversity - the interactive effects of these climate and grazing factors have not been addressed experimentally in cold systems. We investigate the effects of these climate change and grazing factors using 5 years of data collected from a relatively long-term (2009-2015), fully-factorial field experiment in an alpine meadow ecosystem on the central Tibetan Plateau. Specifically, we investigate: 1) how experimental warming, spring snow addition, and yak grazing independently and interactively affect plant community properties, including diversity metrics and relative contributions of different plant life forms to the total plant cover, and 2) how the changes in plant community properties are associated with the proportional cover of the dominant plant species. *Kobresia pygmaea* within the total vegetation cover. We found that warming reduced species richness and increased species evenness and the proportional cover of shrubs within the total vegetation cover. Snow addition also increased species evenness. Grazing increased the proportional cover of K. pygmaea within the total vegetation cover, while decreasing that of grasses. Grazing also counteracted warming-induced increases in shrubs. Treatment-induced changes in K. pygmaea cover were strongly correlated with the indices of plant community properties and were generally in the opposite direction of changes in species evenness and diversity. We conclude that the projected increases in spring snowstorms and maintaining moderate levels of grazing can counteract some warming effects on the plant community. Moreover, the performance of the dominant species can regulate plant community responses to climate change and livestock grazing on the central Tibetan Plateau.

1. Introduction

Global mean temperatures have been increasing exponentially since the pre-industrial period, with alpine and arctic systems experiencing an even stronger magnitude of warming than lowland and temperate regions (IPCC, 2013). Warmer temperatures and more frequent extreme weather events are projected to occur across the Tibetan Plateau (Christensen et al., 2013; He et al., 2016; Jiang et al., 2012; Yang et al., 2012). The Tibetan Plateau encompasses approximately 1.2 M km² of semi-arid alpine grassland (Zhang et al., 2014), equivalent to 0.9% of Earth's total terrestrial land area (Coble et al., 1987), and is among the most vulnerable eco-regions to climate warming (IPCC, 2013). Episodic extreme snowstorms represent one of the key types of extreme events on the Tibetan Plateau that is expected to increase (Jiang et al., 2012; Shen et al., 2015; Wang et al., 2018). Extreme snowstorms can have devastating effects on livestock and livelihoods (Klein et al., 2011), but the ecosystem effects of snowstorms, and their interactions with warming and grazing, have not been explored. Within the semi-arid alpine grassland eco-region, the alpine meadow ecosystem is one of the dominant ecosystem types on the Tibetan Plateau, covering more than

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one-fourth of its total vegetated land surface (Wang et al., 2016), and supporting more than two-thirds of the total livestock population on the Tibetan Plateau according to local official statistics. Livestock grazing is the primary type of land use and has been hypothesized to be the main driver of the formation of alpine meadow ecosystems on the Tibetan Plateau (Miehe et al., 2011b).

The interacting impacts of climate change and livestock grazing on alpine grassland plant communities, including aspects such as species richness, evenness, and composition, are evident on the eastern margin of the Tibetan Plateau (Klein et al., 2004; Wang et al., 2012). The resulting changes in plant community properties can affect ecosystem functioning and the provision of services, such as forage for livestock production (Avolio et al., 2015; Hopping et al., 2018; Ma et al., 2017) and soil carbon sequestration (Chapin et al., 2000; Hopping et al., 2018). However, the complexity of factors mediating plant community responses to interacting global change drivers further underscores the need for more multi-factoral experiments (White et al., 2014). Studies that consider multiple, interacting factors have led to key system insights, including the finding that experimental warming effects on plant community composition are mediated by grazing (Klein et al., 2004; Post and Pedersen, 2008), soil moisture availability (Xu et al., 2016) and permafrost status (Yang et al., 2018). Yet, no arctic or alpine warming studies to date have directly manipulated temperature, grazing and moisture inputs (including extreme events). Understanding the independent and interactive effects of these drivers is essential, particularly for grazed ecosystems such as the Tibetan Plateau, where not only are temperatures increasing, but where the timing and amount of precipitation are also projected to change (Christensen et al., 2013; He et al., 2016; Wang et al., 2018), and where grazing policy changes are also underway (Bauer and Nyima, 2011).

A dominant plant species can exert a strong influence on plant community properties due to its high proportional cover, which is mainly the result of being highly adapted to the local biotic and abiotic conditions (Grime, 1998; Kardol et al., 2010; le Roux et al., 2013). Competition from the dominant species may reduce species richness and evenness, whereas release from competition with the dominant species may allow other species to increase, thereby increasing richness and evenness (Cerabolini et al., 2010). Dominant species may play a significant role in community productivity, by, for example, counterbalancing large declines in rare and uncommon species (Smith and Knapp, 2003), and/or in community composition, by, for example, inducing competitive exclusion of subdominant species under warming if warmer conditions favor highly competitive dominant species over subordinate ones (Olsen et al., 2016). Therefore, understanding the ways in which changing temperatures, precipitation, and land use will affect the dominant species will be important for predicting how plant communities as a whole will respond to climate and land use changes (Kardol et al., 2010). This understanding is particularly important for alpine meadow grasslands on the Tibetan Plateau, where the dominant species, Kobresia pygmaea C. B. Clarke, is both highly palatable for livestock and resistant to grazing (Miehe et al., 2008). Moreover, it is also a shallow-rooted, early-flowering sedge species that is sensitive to upper-soil moisture availability, which could be altered by climate change (Hu et al., 2013).

Thus, the objectives of our study were to quantify:

- 1) How growing-season warming, simulated spring snowstorms, and yak grazing independently and interactively affect plant species richness, evenness, diversity, and proportional vegetation cover of different plant life forms (sedges, grasses, forbs, and shrubs).
- 2) How the variation in plant species richness, evenness, diversity, and the proportional vegetation cover of different plant life forms relates to changes in proportional vegetation cover of the dominant plant species under experimental manipulations.

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season will decrease plant species richness due to non-random species loss (Cross and Harte, 2007) or local extinction (Walker et al., 2006), but that this effect will be dampened by growing-season yak grazing, due to grazers' ability to counteract community composition shifts under warming in other alpine and arctic systems (Klein et al., 2004; Post and Pedersen, 2008). We also hypothesized that spring snow addition will increase plant species richness, evenness, and thus diversity, because the increase in soil moisture availability with snow addition can promote emergence, growth, and population expansion of shallow-rooted, early flowering, rare species in semi-arid ecosystems (Dorji et al., 2013; Porporato et al., 2001). Finally, we expected that yak grazing will promote *K. pygmaea* dominance, given its adaptations to grazing as discussed above.

2. Materials and methods

2.1. Study design

This study was conducted in a semi-arid, alpine meadow grassland near Nam Tso Lake, central Tibet, China (30.72°N, 91.05°E, 4875 m a.s.l). The grassland is dominated by *K. pygmaea*. There are also commonly occurring sub-dominant plant species, such as *Potentilla saundersiana* Royle, *Potentilla bifurca* Linn., *Potentilla fruticosa* Linn., *Carex moorcroftii* Falc. ex Boott, and *Astragalus rigidulus* Benth. (Fig. S1). In total, we found 53 vascular plant species – including 7 sedges, 37 forbs, 7 grasses, and 2 shrubs – in our experiment across all years and treatments.

Mean annual air temperature was -0.71 °C, while mean air temperature in winter (December 1–February 30) was -9.59 °C, in summer (June 1-August 30) was 8.43 °C, and during the growing season (May 1-September 30) was 5.93 °C, as measured by a nearby weather station from 2006 to 2017 (NAMORS, 2018). The mean annual precipitation was 407 mm, but this mainly falls during the summer monsoon season from June to September (NAMORS, 2018). Winter snowfall is typically low in this region and sublimates quickly, primarily due to strong solar radiation and wind at this elevation, leaving the vegetation snow-free during much of its dormant season. However, episodic, severe snowstorms do occur, and these are projected to increase in frequency and severity (Jiang et al., 2012; Shen et al., 2015; Wang et al., 2018). The Plateau is also simultaneously undergoing climate warming at rates above the global mean (IPCC, 2013; Wang et al., 2008) and is projected to face up to an additional 2.0 °C of warming by 2035 and 4.9 °C by 2100 under the RCP4.5 scenario, along with up to a 25% increase in winter precipitation (Christensen et al., 2013), which is expected to fall as snow.

We conducted this study using a factorial study design with three factors (growing season warming - "warming" hereafter, spring snow addition - "snow addition" hereafter, and growing season yak grazing -"yak grazing" hereafter), fully crossed to yield 8 treatments (warming, snow addition, yak grazing, warming + snow addition, warming + yak grazing, snow addition + yak grazing, warming + snow addition + yak grazing, and control without warming, yak grazing, or snow addition). Each of the eight treatments was assigned to 8-m diameter plots in a randomized block design (Fig. S2a). This randomized block design was used to account for topographic and potentially edaphic variability in the study area - specifically along the hillslope and with distance from the adjacent streambed. This resulted in eight blocks, each containing one replicate of each of the eight treatments, for a total of 64 plots. Note that we originally had 16 treatment combinations, which included pika exclusion for half of the eight blocks. However, the pika treatment was ineffective (Dorji et al., 2013; Hu et al., 2013), and we did not attempt to exclude pikas from any part of the experiment after 2012, thus we did not include pika effects in our data analyses.

We established the treatments starting in June 2009 (Dorji et al., 2013; Hu et al., 2013). Each plot contained five permanent, systematically-located, 1-m-diameter subplots (Fig. S2a). Although we treat

We hypothesized that experimental warming during the growing

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