DISSERTATION

CASCADING EFFECTS OF CHANGING CLIMATE AND LAND USE ON ALPINE ECOSYSTEMS AND PASTORAL LIVELIHOODS IN CENTRAL TIBET

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ABSTRACT

CASCADING EFFECTS OF CHANGING CLIMATE AND LAND USE ON ALPINE ECOSYSTEMS AND PASTORAL LIVELIHOODS IN CENTRAL TIBET

Changing climate and land use practices are re-shaping the dynamics of social-ecological systems globally, with alpine regions and subsistence-based communities likely to be among the most vulnerable to the impacts of these changes. The Tibetan Plateau exemplifies a system in which climate warming and projected increases in snowfall, coupled with natural resource management policies that reduce livestock herd sizes and mobility, will have cascading effects not only on the livelihoods of local pastoralists, but also on other globally important ecosystem services that Tibet's alpine meadows provide. To improve our understanding of the impacts of altered climate and grazing restrictions in central Tibet, I conducted interviews with local herders about their knowledge of environmental changes and the ways in which this knowledge is produced and transmitted within the community, performed a 5-year climate change and yak grazing experiment, and carried out observational measurements in plant communities around the landscape. I found that herders are well attuned to the changes that are the most threatening to their livelihoods, and they transfer this knowledge of environmental change within their village primarily as a means for seeking adaptive solutions, rather than for learning from others. Results from the experiment and landscape observations corroborate much of the herders' understandings of the factors driving undesirable changes in the alpine meadows. From the experiment, I found positive feedbacks between yaks, vegetation, and nitrogen cycling, indicating that these meadows are well adapted to moderate grazing under ambient climate conditions. However, they are particularly sensitive to warming-induced reductions in soil moisture. Although decreased plant production and ecosystem CO_2 fluxes with warming were partially mitigated by additional snow before the start of the growing season, results from the landscape observations suggest that in the longer term, climate warming will likely decrease the quantity and quality of forage available to livestock and wildlife, while also reducing the carbon sink strength of alpine meadows in central Tibet. Therefore, my results indicate that instead of continuing to mandate livestock removals, which will do little to reverse undesirable ecological trends, more consideration needs to be given to climate change adaptation strategies for pastoral social-ecological systems in Tibet.

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TABLE OF CONTENTS

Chapter 1

Introduction

Climate and land use change are affecting social-ecological systems globally, but those at high elevations are likely to be especially vulnerable (Beniston, 2003; Körner et al., 2005; Löffler et al., 2011; Sala et al., 2000). The impacts of these changes will affect subsistence-based communities that depend directly on alpine ecosystems for their well-being, but they will also cascade to regional and global scales due to mountains' provision of critical ecosystem services (Körner et al., 2005). Understanding the ways in which these systems will respond to altered climate and land use conditions is a necessary step toward developing adaptation strategies to cope with the impacts of change (Naess, 2013; Smit and Wandel, 2006). Yet, prediction remains difficult due to the complexity of systems dynamics, unforeseen feedbacks, ecosystem heterogeneity, and data scarcity, particularly in rural and mountainous areas, (Klein et al., 2014; Löffler et al., 2011; Shaver et al., 2000; Smith et al., 2009; Zhou et al., 2008).

Ecosystem functioning at high elevations is often assumed to be constrained by cold temperatures, short growing seasons, and low nutrient availability to support primary production (Berdanier and Klein, 2011; Bowman et al., 1993; Ernakovich et al., 2014; Soudzilovskaia and Onipchenko, 2005). However, alpine organisms have evolved to cope with environments that would be considered extreme elsewhere (Bliss, 1962; Körner, 1998), and as a result, current alpine communities will be particularly sensitive to climate changes that alter the abiotic conditions to which they have become well-adapted (Elmendorf et al., 2012a). The higher temperature sensitivity of biological and chemical processes in cold environments will also contribute to how microbial and physiological functioning will be affected by climate warming (Kirschbaum, 1995), with cascading effects for vegetation production, nutrient cycling, and carbon sequestration (Shaver et al., 2000; Wookey et al., 2009). In addition, alpine ecosystems are made more vulnerable by their exposure to global climate change at a faster rate than lowland areas (Gottfried et al., 2012; Mountain Research Initiative, 2015).

Climate change will also interact with changes in land use to affect ecosystem functioning. Pastoralism is the dominant land use at high elevations globally, with an estimated 64% of rural mountain populations depending primarily on livestock for their livelihoods (Huddleston et al., 2003). Herbivory plays a strong role in structuring ecological communities and driving nutrient cycles (Robson et al., 2010), and in some alpine and tundra ecosystems, grazing may even mitigate the effects of climate change on plant communities (Dirnbock et al., 2003; Klein et al., 2007; Post and Pedersen, 2008). However, high-elevation pasture abandonment, decreased livestock mobility, and herd reductions are occurring in mountain systems around the world, driven by land management policies and other socio-economic factors (Dong et al., 2011; Klein et al., 2011; Lasanta-Martínez et al., 2005; Nautiyal and Kaechele, 2007; Streifeneder et al., 2007). This removal of livestock from ecosystems with long histories of grazing will further alter the tightly coupled relationships among biotic and abiotic factors, as well as above- and belowground processes, that determine rates of plant production and biogeochemical cycling (Bardgett and Wardle, 2003; Lamarque et al., 2014; Wookey et al., 2009).

Furthermore, people whose livelihood practices connect them closely to the land tend to hold rich local knowledge of their social-ecological systems and the ways in which they are changing (Berkes, 2009). This knowledge can be a crucial source of information to improve local strategies to cope with change, to inform regional adaptation efforts and, when appropriate, can be integrated with Western scientific understandings of ecosystem dynamics (Alexander et al., 2011; Boillat and Berkes, 2013; Klein et al., 2014; Laborde et al., 2012; Reid et al., 2009; Smith and Sharp, 2012). Thus, local ecological knowledge (LEK) is likely to arise as an important source of resilience to environmental change in marginalized systems that have little external support or access to necessary resources to facilitate adaptation efforts (Fu et al., 2012; Homann et al., 2008). However, although LEK is continuously produced and transmitted within communities, it is also subject to degradation by changing social institutions and livelihood practices (Fernández-Giménez and Estaque, 2012; Oteros-Rozas et al., 2013; Reyes-García et al., 2010; Reyes-García et al., 2007; Zent, 1999). The potential loss of this knowledge could in turn have cascading effects for human-environment interactions, ecosystem health and the continued provision of ecosystem services. Thus, processes of local knowledge production and sharing may serve as important precursors to coping with the impacts of global change in remote, alpine social-ecological systems.

The Tibetan Plateau contains the largest alpine ecosystem in the world (Miehe et al., 2008), and it has supported mobile pastoralists and their livestock for millennia (Miehe et al., 2009, 2014). Its alpine meadow ecosystems serve as a globally important carbon sink (Ni, 2002), but reports of grassland degradation suggest that the meadows' ability to continue providing critical ecosystem services could be threatened (Harris, 2010; Yundannima, 2012). Consequently, policies designed to reduce overgrazing have arisen partly as a means to combat further degradation of the meadows (Yan et al., 2005; Yangzong, 2006; Yundannima, 2012). These laws range from mandating the construction of fences to restrict mobility, to herd reductions, to complete grazing bans in some regions (Bauer and Nyima, 2010), and the scale of the grazing restrictions is expected to continue to grow (Qiu, 2014). The Plateau is simultaneously undergoing climate warming at rates above the global mean (Wang et al., 2008) and is projected to face up to an additional 2.0 ^{0}C of warming by 2035 and 4.9 ^{0}C by 2100, along with a 32% increase in precipitation, which is expected to increase most in winter and spring when it would fall as snow (Christensen et al., 2013). Most studies on ecosystem functioning and the effects of grazing and climate change in Tibet have been conducted in more mesic alpine meadows in eastern Tibet (e.g., Klein et al., 2007; Wang et al., 2012). My work, however, contributes a new understanding of social-ecological dynamics in a relatively more arid region of central Tibet, near Namtso Lake, in the Tibet Autonomous Region.

With this research I seek to improve our understanding of how pastoral, social-ecological systems in central Tibet will respond to changing climate and livestock management practices. I take an interdisciplinary approach by integrating data from three primary sources: interviews with local pastoralists; a fully factorial climate change and grazing experiment, in which I simulated climate warming, additional spring snow fall, and controlled yak grazing; and an observational study in different vegetation communities within the alpine meadow ecosystem at Namtso.

In chapter 2, I combine quantitative and qualitative methods to explore local pastoralists' observations of environmental change. As far as I know, this the first study to go beyond the content of Tibetans' LEK to also begin to examine the processes by which this knowledge is produced and transmitted within a Tibetan pastoral community, which yields insight into how these knowledge systems themselves may be changing. Next, in chapter 3, I present results from the climate change and grazing experiment that shed light on the mechanisms controlling plant production and biogeochemical cycling in central Tibetan alpine meadows. In chapter 4, I couple measurements from the experiment and from healthy, degraded, and shrub meadow communities around the landscape in order to extend the temporal and spatial scale of my findings. This approach allowed me to determine the causes of alpine meadow degradation, as well as to make predictions for how climate warming and livestock removal policies will likely affect forage production and carbon sequestration, two ecosystem services provided disproportionately by Tibet’s alpine meadows. Finally, in chapter 5, I synthesize my findings from the previous chapters and discuss how they support my conclusion that alpine meadow ecosystems are maintained by traditional grazing practices, but that ecosystem functioning and pastoral communities in Tibet are vulnerable to the impacts of climate change. These results highlight the need for collaboratively produced climate change adaptation strategies, rather than a continued focus on livestock removals, in order to maintain ecosystem functioning and improve the well-being of Tibetan pastoral communities facing the pressures of global change.

Chapter 2

Local knowledge production, transmission, and the importance of village leaders in a network of Tibetan pastoralists coping with environmental change[1]

"I've had a lot of experiences and have been paying attention since I was young. I've seen many changes."

- Tibetan pastoralist, age 55

2.1 Introduction

Global change is driving social-ecological systems outside of their historical range of conditions, thereby threatening ecosystem health and human well-being. Gradual increases in temperatures coupled with increasing climate variability and extreme events produce non-linear and often unpredictable ecological feedbacks that in turn interact with natural resource management practices to alter the functioning of ecosystems and social institutions (Nelson 2005, Christensen et al. 2013). Among the people most vulnerable to these changes will be those who depend directly on local ecosystem for their livelihoods (O'Brien and Leichenko 2000). Traditionally these same subsistence-based communities have had an intimate understanding of their environment that has allowed their long-term persistence (Berkes 2008), but these local knowledge systems are increasingly subject to degradation by rapidly changing social institutions (Zent 1999, Reyes-García et al. 2007, 2010, Fernández-Giménez and Estaque 2012, Oteros-Rozas et al. 2013). Furthermore, if traditional knowledge of the environment becomes less accurate under altered climate regimes, people previously seen as local experts may lose credibility within their

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[1] This chapter, co-authored with Ciren Yangzong and Julia A. Klein, is currently in review at *Ecology and Society*.

communities, and trust in local knowledge systems may be eroded (Kronik and Verner 2010). Yet, precisely because of the unpredictability of the local impacts of dynamic and interacting global change drivers, integrating already-existing local ecological knowledge (LEK) with continuous learning and production of new LEK will be critical to subsistence-based communities' ability to cope with and adapt to their changing environments (Crona and Bodin 2006, Berkes 2009, Boillat and Berkes 2013).

Local ecological knowledge, sometimes referred to as indigenous knowledge or traditional ecological knowledge, is a complex of knowledge, practices, and beliefs concerning the biophysical environment and humans' engagement with it (Berkes 2008). LEK is acquired through people's personal observations and experiences, but it is also transmitted through social networks, including learning from elders (Reyes-García et al. 2009), participation in natural resource management institutions (Fernández-Giménez 2000, Crona and Bodin 2006), and discussion with peers (Baival and Fernández-Giménez 2012). Thus, variation in individuals' LEK is explained not only by their livelihood practices and personal characteristics, but also by their ability to access information through their relationships to others (Atran et al. 2002, Crona and Bodin 2006, Hopkins 2011). These networks of information-sharing and learning may enhance households' or communities' resilience to the impacts of global change (Folke et al. 1998, Adger 2003, Baival and Fernández-Giménez 2012). However, power dynamics, local institutions, and government policies also affect the ability of LEK to inform climate change adaptation research, practices, and policies (Smith and Sharp 2012, Naess 2013).

The Tibetan Plateau exemplifies a social-ecological system facing a host of interacting social, political, and environmental changes that threaten its resilience, including the maintenance and ongoing development of LEK. Pastoralists have been herding livestock in Tibet for millennia, which has allowed communities to develop a reservoir of LEK that integrates both practical and cosmological concerns (Huber and Pedersen 1997, Byg and Salick 2009, Fu et al. 2012, Salick et al. 2012, Klein et al. 2014). However, significant climate warming along with changes in the timing and variability of precipitation (Wang et al. 2008, Christensen et al. 2013) are affecting ecosystem functioning (Klein et al. 2007, Wang et al. 2012, Wei et al. 2014). New rangeland policies are altering pastoralists' management of their herds and pastures (Yangzong 2006, Bauer and Nyima 2010, Klein et al. 2011, Cao et al. 2013). Increasing school enrollment and participation in off-range wage labor will likely further decouple young, rural Tibetans from close engagement with the land (Fischer 2011, Iselin 2011), limit their ability to learn from elders, and thus present additional ways by which LEK could be lost (Zent 1999, Reyes-García et al. 2007, 2010).

LEK is an especially important resource for understanding and responding to the impacts of global change in social-ecological systems such as Tibet, where there are a limited range of livelihood, natural resource management practices, and governance options due to political and biophysical constraints (Fu et al. 2012). The erosion of Tibetans' LEK, without replacement by the production of new knowledge suited to new circumstances, could reduce local capacity to cope with environmental changes and have cascading effects for ecosystem health and the provision of ecosystem services. LEK loss also represents a missed opportunity for Tibetan pastoralists' knowledge to inform and improve regional climate adaptation policies, as well as Western scientific understandings of the ways in which this remote system is being affected by global change (Homann et al. 2008, Reid et al. 2009, Fu et al. 2012, Laborde et al. 2012, Oba 2012, Smith and Sharp 2012, Klein et al. 2014).

With rapid social and environmental change occurring in subsistence-based communities around the world, it is critical to move beyond focusing only on the content of LEK to also incorporate a better understanding of the processes by which LEK is produced, transmitted, and used (Zarger and Stepp 2004, Berkes 2009, Naess 2013). Therefore, with this study I examine: (1) the environmental changes that central Tibetan pastoralists are observing and their perceptions of the drivers of these changes, and (2) the factors that influence how this knowledge of environmental change is acquired and shared through social networks. I discuss the implications of these trends for the continued resilience of Tibetan pastoral communities and other social-ecological systems under global change.

2.2 Methods

2.2.1 Study area

I conducted this research in one natural village (the smallest administrative settlement unit in Tibet) in Damzhung County in the Tibet Autonomous Region of China. It is one of six natural villages comprising an administrative village that covers approximately 600 km^2, has an average elevation of 5,000 meters above sea level, and spans alpine meadow and alpine steppe vegetation types. Administrative villages are the second smallest settlement unit and the highest administrative level at which leaders are elected by villagers, rather than appointed by higher officials. Each natural village has one leader and one representative to the administrative village committee, both of whom are also elected by villagers. Livestock herding is the primary livelihood practice, and children begin assisting their parents with herding at an early age. At the time of the interviews, this natural village had 38 households with 179 people and 3538 head of livestock (sheep: 60% of total animals, or 29% of the total sheep equivalent units (SEU); yaks: 27% of total animals, or 66% of the total SEU; goats: 13% of total animals, or 1% of SEU). Engagement in off-range, income-generating activities is becoming increasingly prevalent, primarily due to the village's proximity to a site sacred to Tibetan Buddhists that has been promoted as a tourist destination since the 1990s. This has created year-round and seasonal service-oriented economic opportunities for some households. The majority of adults in the village had never attended school, but reforms in 2007 made nine years of schooling compulsory for all children.

Recent national- and provincial-level policies have also affected mobility and herd sizes in the study village (Bauer and Nyima 2010). In 2005, Han Chinese government officials mandated the fencing of wetlands and established fixed territories for each village in the study area. The construction of fences between villages in 2008 further demarcated their boundaries. Households continue to make four longer-distance migrations per year, in addition to shorter, daily movements. The fences hinder movement for some who would like to move further with their herds into the mountains, while for others they reduce daily labor by allowing livestock to stay penned in the wetlands with less supervision. Herd sizes were capped at 40 sheep equivalent units per person (SEU) in 2005 and were lowered in 2011 by changing the SEU conversion rate for yaks.

2.2.2 Interviews

In 2012, I conducted structured interviews with 48 people about their knowledge of environmental change and how it is acquired and transmitted. The interviews were conducted in Tibetan by a native speaker. I attempted to interview all people 18 years of age or older in the village, but not everyone was able or willing to participate. As in other studies asking pastoralists about environmental change, women tended to opt out of the interviews, usually citing that they did not know how to answer the questions because they are not typically the primary herders in the household (Fernández-Giménez and Estaque 2012, Oteros-Rozas et al. 2013, Klein et al. 2014).

I interviewed 39 men and 9 women from 28 households in the natural village. Their ages ranged from 18 to 72, with a mean of 41 years. Half were heads of their household. Three held official leadership positions: one was the natural village leader, one had previously been the natural village leader for 29 years and was currently serving as representative to the administrative village committee, and one was the deputy administrative village leader. In addition, six others had served in leadership positions in the past. The majority (60%) spend most or all of their time herding livestock, while the others herd seasonally or not at all while they pursue other off-range economic opportunities. Although women also herd livestock in this community, their daily activities are usually closer to home and include milking and caring for livestock.

I asked about people's ways of learning about the environment, the changes they had observed in different climatic and ecological variables over their lifetimes, and the reasons for why these environmental changes are occurring. Closed-ended options for responses to questions about specific environmental changes included "increase/no change/decrease," or "earlier/no change/later," depending on the question. Enough people responded instead with "it depends on the rain" that I subsequently added this as another response option.

I also asked them to name the people within their household and village who were most knowledgeable about the climate and grassland ecosystem, to describe the type of knowledge typically held by women and by men, and, following the question format for information exchange used by Crona and Bodin (2006), to free list the people with whom they talk about the climate and grassland changes they observe.

2.2.3 Data analysis

2.2.3.1 Knowledge of environmental change

To determine the environmental changes on which the community agreed most, I used cultural consensus analysis (CCA), a type of factor analysis used to identify whether a group of people share a common understanding about a particular topic, and if so, the culturally appropriate responses within this group to a set of questions about the topic (Romney et al. 1986, Weller 2007). This approach has also been used in other studies to understand people's perceptions of climate change (Crona et al. 2013, Carothers et al. 2014, Klein et al. 2014). Here, I coded responses to the 50 multiple choice questions about environmental change as -1 for "decreasing" and "earlier," 0 for "no change," and 1 for "increasing" and "later." When people responded that an environmental change "depends on rain," meaning that it varies interannually with the weather, I coded these as "no change" for the CCA because they indicated that there was no single trend. To meet the assumptions of CCA, I removed questions and interviewees so that no interviewee had "don't know" or missing responses to more than 10% of the questions, which left 30 questions and 31 interviewees in the analysis (Miller et al. 2004). For the remaining missing responses, I assigned answers randomly (Weller 2007). I performed the CCA in Ucinet (v. 6.507) using the ordinal data model option (Borgatti et al. 2002).

The output from the CCA showed that the ratio of the first to second eigenvalue was 5.149, indicating that the data met the conditions for finding consensus around a single set of environmental changes observed by the interviewees (Weller 2007). The CCA then gives the strength of consensus among interviewees about the direction of change for each question, weighted by interviewees' "competence" scores. These scores are calculated for each interviewee based on the degree of his or her agreement with all other interviewees across all questions. This step effectively down-weights idiosyncratic responses in the data, including interviewees' guesses, as well as the random responses that I assigned to avoid missing values.

I also tested whether subgroups of people tended to respond more similarly to each other than to the community as a whole when asked about environmental changes. First I created a Gower dissimilarity matrix for nominal variables that compared responses among all interviewees who had answered all 50 questions ($n = 45$). For this I allowed "don't know" and "depends on rain" responses to remain in the data. Next I performed a cluster analysis on the dissimilarity matrix and used the Ward clustering algorithm to minimize within-group variance in responses while maximizing between-group variance. I used the pseudo-t statistic to determine the cut-off point at 6 clusters of people ($r^2 = 0.40$) and used ANOVAs to determine whether any of the resulting clusters tended to be more observant of environmental changes, as indicated by fewer "don't know" responses and more agreement on the direction of changing environmental trends. I performed these analyses in SAS (v. 9.3).

To elucidate interviewees' understandings of causal connections among different components of the social-ecological system, I followed a grounded theory approach (Corbin and Strauss 1990, Strauss and Corbin 1998). I iteratively coded interview transcripts in Atlas.ti (v. 7.1.8), first using *a priori* codes about components of the climate and ecosystem that were the focus of the multiple choice environmental change questions, and then inductively coding other themes that emerged frequently during the interviews, such as "conflict." This produced 23 codes in four general themes: climate, ecosystem, natural resource management, and knowledge. For each of the ten codes that were used most frequently, I populated the network view manager in Atlas.ti with their co-occurring codes and interview quotations. I then recorded all quotations referring to causal relationships among the codes and used these to interpret interviewees' knowledge of the drivers of the changes they observed. I undertook a similar process for analyzing interviewees' perceptions of differences in the types of knowledge held by men and women.

2.2.3.2 Transmission of environmental change knowledge in the social network

To examine with whom people share knowledge of environmental change, I created a full matrix of interviewees and their directional connections, or "ties," to others within and beyond the village who they reported seeking out to discuss changes. Many herders indicated that they discuss these changes with a few specific people, as well as with "all other herders they meet when out herding." The latter response was substantiated both by the frequency with which it was given and during participant observations. To differentiate those who were named specifically from those who were mentioned more generally, I assigned different weights to the ties between people according to the apparent strength of their connection. For each interviewee, I assigned the following tie weights: three to those who were named specifically; two to people who appeared to be named because they were present during the interview (n = 8); one to all other people in the network who were full-time herders if the interviewee responded that he talked with all other herders he met; zero to people who were not named.

I calculated Freeman degree centrality scores, using non-symmetric, weighted ties, to assess the degree to which people seek out and are sought out by others to discuss environmental change. To determine whether people who observed the same environmental changes were also more connected to each other in the social network, I calculated the density of connections for the whole network, as well as within and between the four dominant livelihood groups (mostly herding, current village leader, mostly not herding, women in the home) and the six knowledge groups produced by the cluster analysis. I tested whether any of these groups' members were more densely connected with each other than would be expected by comparing each group's internal density value to the overall network density. Sample variances for each group's density were generated by bootstrapping 5000 random samples from the observed network data. For density analyses I used unweighted ties between actors to capture the degree to which all possible connections between people were actually being used. All network analyses were performed in Ucinet (Borgatti et al. 2002), and network diagrams were created with Netdraw (Borgatti 2002).

2.2.3.3 Relationships among demographic and knowledge data

I tested for relationships between demographic variables and metrics derived from the cultural consensus, cluster, and social network analyses. I used chi-square tests to examine relationships among categorical variables and ANOVAs to test for relationships between continuous and nominal variables, with the Tukey-Kramer adjustment for multiple comparisons. I used a logistic regression to test for factors associated with being nominated as an expert herder, and I used multiple linear regressions to test for demographic predictors of degree centrality in the social networks. The following independent variables were included: dominant livelihood practice, daily herding distance (near vs. far), age, whether people had learned LEK from older generations, household herd diversity (calculated using the Simpson diversity index; Ndikumana et al. 2000), and gender (degree centrality models only). Education level and literacy were negatively and positively correlated with age, respectively, and household sheep equivalent units per capita were positively correlated with herding distance, so these were not included in the models. All regression analyses used stepwise model selection with a significance threshold of 0.05 for parameters to be retained. I performed statistical analyses in SAS (v. 9.3) and made figures in R (v. 3.0.3) unless otherwise noted.

2.3 Results

2.3.1 Knowledge of environmental change

2.3.1.1 Consensus view of changes

CCA results indicate that people tend to agree on multiple indicators of alpine meadow degradation (Figure 2.1a). These trends include declines in beneficial properties, such as production of the sedge *Kobresia pygmaea* C. B. Clarke, which is the dominant plant species and primary forage for livestock in alpine meadows. When describing alpine meadow changes, people often referred to how forage plants are not as tall as in the past, and there are fewer flowers in general. They also strongly agreed that livestock milk production has decreased. In contrast, increasing trends were only observed for problematic elements of the system, such as the proliferation of plants that are toxic to livestock (*Oxytropis glacialis* Benth), lichens that form a black crust on the soil, and pikas, which many interviewees viewed as a rangeland pest.

People also tended to agree on the main climate trends (Figure 2.1b). They observed that precipitation has decreased, especially in winter. They reported decreases in winter temperatures, while summer temperatures have increased during their lifetimes. Some disagreed with the consensus view of colder winters; as one village leader put it, “people say that many years ago, you still weren’t warm enough wearing a *lokpa* [traditional sheep-skin robe]. Now you can be warm enough wearing Han Chinese clothes [that are less insulating]. So it must be warmer now than a long time ago.” Consistent with summer warming trends, people observed decreasing snow on permanently snow-covered mountains, which have a distinct term in Tibetan (*gangs ri*). Responses were nearly unanimous about rising water levels in the closed-basin lake. Although some recalled that the lake had started rising as early as the 1960s and 1970s, many reported relatively recent, rapid changes, such as newly constructed fences becoming submerged by the lake. One man said, “In the beginning I put prayer flags close to the water, but they were covered more and more every year. I moved them higher, and they were covered again.”

2.3.1.2 Drivers of ecological change

Interviewees attributed the grassland changes they had observed to the impacts of changing climate, but they viewed decreasing livestock health as a result of both environmental changes and changing land management practices (Figure 2.2). They described how the quality, quantity, and phenology of plants and the timing of livestock milk production all depend on the weather. Interviewees overwhelmingly attributed declining meadow health to decreasing precipitation. Overall, they said that less rainfall is responsible for decreases in flowers, medicinal and edible plants, and shorter heights of the dominant plant species, *K. pygmaea*. When lack of rain causes plants to die, lichen takes their place, forming a crust over exposed soil and dead root-mats. Toxic plants (*O. glacialis*) respond positively to drier conditions. People consistently listed *O. glacialis*, a type of locoweed (Lu et al. 2014), as the worst type of plant, and the local traditional animal doctor estimated that 10% of the village’s livestock die each year from eating *O. glacialis*. The many undesirable effects of reduced precipitation led one herder to comment, “If the grassland continues to degrade, then we will have to change our livelihoods. But if we have good rain, then this could reverse.”

Rather than linking changing temperatures to vegetation directly, people primarily connected temperature change to increasing snowmelt in the mountains. A subset of people also identified how increased mountain snowmelt runs off into the closed lake basin, thereby causing the lake to rise and inundate pastureland. Thus, interviewees view precipitation as directly affecting the quality and quantity of vegetation, while temperature indirectly affects the spatial extent of the grassland.

People more frequently described bottom-up effects of the grassland condition on livestock than top-down effects of grazing on the grassland. They agreed that livestock health, body size, and milk production are decreasing, and they mainly attributed these declines to insufficient access to forage and increases in toxic plants and livestock parasites. In addition to the role of weather in driving reductions in forage availability, some people also mentioned competition for forage among growing livestock populations as well as between livestock and pikas. One older man said, “Many years ago, because there weren’t as many livestock, livestock could choose the best grassland to eat. Now they can only eat to fill their stomachs, but they can’t choose the best quality [plants].” Fences that restrict livestock mobility were often cited as being bad for livestock because they restrict their ability to move and graze freely. Conversely, some said that fences are good because they encourage people to care for the land.

Although interviewees’ views on the relationships between the grassland, livestock, and management practices were more mixed than their understanding of climate-grassland relationships, people were nearly unanimous in their concern that fences are creating conflicts over access to grazing land, which had not been a problem before the grassland reform. These conflicts primarily arise between people from different villages when livestock graze others’ land during their seasonal migrations. They also anticipate that fences will hinder their ability to move their livestock to snow-free areas during severe snowstorms, which has been an important coping strategy in the past (Yeh et al. 2014).

A few older people also invoked cosmological explanations for the changes they observed. Smaller body size of animals and declining soil quality were cited as specific markers of the coming of the "end of the world." They attributed the impetus for this decline to increased human and livestock populations, the presence of electricity and non-Tibetan people in Tibet, and desecration of sacred mountains by mining and of the sacred lake by swimming and washing in it.

2.3.2 Knowledge subgroups

Although results from the CCA indicate the environmental changes on which the community agreed most strongly overall, I was also interested in whether the heterogeneity in interviewees' responses could be explained by the existence of subgroups of people who hold different knowledge from the consensus view. First, I briefly examine whether men and women are perceived to hold different LEK in this community. Next, I identify who are regarded as LEK experts. Finally, I determine whether other individuals emerge as particularly knowledgeable about environmental changes based on responses to closed-ended questions and examine the additional insights they provide.

When asked about gender differences in LEK, men and women alike agreed that men know more about everything related to the climate and grassland, though women know more about caring for livestock. Indeed, I found that men were often unable to answer questions about changes in livestock milk production and tended to defer to women in the household, whereas women often said that they could only answer these milk-related questions. One herder, who made frequent reference to the LEK he had learned from his own father, explained another dimension of these gender differences beyond household labor division: "If you have lots of traditional customs and observations, then you must teach your sons. Daughters get married and leave the family, so the family knowledge must be passed on to the sons."

When interviewees were asked to name those who know the most about climate and the grassland, ten men were nominated by at least one person outside of their own household. Three of the ten people were current village leaders, six were full-time herders, and one was an elderly man no longer actively engaged in herding. Due to the unique role that current village leaders play in the social network (as described below), I removed them from all subsequent analyses on the remaining seven "expert herders" to avoid confounding interpretation of results. However, the following significant predictors of "expert" status remain the same whether the current leaders are included or excluded from the regression. The "experts" tend to move longer distances daily with their livestock ($\chi^2 = 6.80$, df = 1, $p = 0.009$) and are significantly older ($\chi^2 = 5.54$, df = 1, $p = 0.02$) than non-experts. The odds of someone being nominated as an expert increase by a factor of 2.9 with each 10-year increase in age. The expert group also has a significant number of people who were village leaders in the past ($\chi^2 = 20.72$, df = 1, $p < 0.0001$). The expert herder group's knowledge of environmental change was similar to the consensus view.

The similarity of interviewees' responses across 50 environmental change questions produced six knowledge clusters (Table 2.1). If clusters contain people who gave more "don't know," "no change," or "depends on rain" responses, this indicates that they may be less knowledgeable about longer-term environmental trends than clusters of people who gave more "increase," "earlier," "decrease," and "later" responses. Theoretically, any of the environmental changes could have increasing or earlier trends, but these responses were used infrequently by all interviewees, and there were no significant differences in the frequency with which any group reported these trends ($F_{5,39} = 1.82$, $p = 0.13$). "Decrease" and "later" responses were reported more often, and Group A observed significantly more of these trends than any other group (Table 2.1). On average, Group A's members responded with "don't know" only 8% of the time, less than any other group, which further indicates that people in this cluster appear to be most knowledgeable about directional changes in the environment.

Group A agreed strongly about the trends detected by the consensus analysis as well as about other questions that were excluded from the CCA due to too few responses. For example, Group A detected a suite of phenological trends that were not captured well by others, including a shortened duration of lake ice in winter and a delayed, shorter growing season in summer (Figure 2.3).

2.3.3 Production and transmission of local ecological knowledge

2.3.3.1 Learning LEK

Most interviewees (64.4%) reported learning about LEK from elders in the community, saying that oral teaching is a nomad custom, and people always meet and talk together about the land. They also learn from personal observations, starting in childhood when they "play in the grassland and learn on their own." Yet, interviewees expect that these modes of LEK acquisition will decline, since children today are learning less about the environment due to being in school and generally paying less attention to the grassland. As one herder put it, "Old people have lots of experiences, and young people have good educations." Among all people in the interview households (n = 88), only 16% of those over the age of 30 had ever attended school, and most had gone for a few months or less. In contrast, of the 23 children between 7-17 years of age in the interview households, 87% had attended at least some primary school, with several advancing to middle and high school. Some interviewees said that they wanted young people to return to herding eventually, but others had aspirations for them to participate in off-range livelihood activities if they were able to get a formal education. One man whose household engages only in the local tourist economy confirmed that people who already live at the sacred/tourist site, rather than herding, “don’t talk about the climate and grassland anymore.”

2.3.3.2 Sharing LEK in the social network

Livelihood activity is a strong predictor of who is most sought out (in-degree) to discuss environmental changes in both the climate (full model $R^2 = 0.85$, $F_{3,42} = 86.49$; livelihood $p < 0.0001$) and ecology networks (full model $R^2 = 0.88$, $F_{3,42} = 107.22$; livelihood $p < 0.0001$). Among the four livelihood groups, current village leaders are significantly more sought out than anyone else, followed by full-time herders, who are significantly more sought out than people who are mostly not herding and women who tend to stay at home (Table 2.2). Those identified as expert herders are also more sought out than non-experts are (climate network $F_{1,43} = 18.29$, $p = 0.0001$; ecology network $F_{1,43} = 6.17$, $p = 0.02$).

Demographic variables are less able to predict the degree to which people seek out others (out-degree) in the climate ($R^2 = 0.24$, $F_{4,41} = 4.61$) and ecology networks ($R^2 = 0.12$, $F_{3,42} = 2.99$). The most significant predictor was that people who learned LEK from older generations sought out more people to discuss climate changes ($p = 0.008$). Livelihood practice was also significant in both the climate ($p = 0.03$) and ecology networks ($p = 0.04$), with full-time herders seeking out significantly more people than non-herders and women do (Table 2.2). Status as an expert herder was not a significant predictor of out-degree scores.

The six knowledge clusters were not significantly different in the degree to which their members are sought out by others in the climate or ecology networks, nor for how much they seek out others in the climate network. However, in the ecology network, people in the “observant” group (A) seek out significantly more people than do those in the youngest group (B; $F_{5,39} = 2.79$, $p = 0.03$).

Overall, centrality scores show that village leaders, full-time herders, “expert” herders, people who learned LEK from elders, and members of the “observant” group (A) are more central to the network because of their higher degree of connection to others (Figure 2.4). Notably, former village leaders, unlike current village leaders, are not significantly more sought out than people who had never been leaders. Women tend to be more peripheral to the core structure of the network. This was partly an artifact of my inability to interview as many women as men, but it is also due to women seeking out only 1.4 people on average to discuss environmental changes, versus men seeking out 7.2 people on average. Furthermore, of the people who said they seek out others, 83% of women named members of their household, whereas only 41% of men named members of their household.

2.3.3.3 Linking knowledge sharing with knowledge holding

To determine whether people tend to hold the same LEK as others with the same livelihoods or as those with whom they discuss environmental changes, I compared the density of connections among the four livelihood groups and among the six knowledge clusters. Within- and between-group densities indicate the extent to which all of the possible connections are actually made between people in the network. The whole-network densities and subsequent results are not significantly different between the climate and ecology networks ($t = -1.35$, $p = 0.16$), so I only report results for the ecology network.

Densities show that herders talk more among themselves than with non-herders and that they also seek out the village leaders at higher rates than any other livelihood group does (Table

2.3). The density of connections among herders, among village leaders, and between herders and village leaders are significantly higher than the average density of connections throughout the whole network. People who are not primarily engaged in herding activities and women who tend to stay in the home are less densely connected among themselves and with others in the network. There are no significant trends in the density of connections for herders nominated as "experts."

In contrast to the differences between livelihood groups, there are few differences in density among the knowledge groups (Table 2.4). Only Group C has marginally significantly more connections among its members than would be expected based on the density of the whole network. Furthermore, several knowledge groups' members are more densely connected to members of other groups than to members of their own. This demonstrates that although people in the knowledge groups have, by definition, tended to observe the same environmental changes as each other, they discuss these issues across knowledge groups.

2.4 Discussion

2.4.1 Importance of environmental change LEK

I found that rural Tibetans' LEK tends to correspond well with current Western scientific knowledge of environmental changes on the Plateau, in addition to suggesting areas that could benefit from further inquiry. Herders emphasized the importance of precipitation in controlling grassland dynamics in central Tibet, and this relationship is increasingly being examined by ecological studies (Dorji et al. 2013, Hu et al. 2013, Shi et al. 2014, Wei et al. 2014). Interviewees' observations of delayed and shortened growing seasons also continue to contribute to the debate in the scientific literature over the direction of phenological trends on the Plateau (e.g., Yu et al. 2010, Zhang et al. 2013, Klein et al. 2014). However, herders' perceptions of causal links between reduced precipitation, vegetation die-back, and expansion of lichen crusts call into question the Western scientific assumption that increasing coverage of lichen crusts can be attributed solely to livestock overgrazing (Unteregelsbacher et al. 2011).

Being well attuned to their environment has allowed Tibetan pastoralists to sustain their livelihoods under dynamic and extreme climatic conditions for millennia, and their LEK will likely be key to their continued resilience under global change. Put simply by one herder, "for nomads, everything depends on the weather." Since herders are keenly aware of the environmental trends that have the strongest effect on their daily lives, the changes for which they have a high degree of consensus and concern also point toward often under-studied trends that threaten social-ecological resilience. For example, although herders' perceptions of lake level rise corroborate results of hydrological studies (Zhang et al. 2011), their insights into the consequences of pasture inundation by lakes deserve further social-ecological research that can inform policy and land tenure decisions.

2.4.2 Understanding LEK production and transmission

These results suggest that processes relating to production and transmission of environmental change knowledge may have fundamental differences from other types of LEK that are more theoretical or temporally stable, such as forage plant identification and traditional livestock management practices (Molnár 2014). Having baseline knowledge of the environment is undoubtedly a prerequisite to being able to observe changes to it, and the majority of interviewees reported learning this foundational LEK from elders. The herders named as experts about the climate, pasture, and livestock are likely more knowledgeable about these domains due to their longer time spent herding and higher degree of mobility, and they were, in fact, relatively more sought out in the climate and ecology networks. However, these “experts” were not consistently more knowledgeable about environmental changes.

As in other pastoral systems, interviewees report acquiring much of their knowledge of environmental changes through personal observations (Fernández-Giménez 2000, Oba 2012). While the youngest knowledge group (B) had the least time to accrue observations of change and subsequently had the most “don’t know” responses,” the oldest groups (D and F) contain older men who are no longer herding as often as in the past and are therefore not updating their knowledge of subtle environmental changes as frequently as those who continue to herd more actively (Oteros-Rozas et al. 2013, Klein et al. 2014). However, these practice-based means of knowledge acquisition are also tempered by beliefs concerning the nature of the world (Huber and Pedersen 1997, Berkes 2008, Salick et al. 2012). Cosmological explanations were cited more frequently by older men, as well as by younger people referring to how elders’ views differ from their own understandings of environmental change.

Overall, the dense connections among herders and to village leaders, but not within knowledge groups, indicate that knowledge of environmental change is produced through personal observations and then discussed with others primarily so that actions can be taken, rather than for knowledge transmission per se. However, the group of people who emerged as most observant of climatic and ecological changes (Group A) tended to seek out more people on average to discuss the environmental changes they were observing, in spite of being relatively diverse in terms of their age, gender, herding experience, and primary livelihood practices. While this observant group included accomplished herders, it also included a 35-year-old woman who cares for livestock only during the winter and spends the rest of the year running a small business reselling store-bought goods to local herders. She described how her interactions with many villagers who come to her shop have allowed her to overhear and learn about the environmental changes taking place. Thus, people may arise as important holders and gate-keepers of environmental change knowledge through their observations while practicing subsistence-based livelihood activities, as well as through their connections to others. In particular, these results suggest that those who seek out more people in the network may also be the most knowledgeable about environmental changes, though I cannot determine the direction of causality; people may be more knowledgeable due to a greater degree of seeking out others to learn from them, or those who are already more knowledgeable may seek out more people with whom to discuss the changes they observe.

Although social network analysis is a useful tool for elucidating patterns of connection, it can also reduce complexity in a way that obscures other dynamics. For example, the members of knowledge group D ("neighbors") were not significantly densely connected to each other, which suggests that they did not hold similar knowledge due to having a high number of knowledge-sharing connections among themselves. Yet, five of this group's seven members are neighbors in the summer and winter pastures, and so the strength of their interpersonal relationships or the frequency with which they encounter each other to discuss these issues could be more important as a metric of knowledge transmission than the density of their connections alone. While I acknowledge that network density measures may fail to capture the importance of the quality of relationships for shaping peoples' LEK, it remains clear that village leaders are playing a unique role in the social network.

2.4.3 Political dimensions of global change knowledge and action

Current village leaders emerge as brokers who connect many pairs of actors in the network of people discussing environmental changes. It is possible that interviewees who had difficulty recalling with whom they had actually discussed environmental changes may have tended to default to naming leaders because this was a culturally expected response (Bernard et al. 1986). However, in spite of problems with any single interviewee's recall accuracy, people who were named the most frequently across all interviews are likely to be the people who were most sought out in the network in reality (Bernard et al. 1982). This strong tendency to consult with local leaders about environmental concerns has also been reported by Mongolian pastoralists seeking ways to cope with the changes they face (Baival and Fernández-Giménez 2012).

Current and former leaders were disproportionately nominated as experts about pastoral LEK, but on average, their responses to interview questions did not distinguish them as being exceptionally knowledgeable about environmental changes. Furthermore, former leaders were not disproportionately sought out within the network. This indicates that leaders' role as brokers has more to do with their current position of relative power and leadership than with their understanding of environmental change or other inherent traits associated with being elected as a leader. The one outlier was the current natural village leader, who in addition to being the youngest leader was also the only leader to be part of the "observant" knowledge group. Interviewees described how he encouraged them to inform him about their concerns about the changing ecosystem, and his more active engagement in the network relative to the other leaders may explain his comparatively greater knowledge of environmental changes.

Village leaders in Tibet form the only direct link between local and higher administrative levels. While leaders of the natural and administrative villages continue to be responsible for local decision-making, such as when to make seasonal migrations, they also act as conduits to transmit and implement natural resource management decisions made by the Chinese government. As the national and provincial government increasingly extends its reach into the management of and rhetoric surrounding Tibetan rangelands, it also affects the interplay of power, knowledge, and decision-making in what were historically relatively isolated parts of the Plateau (Klein et al. 2011, Yeh et al. 2014). For example, provincial-level government pamphlets about the role of overgrazing as a driver of grassland degradation are distributed to herders via the village leader, thereby introducing a new, authoritative source of knowledge that may be at odds with herders' own LEK. The apparent authority of governmental knowledge seemed to lead some interviewees to believe that administrators should also know how to solve undesirable environmental conditions, by, for example, curbing the spread of toxic plants. Therefore, as some herders look more toward external support to address environmental changes, they may also seek out village leaders as their closest link to government authorities with the perceived ability to "fix" environmental problems.

The environmental changes occurring in Tibet also have an explicitly political dimension, as climate change impacts on pasture resources are entangled with the effects of top-down natural resource management policies. As a result of the combined pressures of restricted grazing practices, declining rangeland health, and growing local human populations, people report having more problems with grassland management than in the past, which produces conflicts among people and leads them to seek out village leaders to resolve both environmental and interpersonal issues. As in other subsistence-based communities, social and political changes, such as population growth and the implementation of fences, may be perceived as having more pressing impacts on local livelihoods than the direct effects of climate change (Boillat and Berkes 2013, Boissière et al. 2013). A global meta-analysis also shows that land management practices have a stronger effect on grassland functioning than does climate change alone (Thébault et al. 2014). Thus, in a bureaucratic system in which local herders are the recipients of top-down land management decisions, village leaders emerge as being better positioned to attempt to address the environmental changes occurring and to seek adaptive solutions to them.

2.4.4 Implications for the future of LEK and adaptive capacity

LEK of past conditions, often held by elders and knowledge "experts," provides a reservoir of practical knowledge that could prove useful in response to current and future challenges (Berkes 2009, Fernández-Giménez and Estaque 2012), but it must also be updated with the production of new LEK relevant to changing environmental conditions. New education requirements that remove children from the rangeland at an early age to attend boarding schools pose a threat to their ability to continue acquiring LEK through personal observations, practices, and from elders. Whether members of this younger generation seek off-range employment or return to herding, they are less likely than in the past to hold the LEK necessary to aid this social-ecological system in coping with the challenges posed by global change (Reyes-García et al. 2007, 2010). Yet, young Tibetans seeking to navigate their changing identity as contemporary pastoralists may find innovative ways to couple the LEK of their elders with what they have learned in school (Iselin 2011), as well as through other experiences and connections, in order to bolster their communities' social and environmental well-being.

The extent to which community members sought out village leaders to discuss their observations of environmental changes indicates that strong local leadership could emerge as being particularly important for improving Tibetan pastoralists' ability to cope with and adapt to the interacting pressures of social, political, and environmental changes. Interviewees sought out not only the natural village leader who encouraged them to do so, but they also proactively sought out the higher-ranking representative to the administrative village committee and the deputy administrative village leader to discuss environmental changes. All three of these local leaders talked about ways in which they might be able to manage the rangeland more adaptively in order to alleviate the strain felt by villagers, though their ability to do so is constrained by the management parameters imposed by the regional and central government.

In Tibet and other social-ecological systems, open communication between villagers and leaders who bridge administrative levels is therefore likely be a useful strategy for creating adaptive solutions to the environmental problems that communities face (Reid et al. 2009, Baival and Fernández-Giménez 2012, Naess 2013). Yet, for substantive adaptations to be possible, it is also imperative that administrators beyond the local level are receptive to LEK from village leaders and other local-level stakeholders.

2.5 Conclusion

Tibetan pastoralists hold varied knowledge of environmental changes, but they have strong consensus on trends that are most threatening to the sustainability of their livelihoods, and which thus represent key areas for further collaborative inquiry. Their environmental concerns are also entangled with land management practices and policies, which they often view as more pressing than the direct impacts of climate change alone. Local knowledge of these complex and interacting global change factors appears to be held and shared differently than other types of more temporally stable LEK. A diverse group of people, rather than those perceived as experts about local pastoral knowledge, emerged as being the most knowledgeable about environmental changes. Although members of this observant group also tended to seek out more people to discuss ecological changes, overall, people were not primarily learning about these changes through talking with others. Instead, the disproportionate degree to which people sought out local village leaders reveals that they share this knowledge more as a precursor to taking action, and that local leaders are emerging as brokers of environmental change knowledge. Local leaders' ability to act as conduits for knowledge exchange within and beyond the village thus suggests that in small and relatively marginalized communities, leaders can play a key role in aggregating LEK from many peoples' observations. When possible, this knowledge can then be used to develop adaptive local resource management practices, guide scientific inquiry, and collaboratively inform policy decisions, thereby enhancing communities' social-ecological resilience to the impacts of global change.

2.6 Tables

Table 2.1. Description of the six knowledge clusters determined by observations of environmental changes. Names are assigned to groups based on their defining feature, some of which are described under the social network results. Dominant responses were given significantly more by one group than by the others across all environmental change questions.

	Knowledge Group						Group Differences	
	A: Observant	B: Younger	C: Well-connected	D: Neighbors	E: Depends on rain	F: Older	Test statistic	*p*-value
Number of members	8	9	7	7	5	9		
Mean age (range)	39.3 (23-57)	31.1 (18-47)	41.6 (32-67)	48.6 (29-72)	38.2 (27-59)	49.8 (33-61)	$F_{5,39} = 2.20$	0.07
Number of current, former leaders	1, 0	0, 0	0, 0	0, 2	1, 0	1, 3	$\chi^2_5 = 14.21$	0.16
Number of "expert" herders	1	1	1	2	0	1	$\chi^2_5 = 1.93$	0.86
Number of full-time herders	5 (63%)	4 (44%)	4 (57%)	5 (71%)	2 (40%)	6 (67%)	$\chi^2_5 = 2.69$	0.75
Number of women	2 (25%)	1 (11%)	2 (29%)	0	2 (40%)	0	$\chi^2_5 = 6.80$	0.24
Dominant response	Decrease / Later***	Don't know**	Mixed	No change**†	Depends on rain*	No change**†		

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.0001$

† This response was given significantly more relative to Groups A, B, E, but not C.

Table 2.2. Mean (and standard error) in- and out-degree scores for each livelihood group in the climate and ecology social networks. Out-degree scores were log-transformed to normalize the data before performing statistical analyses.

	Livelihood Practice				**ANOVA**	
	Mostly herding	Current leaders	Mostly not herding	In the home	*F*-statistic	*p*-value
Number of people	27	3	12	6		
Climate in-degree	7.96 (0.54)	31.67 (1.61)	3.75 (0.81)	2.33 (1.14)	$F_{3,44} = 89.10$	$p < 0.0001$
Climate out-degree	12.07 (1.96)	5.00 (5.88)	7.42 (2.94)	2.50 (4.16)	$F_{3,44} = 3.78$	$p = 0.02$
Ecology in-degree	8.96 (0.52)	34.00 (1.55)	3.58 (0.78)	3.17 (1.10)	$F_{3,44} = 111.24$	$p < 0.0001$
Ecology out-degree	13.48 (2.44)	6.00 (7.31)	6.67 (3.66)	3.17 (5.17)	$F_{3,44} = 3.52$	$p = 0.02$

Table 2.3. Density of connections within and between primary livelihood groups in the ecology network. Values indicate the density of connections from people in each row seeking out people in each column. T-tests on bootstrapped data compare within-group density to the whole-network density of 0.114. The only between-group density that is significantly higher than the whole-network density is full-time herders' connection to village leaders (z = 4.12, $p < 0.001$).

	n	Livelihood Practice				t-test	
		Mostly herding	Current leaders	Mostly not herding	In the home	z-score	*p*-value
Mostly herding	27	0.234	0.284	0.04	0.037	z = 1.66	$p = 0.05$
Current leaders	3	0.012	0.833	0	0	z = 2.75	$p < 0.001$
Mostly not herding	12	0.09	0.139	0.038	0	z = -2.54	$p < 0.001$
In the home	6	0.019	0.056	0.014	0.033	z = -1.96	$p < 0.001$

Table 2.4. Density of connections within and between knowledge groups in the ecology network. Values indicate the density of connections from people in each row seeking out people in each column. T-tests on bootstrapped data compare within-group density to the whole-network density of 0.114.

		Knowledge Group						t-test	
	n	A	B	C	D	E	F	z-score	*p*-value
Group A	8	0.143	0.069	0.161	0.125	0.125	0.139	z = 0.41	*p* = 0.36
Group B	9	0.083	0.069	0.095	0.095	0.067	0.086	z = -0.78	*p* = 0.65
Group C	7	0.232	0.127	0.310	0.204	0.171	0.254	z = 1.62	*p* = 0.05
Group D	7	0.036	0.048	0	0.119	0.029	0	z = 0.07	*p* = 0.40
Group E	5	0.175	0.089	0.171	0.143	0.10	0.20	z = -0.17	*p* = 0.50
Group F	9	0.194	0.099	0.19	0.159	0.222	0.181	z = 0.54	*p* = 0.28

2.7 Figures

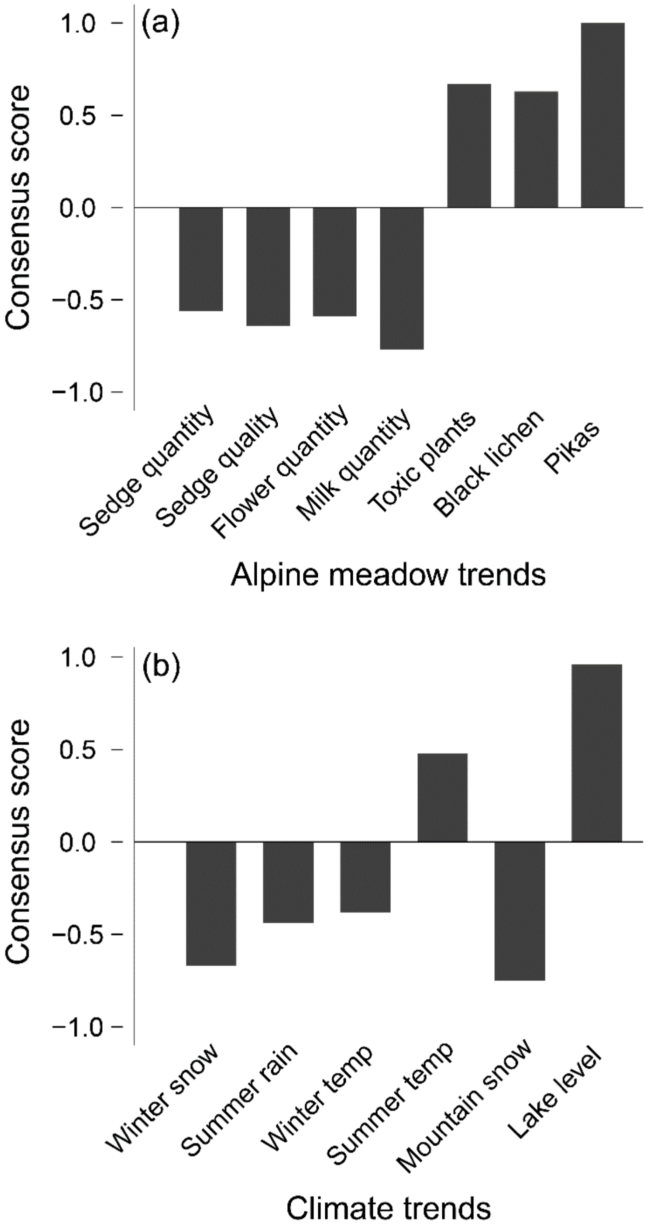

Figure 2.1. Predominant observations of (a) alpine meadow and (b) climate trends from the CCA. Scores closer to 1 indicate strong consensus on an increasing trend, scores closer to -1 indicate strong consensus on a decreasing trend, and scores closer to zero indicate either observations of “no change” or a mix of “increase” and “decrease” responses.

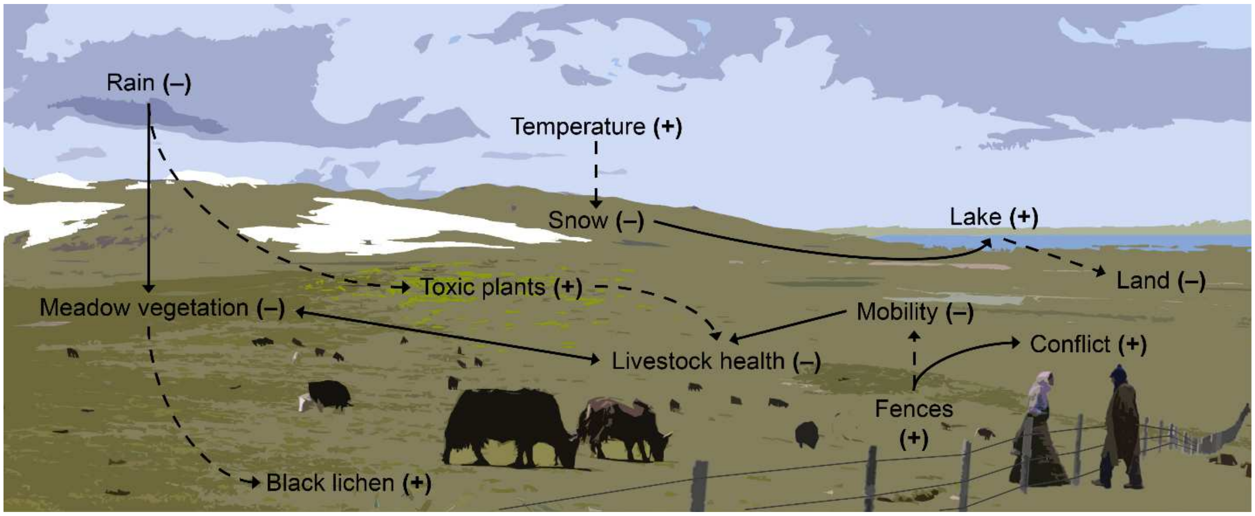

Figure 2.2. Conceptual model of the drivers and consequences of environmental changes, according to interviewees. Arrows with solid lines represent promoting relationships between system components, and arrows with dashed lines represent inhibiting relationships. Pluses indicate increasing trends, and minuses indicate decreasing trends.

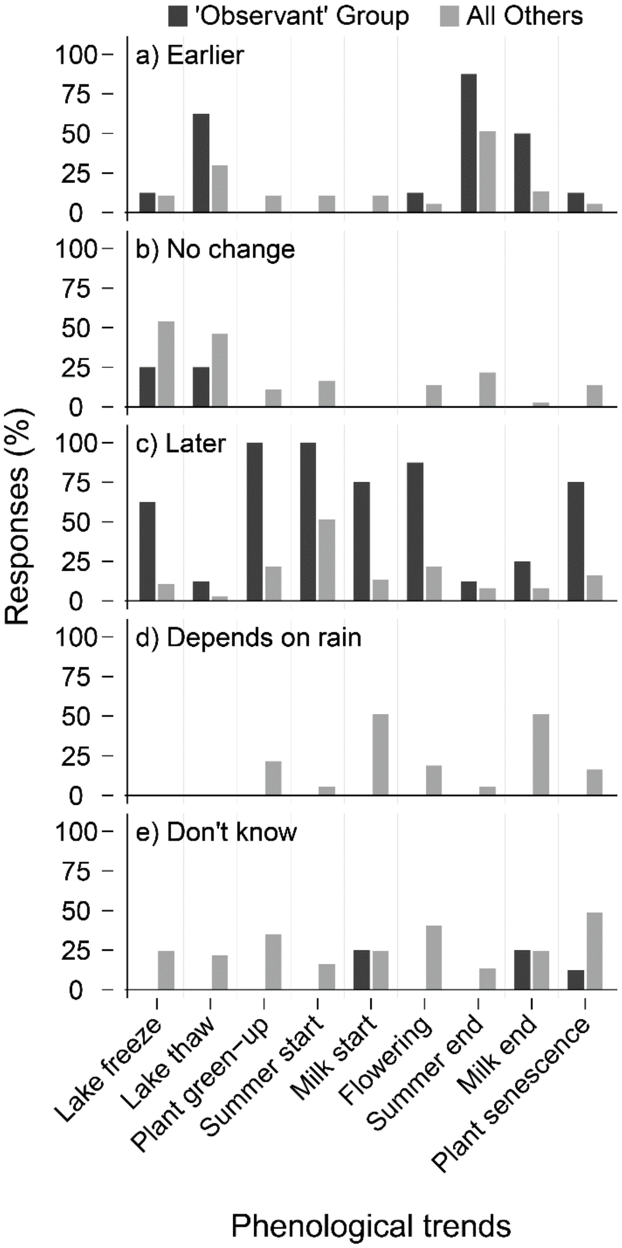

Figure 2.3. Seasonal trends observed by knowledge group 1, the "observant group" (black), and all others (gray). Panels (a-e) show closed-ended response options. Phenological events are arranged in order of their occurrence, starting in January and ending in September.

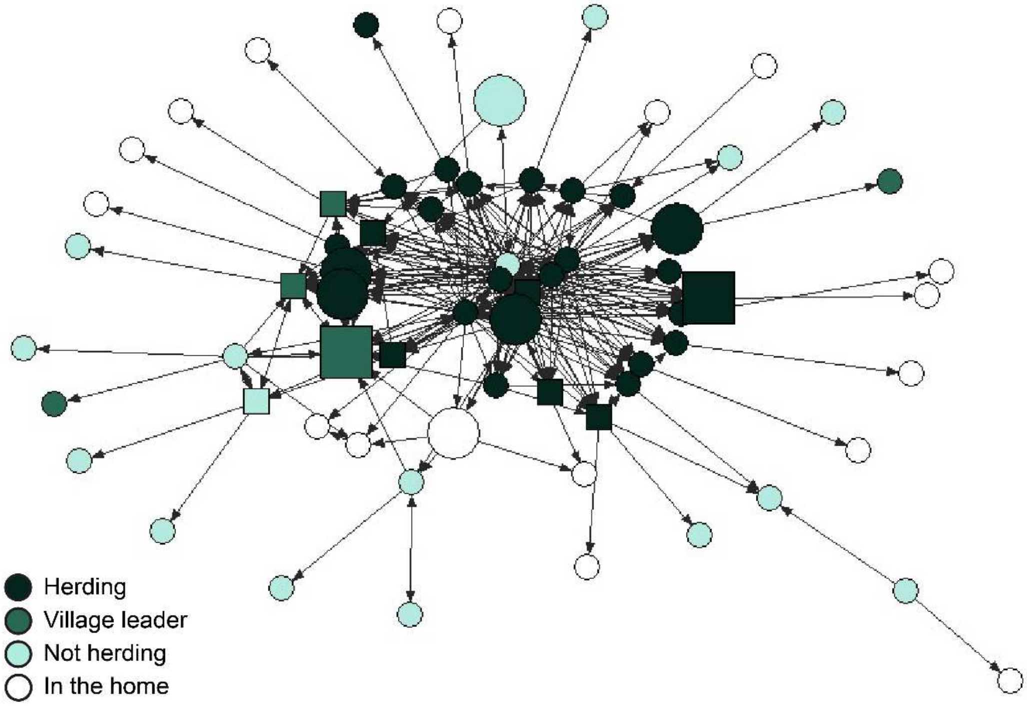

Figure 2.4. Social network of interviewees and others with whom they talk about climate and ecological changes. Nodes represent individuals, and arrows indicate directional connections between people. Squares show people nominated as LEK experts. Larger nodes are members of the "observant" group, and color is scaled from people who herd full time (dark) to men who spend little time herding and women who mostly work close to home (light). Two leaders from other villages are near the network perimeter.

Chapter 3

Plant production, nitrogen cycling, and CO_2 fluxes in Tibet's alpine meadows are maintained by yak grazing but vulnerable to climate change[2]

"Probably the soil quality is getting worse and worse. That's why the grasslands are not as good, and then of course the livestock quality is not as good."

- Tibetan pastoralist, age 55

3.1 Introduction

3.1.1 Climate and grazing controls on tundra ecosystem functioning

Organisms in alpine ecosystems are well adapted to low temperatures, short growing seasons, and in many cases, to traditional land uses, such as livestock grazing, that have been practiced in these systems for millennia (Bliss, 1962; Körner, 1998; Miehe et al., 2009). Consequently, changing climate and land use practices will alter the tightly coupled relationships between abiotic and biotic and above- and belowground processes that have evolved in these high-elevation systems (Bardgett and Wardle, 2003; Elmendorf et al., 2012a; Gottfried et al., 2012; Robson et al., 2010; Wardle et al., 2004). Changes in these relationships will have cascading effects on production, community structure, nutrient cycling, and other ecosystem services on which humans depend (Beniston, 2003; Lamarque et al., 2014; Smith et al., 2009; Wookey et al., 2009), necessitating the need for an increased understanding of how climate and land use changes will interact to impact alpine ecosystem functioning.

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[2] This chapter will be submitted for publication with co-authors Beth A. Roskilly, Jia Hu, Tsechoe Dorji, and Julia A. Klein.

Short growing seasons and low resource availability limit production in alpine environments (Berdanier and Klein, 2011), making them particularly sensitive to changes in climate (Körner et al., 2005; Sala et al., 2000). Due to plants' physiological adaptations to low soil moisture (Oberbauer and Billings, 1981), in the past drought stress was considered to be uncommon in low-stature alpine vegetation, even in arid regions (Bliss, 1964; Sveshnikova, 1973). Instead of experiencing direct water limitation, plant and microbial growth in tundra ecosystem is commonly thought to be more constrained by the availability of nutrients, such as nitrogen (N) (Bowman et al., 1993; Shaver and Chapin, 1980; Soudzilovskaia and Onipchenko, 2005). Nitrogen availability is in turn affected by soil moisture and temperature, which interactively control rates of soil organic matter decomposition, N mineralization, nitrification, denitrification, and diffusion of N through the soil to reach plant roots (Bardgett et al., 2007; Chapin et al., 2002; Fisk et al., 1998; Malhi et al., 1990). Thus, rather than affecting plant water status by reducing turgor, soil moisture limitation is more likely to reduce alpine plant productivity indirectly by limiting nutrient availability in the soil (Körner, 2003). Although warmer temperatures may accelerate rates of N mineralization, thus making more inorganic N available to plants (Lu et al., 2013; Nadelhoffer et al., 1991; Rustad et al., 2001), warming can also have opposing effects on N availability if it dries upper soil layers (Saleska et al., 1999) or drives shifts in species composition and changes in plant tissue stoichiometry that increase the recalcitrance of litter for decomposition (Cornelissen et al., 2007; Cornwell et al., 2008). Therefore, projected climate changes will likely affect the availability of soil resources to support vegetation production in alpine ecosystems.

In ecosystems with long histories of grazing by wildlife and livestock, herbivores may also stimulate plant growth and accelerate nutrient cycling through their effects on vegetation and soil microbial communities (Bardgett and Wardle, 2003; McNaughton, 1979; Milchunas and

Lauenroth, 1993; Ruess and McNaughton, 1987), but the ability of grazing to increase primary production also depends on other environmental conditions. Theoretical and empirical work suggests that grazing should promote aboveground net primary production (ANPP) when herbivores increase a limiting resource, such as nitrogen (De Mazancourt et al., 1998), or when soil fertility is already high and soil moisture is adequate (Augustine and McNaughton, 2006; Bonnet et al., 2010; Chapin and McNaughton, 1989). In addition to sufficient availability of resources, temporally intermittent, relatively high rates of consumption by herbivores may be required to maintain positive feedbacks between grazing and the processes driving plant growth and decomposition (Augustine and McNaughton, 1998; Bardgett and Wardle, 2003; Wardle et al., 2004). Intermittent grazing in livestock production systems is achieved through extensive management practices, which also tend to promote fungal-dominated microbial communities (Bardgett and McAlister, 1999) that increase nitrogen cycling efficiency by enhancing immobilization by microbes and plant roots while reducing losses to leaching and denitrification (de Vries et al., 2012; van der Heijden et al., 2008). Thus, grazers can serve as important mediators of ecosystem functioning, but their effects on plant production and biogeochemical cycling interact with abiotic controls and may differ under different management regimes.

Increased rates of nutrient cycling with grazing can also alter community structure by creating positive feedbacks between plant growth, palatability, and herbivore preference, leading to a competitive advantage for grazing-tolerant species (Augustine and McNaughton, 1998; McNaughton, 1984). Selection for grazing-tolerant traits, such as short-statured, prostrate plants with stoloniferous and rosette architecture (Díaz et al., 2007) should also confer drought tolerance because short, dense vegetation with high belowground nutrient reserves are adaptive not only for plants exposed to disturbances, such as grazing, but also for avoiding or tolerating stressful environments (Augustine and McNaughton, 1998; Coughenour, 1985; Grime, 1977; McNaughton, 1984; Milchunas et al., 1988)[3]. Grazing may also promote selection for drought-tolerant traits directly by aridifying the ecosystem through two pathways: via higher rates of evaporative losses when grazers remove biomass from the canopy, and via reduced water infiltration to roots when trampling compacts the soil (Veldhuis et al., 2014). Similarly, convergent selection for grazing-tolerant and cold-tolerant traits likely occurs in alpine vegetation. Short, dense plant canopies selected for by grazing are also adaptive in cold environments because they can retain heat by remaining relatively de-coupled from atmospheric mixing (Chapin et al., 2002; Körner, 2003). The resulting low-stature alpine turf systems are also more resilient than alternative canopy architectures to herbivore trampling (Körner, 2003). Consequently, selective pressures from grazing and dry and/or cold climates can converge to promote dominance of palatable, short, dense vegetation, which may lose its competitive advantage under altered climatic and land use conditions.

The species that are most abundant in a community will drive the bulk of ecosystem functioning and thereby the provision of ecosystem services, such as carbon sequestration (Grime, 1998; Smith and Knapp, 2003; Winfree et al., 2015). For example, a shift toward more drought- or grazing-tolerant but less productive species in response to warming or changes in grazing intensity can lower the carbon sink strength of an ecosystem by reducing its net CO_2 uptake (Cahoon et al., 2012; Metcalfe and Olofsson, 2015; Saleska et al., 1999; Väisänen et al., 2014). Changes in multiple climate and land use factors can also interact in the ways that they affect carbon cycling. Grazing may suppress shifts in composition toward more productive species that

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[3] It should be noted that when ecosystems have experienced long evolutionary histories of exposure to potentially harsh or disruptive conditions, such as low temperatures and chronic grazing, these do not truly represent "stresses" or "disturbances" if the organisms have become adapted to this environment (Körner, 1998, Milchunas et al., 1988).

would otherwise occur in response to warming, thereby counteracting the effects of climate change (Cahoon et al., 2012), or grazers may alleviate nitrogen limitation to support increased gross primary production (GPP) under warming (Väisänen et al., 2014). Increased precipitation in the form of spring snow may alleviate warming-induced drought to drive higher rates of GPP (Sloat et al., 2015), or alternatively, increased snow can compound the effects of warming on ecosystem respiration (ER) to driver even higher rates of CO_2 efflux (Welker et al., 2000). Therefore, the direct, indirect, and interactive effects of climate and land use will alter ecosystem functioning through their impacts on resource availability, community composition, and physiological processes, such as photosynthesis and respiration. The complexity of these processes make it difficult to predict outcomes for a particular system, but if a single species has strong dominance in the community and is sensitive to changes in climate or land use, then its response to changing conditions should have particularly strong and cascading impacts on the whole ecosystem.

3.1.2 Tibet's alpine meadows

Alpine meadows on the Tibetan Plateau exemplify a system that is being rapidly exposed to changes in climate and land use that will affect ecological processes and the services on which people depend, including forage production for livestock and carbon sequestration to prevent further atmospheric CO_2 accumulation and climate warming. Tibet's alpine meadow plant community type comprises the largest alpine ecosystem in the world, covering 450,000 km^2 (Miehe et al., 2008, 2014). It has co-evolved with wildlife and livestock herbivores for thousands of years, leading to a grazing-tolerant vegetation assemblage (Miehe et al., 2009, 2014). Alpine meadows are strongly dominated by a single species of rhizomatous, turf-forming dwarf sedge, *Kobresia pygmaea* C. B. Clarke, which is the preferred summer forage of livestock and wild herbivores (Kaiser et al., 2008; Miehe et al., 2008, 2014). *K. pygmaea* is well adapted to its cold environment and to herbivory, with high rates of tetraploidy and clonal reproduction, a persistent seed bank, inflorescence production resilient to grazing, and improved germination after seeds undergo processes similar to those that would occur if passed through the gut of a herbivore (Fawcett and Van de Peer, 2010; Seeber et al., 2015). Consistent with predictions for grazing-tolerant species, its cover and belowground allocation of resources also increase when grazed by livestock (Gao et al., 2008; Hafner et al., 2012). Partly as a result of these adaptive mechanisms of the dominant species, even in spite of the short growing season during which vegetation is photosynthetically active, the alpine meadows are a significant carbon sink (Kato et al., 2006), storing 26% of the carbon in China's grassland soils (Ni, 2002).

Abiotic conditions vary across the distribution range of Tibet's alpine meadows due to a strong east-west precipitation gradient, these differences should mediate interactions among vegetation, climate, and grazing (Saccone et al., 2014). Observational transects across the Plateau's rainfall gradient indicate that precipitation and soil moisture are strongly correlated with net primary production (Luo et al., 2009; Shi et al., 2014; Yang et al., 2009b), rain use efficiency (Yang et al., 2010), N availability (Baumann et al., 2009), and soil respiration (Geng et al., 2012) at a regional scale. Water is found to be most limiting to plant growth at drier sites, whereas N only becomes limiting when soil water is sufficient (Luo et al., 2009). The start of the growing season is more sensitive to temperature in mesic areas, whereas plant green-up is more sensitive to preseason precipitation in more arid parts of the Plateau (Shen et al., 2015). In drier, central Tibetan meadows, earlier and increased vegetation production in the summer following large snowstorms provides further observational evidence for the importance of soil moisture to support plant growth in more semi-arid alpine meadows (Klein et al., 2014). Vegetation species composition also changes along this precipitation gradient (Miehe et al., 2011), with evidence that species in more mesic, eastern meadows tend to have more competitive growth strategies than those in relatively more arid central Tibet (Grime, 1977; Klein et al., 2007; Wang et al., 2012).

However, changes in climate and land use practices will interfere with the ways in which alpine meadows functioned historically. The Plateau has already undergone significant climate warming since at least the 1960s (Wang et al., 2008), and temperatures are projected to continue to increase at rates greater than the global average, reaching up to 2.0 ^{0}C warmer by 2035 and 4.9 ^{0}C by 2100 (Christensen et al., 2013). The timing and amount of precipitation is also changing, with increased winter snow depths and spring precipitation, but strong decreases in summer rainfall since the 1960s (Qin et al., 2006; Xu et al., 2008). Climate models project precipitation increases of up to an additional 35% annually on the Plateau by 2100 (Christensen et al., 2013). Simultaneously, policies are significantly reducing the mobility and herd sizes of pastoralists, and grazing bans have been established in some regions in an attempt to reverse observed trends of declining grassland production (Bauer and Nyima, 2010; Klein et al., 2011). Livestock removal will not only directly affect the livelihoods of millions of Tibetan pastoralists (Miller, 2000), but will also interact with climate change impacts to alter the conditions that were previously limiting or promoting to plant production and biogeochemical cycling. These effects may differ between relatively more mesic (eastern) and semiarid (central) regions of the Plateau.

Most of the ecological research on the Plateau to date has been conducted in more mesic, eastern meadows (e.g., Gao et al., 2008; Kato et al., 2006; Klein et al., 2007; Ren et al., 2009; Rui et al., 2011; Seeber et al., 2015; Wang et al., 2012). Many of these studies do not agree on the impacts of climate change and grazing, making it more difficult to extrapolate from their findings to drier meadows in central Tibet. While some studies from the eastern Plateau showed that grazing increases N mineralizing and nitrifying microbes, decreases denitrifying microbes (Yang et al., 2013), and that both grazing and warming increase net N mineralization (Rui et al., 2011), another found that neither grazing nor warming significantly affect N availability (Wang et al., 2012). Experimental manipulations find conflicting evidence for whether N is limiting to plant growth in eastern Tibetan alpine meadows (Ren et al., 2009; Wang et al., 2012). Contradictory results have also been found for whether warming and grazing each reduce or promote ANPP at the same site but in separate studies in eastern Tibet (Klein et al., 2007; Wang et al., 2012), while further west, exclusion of grazers increased total and *K. pygmaea* ANPP, with larger increases at sites with higher mean annual precipitation (Xiong et al., 2014).

The ways in which changes in grazing and climate affect vegetation production, composition, N availability and microclimate will also interactively drive ecosystem CO_2 fluxes. Manipulative studies suggest that at higher grazing pressures in eastern Tibet, soil CO_2 efflux may be reduced and less sensitive to increases in temperature in eastern Tibet (Cao et al., 2004), whereas in central Tibet, grazing removal could have little effect on net CO_2 exchange, at least in the short term (Ingrisch et al., 2015; Peng et al., 2014). A warming experiment in central Tibet showed that higher temperatures reduce net CO_2 uptake (NEP) by reducing GPP (Hu et al., 2013), while a two-year experiment from a more arid alpine meadow found that warming could, in fact, stimulate NEP via increasing GPP, but only in a wet year (Peng et al., 2014). Thus, the complexity of understanding the effects of multiple global change factors on these ecosystems is compounded by heterogeneous conditions and responses even within the alpine meadow zone.

With this study I seek to improve our understanding of how ecosystem functioning on the central Tibetan Plateau will be affected by changes in climate and livestock grazing that alter the conditions under which these alpine meadow systems evolved. I simulated spring snowstorms, climate warming, and livestock grazing removals within a fully factorial experiment. I use measurements of microclimate (soil moisture, soil and air temperature), vegetation (species and functional group ANPP, cover, leaf C:N and natural abundance C and N isotopes), soil resources (inorganic N supply rates, total soil N and C), and ecosystem CO_2 exchange as a means to investigate the mechanisms driving vegetation production and biogeochemical cycling in semi-arid alpine meadows and how these will be affected by changes in climate and land use. Building on predictions from theory and previous research in Tibet and across the tundra biome, I hypothesize that:

(1) Snow additions will alleviate pre-monsoon water limitation and increase nitrogen availability to support plant production and CO_2 uptake;

(2) Warming will increase temperature and decrease soil moisture and nitrogen availability, reducing plant production and net CO_2 uptake;

(3) Yak grazing will maintain the *Kobresia pygmaea*-dominated community, accelerate nitrogen cycling, and stimulate plant production if soil moisture is also sufficient;

(4) Single or interacting climate and grazing factors that produce a significant change in *K. pygmaea* dominance will drive ecosystem-level responses in production and CO_2 exchange.

Furthermore, I predict that the net effects of the two- and three-way combinations of climate and grazing treatments will depend on how they interactively affect the potentially limiting conditions of temperature, soil moisture, and nitrogen.

3.2 Methods

3.2.1 Study system

This study took place on the central Tibetan Plateau, near Namtso Lake and in the northern foothills of the Nyenchen Tanglha Mountains. This area is dominated by alpine meadows that are used as summer pastures by local pastoralists who herd yak, sheep, goats, and horses. The Plateau experiences a monsoon climate, with 60-90% of precipitation falling between June and September, during the vegetation growing season (Xu et al., 2008). Mean annual temperature is -0.5 ^{0}C, and mean annual precipitation is 461 mm (data from 2006-2013; NAMORS). This region is more arid than other alpine meadow ecosystems on the eastern part of the Plateau, where much of the previous research on the effects of grazing and climate warming has been conducted (Fig. 3.1; e.g., Haibei Alpine Meadow Ecosystem Research Station: Klein et al., 2007; Rui et al., 2011; Wang et al., 2012). As a result, alpine meadows in central Tibet, including my study site at Namtso, have a higher deficit in the amount of water available to meet evaporative demands and support plant growth (Fig. 3.1).

3.2.2 Experiment

To test the independent and interactive effects of climate change factors and livestock grazing in central Tibet, I set up a fully factorial experiment in 2009. The experiment covers approximately 1.8 ha and is located in an alpine meadow ecosystem at 4875 m a.s.l. (30.72 ^{0}N, 91.05 ^{0}E). It consists of three factors (summer warming, spring snow additions, and yak grazing), which are applied at the plot level and fully crossed to create 8 treatments. A fourth factor, plateau pika exclusion, was applied at a larger spatial extent with the other treatments nested within it, but difficulty with fully excluding pikas caused us to subsequently treat my attempts to exclude them as a random effect when analyzing the other fixed treatment effects. As a result, the 8 warming, snow, and yak treatments are embedded in a randomized block design with 8 blocks, for a total of 64 plots. For a visualization of the experiment layout, see Hu et al. (2013). Within each approximately 8-m-diameter plot I established five 0.75-m-diameter subplots. This allowed us to compartmentalize the type of measurements made in each subplot so that destructive harvests and sensor installations were never made in the subplot in which I measured plant species composition every year.

I simulated climate warming with conical, open top chambers that I installed on each subplot of the warming treatment plots (n=32). The chambers are made of Sun-Lite HP fiberglass and followed the design of those used in the International Tundra Experiment (Solar Components Corporation, Manchester, New Hampshire, USA; (Hollister and Webber, 2000; Marion, 1996; Marion et al., 1997). Each chamber is 1.5 m in diameter at the base, 0.40 m tall, and elevated 5 cm above the ground to allow pikas to enter and air to flow through. I installed the chambers in May every year, except in 2009, when installations occurred from mid-June to early July because I was still in the process of setting up the experiment. Every year I removed the chambers in late August or early September (see figures in Appendix 1) to prevent them from becoming damaged or from altering ambient snow conditions during the rest of the year.

Climate models project that that precipitation will increase on the Tibetan Plateau in winter and spring (Christensen et al., 2013), when low temperatures will cause it to fall as snow. To simulate this change, I had snow added to half of the plots (n=32) in late April and early May when the site became accessible each year (Table 3.1). In central Tibet, winter snow depths greater than 1.5 m have been reported in years with anomalously high snowfall (Li et al., 2001), although less than 0.5 m of winter snow is more typical (Li et al., 2001; Sato, 2001; Ueno et al., 2007).

Therefore, I chose to add snow equivalent to at least 1 m of fresh snowfall to ensure that the treatment represented a significant increase in non-growing-season precipitation, mimicking extreme snowstorm conditions, yet remained within a realistic range of snowfall for this region (Table 3.1). No snow or only light dustings of snow were present at the experiment site each year during the snow addition treatment, so I had snow transported to the experiment site from where it had accumulated nearby, such as in sheltered streambeds. I used cylindrical wire frames 1.0 m in diameter and 0.5 m high to contain the snow shoveled onto each 0.75-m diameter subplot. When the snow had stabilized on the subplots, the wire frames were removed, and the cylinders of snow were covered with mylar sheets. This protected them from radiation and wind so that the snow could melt gradually, rather than sublimating and losing mass from the sides of the cylinder, which wouldn't realistically replicate conditions when the entire area is covered by snow. The mylar was removed before the snow had melted completely to ensure that it did not create unintended shading effects. Snowmelt wetted the ground surface up to 5-25 cm away from the edge of the snow cylinders. Gravimetric soil moisture measurements at 10-cm intervals to 30 cm depth indicated that most of the snow melt water stayed in the top 10 cm of soil, and not much penetrated below 20 cm.

Throughout each summer herders brought local yaks to the grazing treatment plots (n=32) to simulate ambient levels of livestock grazing in this region. The yaks were tethered to a stake at the center of the plot with a rope that allowed them to reach all subplots within the plot, but not neighboring plots. Yaks were present on the plots for about seven hours per day for 3-day periods three to four times per summer. In 2009 and 2013, however, there was only one period of yak grazing in August, due to limited labor availability. When yaks were present on the plots, I removed warming chambers and air temperature sensors to prevent them from interfering with grazing and from getting damaged by the yaks. To estimate the biomass removed through grazing, I measured the area and height of grazed patches before and after yaks came to the plots. I then applied off-plot regressions to estimate the amount of biomass removed based on the measured volume of the grazed patches (Harte and Shaw, 1995; Klein et al., 2007). I made the same measurements outside of the experiment throughout the growing season to verify that the grazing treatment accurately represented observed levels of grazing pressure around the landscape. Herders collected dung from the experiment site in the same way that they remove it from around the landscape for use as fuel.

3.2.3 Microclimate

I measured growing season air temperature, soil temperature, and soil moisture at hourly intervals in 48 plots in 2009 and at 15-minute intervals in all 64 plots in 2010-2013. Decagon EM50 loggers recorded measurements from ECT air temperature sensors with radiation shields at 10 cm above the canopy and from Decagon EC-TM and 5TM soil sensors that integrated across the top 10 cm of soil (Decagon Devices, Inc., Pullman, Washington, USA). Since I was in the process of setting up the experiment in 2009, most sensors that year weren't installed until June 25, while in subsequent years the sensors were installed in late April or early May. The sensors were located in the center of the same subplots each year. I calculated volumetric soil water content by applying custom EC-TM and 5TM sensor calibrations for the field soil to the raw dielectric moisture data.

For soil moisture, soil temperature, and air temperature I removed all erroneous values due to sensor or logger failure and computed daily means in each plot. On days when air temperature sensors were removed for yak grazing, I removed the daily means from subsequent analyses since these lacked daytime measurements and thus skewed the data toward colder, nighttime temperatures. When calculating growing season averages, I also eliminated plots that were missing more than a week of consecutive data to prevent these missing periods from affecting the results, particularly because many missing values early in the season when temperatures were colder across all plots and the soil was drier or wetter, depending on whether snow was added, could also substantially alter the growing season mean.

3.2.4 Soil resources

Each August from 2009-2012 I collected soil cores to 10 cm depth in each plot to measure their nitrogen and carbon content. In addition, in 2010 I collected soil from an area in the center of the experiment site to analyze soil texture and resources in the top 0-5 cm, 5-10 cm, and at 10-cm increments down to 80 cm depth. I sieved the cores and subsets of the soil texture samples and removed all roots and rocks larger than 2 mm. I tested soil from each plot with HCL and found no evidence of carbonates. Then I oven dried the remaining soil at 110 ^{0}C for 24 hours, ground it to a fine powder, and analyzed subsamples with a LECO Tru-Spec CN analyzer (LECO Corp., St. Joseph, MI, USA) at the Natural Resource Ecology Lab in Fort Collins, Colorado.

In addition to measuring total nitrogen in the soil, I also measured nitrogen supply rates using Plant Root Simulator (PRS™) probes (Western Ag Innovations, Inc., Saskatoon, SK, Canada) over a 16-month period from 2010-2011. These probes have a thin ion exchange resin membrane that adsorbs either nitrate (NO_3^-) or ammonium (NH_4^+) to their surfaces, thus acting as a surrogate measurement for plant roots' ability to access inorganic nitrogen (Qian and Schoenau, 1995). During each sampling interval I buried two pairs of NO_3^-- and NH_4^+-adsorbing probes to 10 cm depth in the same subplots from which I took soil cores. The probes remained buried for approximately month-long periods, except for the over-winter burial from 2010 to 2011 that also included the last part of the 2010 growing season. In subsequent graphs and descriptions these sampling periods are labeled according to the months in which they spent the majority of their time buried in the plots. Immediately upon removing probes from the field, I rinsed them with deionized water. Then I took them back to the laboratory where I thoroughly rinsed and scrubbed them with Milli-Q purified water to ensure that they were completely free of soil and debris. I kept them frozen until they could be sent to Western Ag Innovations for analysis.

3.2.5 Vegetation production and quality

Near the peak of the growing season in August, 2009-2012 I visually estimated the areal cover of plant species in one subplot of each plot using a 0.75 x 0.75 m quadrat divided into 400 squares (Bonham, 1989). Due to the small statute of the vegetation, I estimated cover at a resolution down to 1/6th of a square. I placed the corners of the quadrat on metal pegs permanently embedded at the corners of a subplot so that I could sample the same area each year. I measured heights of dominant species, *K. pygmaea*, in a subset of plots in 2009-2011 and the shrub, *P. fruticosa*, in all plots from 2010-2012. In 2012 I also measured the average height of un-grazed shoots for all species without prostrate growth forms in every plot. Then I used a non-destructive biomass estimation method modified from Klein et al. (2007) and Harte and Shaw (1995) to estimate aboveground net primary production (ANPP) for each plot. For this I performed the same cover and height measurements in areas outside of the experiment plots. Then I clipped all biomass for each species within the quadrat, which I oven-dried and weighed. I regressed the dry weights against areal cover from the clipped plots to create a linear relationship with an $R^2 > 0.90$ for every species. Then, for each experiment plot, I applied these regressions to their species cover estimates and multiplied the resulting biomass value by the proportion of the species' height in that plot relative to the species' height in the clipped plots in order to derive a final estimate of ANPP for all species in all plots. I calculated ANPP for *P. fruticosa* from 2010-2012 since I had comprehensive height data for this species for these years.

I selected five focal species for leaf tissue analysis: *Kobresia pygmaea* (shallow-rooted graminoid), *Carex moorcroftii* Falconer ex Boott (deep-rooted graminoid), *Leontopodium pusillum* (Beauverd) Hendel-Mazzetti (shallow-rooted forb), *Astragalus rigidulus* Bunge (deep-rooted forb), and *Potentilla fruticosa* Linneaus (deep-rooted shrub). In August, 2012 I clipped leaf samples from these five species in all plots where they were present. I also clipped leaf tissue from *K. pygmaea*, the dominant species, in all plots in August, 2009-2011 and from 32 plots in July, 2011 to capture whether there were intra- or interannual differences. In addition, in 32 plots in June, 2012 I collected standing dead *K. pygmaea* that had grown and senesced during the 2011 growing season to examine litter quality (Bowman et al., 1995).

In the lab, I oven-dried each leaf sample at 110 ^{0}C for 24 hours, then homogenized them to a fine powder. *K. pygmaea, C. moorcroftii*, and *A. rigidulus* were sufficiently ground with a ball mill, but the thicker leaves on *P. fruticosa* required additional grinding on a Wiley mill, while the dense trichomes on *L. pusillum* required the leaves to be frozen with liquid nitrogen and pulverized with a mortar and pestle. I analyzed green leaf tissue for its %C and %N concentrations and δ^{13}C (‰) using a Carlo Erba NA 1500 elemental analyzer (Carlo Erba Strumentazione, Milan, Italy) coupled to a VG Isochrom isotope ratio mass spectrometer (Isoprime Inc., Manchester, UK). For the senesced *K. pygmaea* tissue, I analyzed δ^{15}N (‰) instead of δ^{13}C. For *L. pusillum* leaf tissue, I analyzed its %C, %N, δ^{13}C, and δ^{15}N with a Costech ECS 4010 Elemental Analyzer (Costech Analytical Technologies Inc., Valencia, California) coupled to a ThermoFisher Delta V isotope ratio mass spectrometer (ThermoFisher Scientific, Bremen, Germany). The instruments' thresholds for detecting differences in $\delta^{13}C$ and $\delta^{15}N$ are 0.8 ‰ and 1.2 (‰), respectively.

3.2.6 Ecosystem CO_2 fluxes

To quantify the balance of CO_2 taken up through photosynthesis and released through respiration, I measured net ecosystem production (NEP) and ecosystem respiration (ER), and then I subtracted ER from NEP to derive gross primary production (GPP). I attempted to measure CO_2 fluxes on mostly cloud-free days at approximately 2-week intervals throughout the growing season. However, monsoon storms, equipment failures, and site inaccessibility prevented me from keeping this schedule. Instead, I was able to make 4 to 5 measurements between June and September each year from 2010-2012 and on one day in August, 2013 (see figures in Appendix 1). I measured the fluxes in the same subplots that I used for species composition measurements, with three replicates per treatment (n=24) because the time-intensive nature of the measurements precluded sampling additional replicates. In plots with the warming treatment, I placed the ecosystem CO_2 chamber inside the open top warming chambers during flux measurements. In 2010 and 2011 I made diurnal measurements at five times throughout the day (7:00, 11:00, 15:00, 19:00, 23:00, China Standard Time). In 2012 and 2013, I made measurements only at 11:00 and used the strong relationship between midday and net daily values in 2010-2011 to estimate net daily fluxes in 2012-2013 as well.

I measured ecosystem CO_2 fluxes by attaching a LI-6400 portable photosynthesis system (LI-COR Inc., Lincoln, Nebraska, USA) to a custom ecosystem chamber (0.50 x 0.50 x 0.25 m) that I modified from Saleska et al. (1999) and Vourlitis et al. (1993), and which is described in more detail by Hu et al. (2013). I moved the chamber and a portable base between plots, creating a temporarily sealed volume over each plot during measurements by using a heavy chain to weigh down a plastic skirt surrounding the base. Two small fans mixed air inside the chamber during measurements, and pressure build-up inside the chamber was prevented by a tube venting to the outside. The LI-6400 also recorded air temperature and photosynthetically active radiation (PAR) measured by a thermocouple and quantum sensor.

I made three consecutive measurements in each plot under ambient light conditions to estimate NEP. Then I covered the flux chamber with an opaque shroud to block all light, thus stopping photosynthesis and yielding an estimate of ER. In 2010 I also took three replicates of ER measurements, but since ER replicates were less variable than NEP, I took one ER measurement per plot in 2011-2013 to increase sampling efficiency. During nighttime measurements, I made three measurements without the shroud because when photosynthesis stops at night, NEP equals ER.

In 2010 I logged single CO_2 flux values, whereas in 2011-2013 I calculated fluxes based on changing CO_2 concentrations across 60-second measurement periods. I found that results did not differ dramatically due to the change in methods, but I preferred to calculate the fluxes from concentrations since this more closely resembles the way in which similar measurements are made for soil CO_2 efflux. In 2010 I set the chamber on its base, allowed the CO_2 readings to stabilize, and logged the flux value at that instant (Hu et al., 2013; Welker et al., 1999; Welker et al., 2004). In 2011-2013, I first recorded the ambient CO_2 concentration over the plot, which I later used to calculate CO_2 fluxes at that ambient level. Then I set the chamber on its base, and after waiting 20 seconds for the conditions inside to stabilize, the LI-6400 logged the CO_2 concentrations at 2-second intervals for one minute (Saleska et al., 1999; Street et al., 2007). For both methods in

2010 and in subsequent years, I vented the chamber between each replicate to allow conditions in the plot to return to ambient before taking the next measurement.

For CO_2 measurements in 2010, I logged individual flux values three times in each plot and then calculated the mean flux from the three replicates (Hu et al., 2013). For measurements made in 2011-2013, I calculated a single flux value from CO_2 concentrations that logged every two seconds inside the measurement chamber over a 60-second period (see chapter 4 for more detail). I again took the mean of three replicates to obtain a final flux value for each plot. Following the convention of Chapin et al. (2006), I report net CO_2 uptake and GPP as positive values and net CO_2 efflux and ER as negative values.

To calculate net daily CO_2 balance from diurnal flux measurements, I fit a first-order harmonic regression function to NEP measurements made at 4-hour intervals throughout a 24-hour period. I made the measurements nearly continuously from 7:00-23:00 as I cycled through the plots during each of the five measurement time periods. Previous research in a high-elevation meadow has shown that NEP fluxes don't change significantly throughout the night (Saleska et al., 1999), so when fitting the harmonic function I duplicated the 23:00 measurement for the 3:00 period, during which I didn't take measurements. This allowed extrapolation of the harmonic function to the boundaries of the 24-hour period in a manner that made sense ecologically and statistically. To prevent transient clouds from affecting the fit of the harmonic function, I removed flux values with substantially lower photosynthetically active radiation (PAR) than the mean for that sampling period (removed measurements from a single 4-hour sampling period for 11 plots in 2010 and 18 in 2011). Then I integrated the area between the fitted harmonic curve and zero to obtain final estimates of the net daily CO_2 balance in each plot.

In 2012 and 2013, I only measured CO_2 fluxes at midday. To estimate net daily values from these midday measurements, I regressed midday values against net daily values in 2010-2011. I included the experiment treatments and day of year (DOY) as covariates and used backward elimination to remove non-significant covariates from the model. I determined that there was a significant, linear relationship between midday and net daily values, with DOY, the snow treatment, and DOY x snow retained as covariates (R^2=0.55). I then applied this relationship to the 2012 and 2013 midday values to derive estimates of their daily net CO_2 balance.

3.2.7 Statistical analyses

For analysis of annual nitrogen supply rates, I summed the data from the PRS probe burial periods over a 365-day interval from 2010-2011. For summer totals, however, I took the sum of the first three burial periods from April to early August in 2010 and for four burial periods from April to late August in 2011. Although these aren't directly comparable to each other due to their different durations, the final probe removals each summer do correspond to the time when vegetation cover sampling was completed in all plots in 2010 and 2011, making total summer available nitrogen a relevant predictor variable for plant cover regressions within each year. Since the nitrogen supply rate data were strongly skewed by high values in some grazing plots, I box-cox transformed these data to normalize their distribution. The transformed data are used in all subsequent analyses.

When analyzing vegetation production data, I generally grouped species into forbs, graminoids, and shrubs, with the exception of *K. pygmaea*, which I treated separately to prevent its strong dominance from skewing the results for other graminoids. To eliminate interannual differences in how I estimated plant cover, since in years after 2009 I improved my estimation technique to capture more litter and lichen cover, I computed log response ratios as $\log_e$(treatment cover/control cover) within each block (Tilman et al., 2012). This gives comparable treatment effects relative to control plots within each year, so that positive values indicate positive responses to a treatment, and negative values indicate negative responses.

To identify significant treatment effects, I used linear mixed effects models with warming, snow, and yak treatments and their interactions as fixed effects. These treatments were nested within the eight experiment blocks, which I treated as random effects. I used repeated measures on data collected in the same plots multiple times, and I log-, square-root-, or arcsine-square-root-transformed data, as necessary, to meet the model assumptions of normality and homogeneity of variance. I ran the models with proc mixed in SAS, using residual maximum likelihood estimation and the Kenward Roger specification for computing denominator degrees of freedom (v. 9.3, Cary, North Carolina, USA). For significant interactions I performed post-hoc Tukey-Kramer adjustments. I report least squares means and modeled error estimates unless otherwise noted.

I assessed vegetation responses to potential limiting factors by regressing proportional areal cover of total vegetation, *K. pygmaea*, other graminoids, and forbs against soil moisture, soil temperature, and total nitrogen availability. I used mean soil moisture and temperature values for each plot from May 11 through August 25 each year, but since the microclimate sensors weren't installed until later in the summer during the first year of the experiment, I excluded 2009 mean seasonal data from the analyses. I calculated total nitrogen availability as the sum of NO_3^--N and NH_4^+-N across all summer measurement periods within each year. Since these nitrogen supply rates were only measured in 2010 and 2011, I dropped nitrogen from the analysis if it didn't have a significant effect and re-ran the regression without it in order to be able to also include data from 2012 in the model. I included all possible 2- and 3-way interactions between soil moisture, temperature, and nitrogen, as well as with warming, snow, and yak treatments as categorical predictors. Then, with proc glmselect in SAS, I used lasso selection to determine the most important parameters for predicting plant cover and Schwarz's Bayesian information criterion to select a parsimonious model. The lasso penalized regression method is well suited to handling relatively small sample sizes with many collinear predictor variables (Dahlgren, 2010; Tibshirani, 1996), as is the case with my independent variables. Categorical variables are split so that, for example, warmed and un-warmed treatments can be considered separately. The lasso method then performs variable selection by shrinking some coefficients to zero, including the split categorical variables. For each plant cover regression, I sampled the dataset 1000 times with replacement and used model averaging to obtain the final parameter estimates. Then I obtained R^2 values using ordinary least squares regression for the final models.

3.3 Results

3.3.1 Climate

During the growing season in each year of the experiment, rates of actual evapotranspiration (AET) at Namtso were generally less than half the magnitude of rates of potential evapotranspiration (PET), indicating that plant growth in this region are likely constrained by water availability (Fig. 3.2). This ratio also shows that AET was closest to meeting PET in 2011, due to it being the wettest summer during this study (Fig. 3.2, Appendix 1). There were also interannual differences in the amount and timing of precipitation each summer, with much stronger dry-down of soil moisture between soil thaw (April) and the start of the monsoon (July) in 2010 and 2012 than in 2011 and 2013 (Appendix 1).

The warming treatment increased air temperatures by 1.2 ^{0}C on average across the growing season and across years, with the largest increase in 2010, the warmest and driest year. The warming treatment also increased soil temperature by 1.6 ^{0}C and reduced soil moisture by 25% on average, though these changes were partially mitigated by the effect of the snow addition treatment, which tended to persist for several weeks after the snow had melted. (Table 3.2, Appendix 1).

3.3.2 Soil resources

The soil texture in the experiment site is coarse, ranging from sandy loam in the top 10 cm to fine sand below 70 cm (Table 3.3). Most of the nitrogen and carbon is stored in the top 30 cm of soil, with approximately half of that nitrogen and carbon in only the top 5 cm, which also includes most of the dense roots of *K. pygmaea*.

Across all experiment treatments, total soil nitrogen concentrations measured in soil cores increased significantly after 2009 (year: $F_{3,\,208} = 9.88$, $p < 0.0001$; Fig. 3.3a). There were no significant treatment effects in 2009, but in subsequent years the interaction between warming and yak grazing had the strongest effect on soil nitrogen (warm x yak: $F_{1,\,207} = 10.40$, $p = 0.002$), with warmed plots having significantly higher concentrations than control and warm x yak plots (Table 3.4, Fig. 3.3b). The snow treatment also increased nitrogen concentrations, though this effect was weaker (Snow effect: $F_{1,\,207} = 3.80$, $p = 0.05$). Soil carbon followed the same trends, which caused soil C:N to be significantly higher after the first two years of the experiment and in warmed plots relative to warm x yak plots (Table 3.4).

In contrast to total soil nitrogen, which includes all forms of organic and inorganic nitrogen in the bulk soil sample, I define net N supply rates as the sum of NO_3^--N and NH_4^+-N measured by PRS probes, which, by acting as a surrogate for plant roots, indicate the amount of inorganic N in the soil that is available to plants. The net N supply rate was 35.9 μg N 10 cm^{-2} $year^{-1}$ on average in control plots from April, 24 2010 to April 24, 2011. The average in control plots spanning the following growing season (April 24 to August 31, 2011) was 28.0 μg N 10 cm^{-2} 129 $days^{-1}$. Total inorganic N supply in the soil aren't directly comparable between years because probes buried in early August, 2010 were left in the ground until the following April, whereas they were removed at the end of August in 2011.

Nonetheless, seasonal patterns were similar in both years, with a general decrease in inorganic N availability as the growing season progressed, likely due to increasing immobilization by microbes and plants (Fig. 3.4). The depletion of NO_3^- in June and July was significantly stronger in 2010, when soils were drier across all treatments than in 2011 (Table 3.2, Fig. 3.4, Appendix 1). Although there weren't large changes in NH_4^+ supply during the over-winter period relative to the months preceding and following it, NO_3^- became significantly more abundant over winter. NO_3^- then decreased in the subsequent sampling month, corresponding with the start of vegetation growth in mid-May that year (MODIS Vegetation Indices, data not shown). Total nitrogen supply rates, driven by NH_4^+, increased again in June when the yak treatment began for the summer.

The yak treatments caused the largest increases in total inorganic N availability across all sampling periods ($F_{1,441} = 36.73$, $p < 0.0001$; Fig. 3.5). On an annual basis, the total inorganic N supply rate nearly doubled from 35.6 μg N 10 cm^{-2} $year^{-1}$ on average without yaks to 62.2 μg N 10 cm^{-2} $year^{-1}$ on average with yaks. This effect was likely due in part to yaks' urine and dung deposition close to probes, which caused NO_3^- and particularly NH_4^+ values to spike by up to two orders of magnitude. Yet even when the highest NO_3^- and NH_4^+ data points were removed from analyses (n = 9 measurements with total inorganic N > 50 μg 10 cm^{-2} during a single sampling period), the yak effect was still significant ($F_{1,432} = 27.44$, $p < 0.0001$). There was also an interaction between yaks, snow, and year ($F_{1,111} = 4.93$, $p = 0.03$), which caused total available N during the growing season in 2010, a dry year, to be significantly higher in yak-grazed plots than non-yak plots only when snow was also added. However, in 2011, a much wetter year, total available N was significantly higher in yak-grazed plots regardless of whether snow was added too.

When NO_3^- and NH_4^+ are considered separately, there is a significant warm x yak interaction for NO_3^- availability ($F_{1,441} = 4.55$, $p = 0.03$). Rates of NO_3^- supply, and thereby also the ratio of NO_3^- to NH_4^+ in soil ($F_{1,447} = 7.13$, $p = 0.008$), were significantly higher across sampling periods in plots with warming and yak grazing together than in those with only warming, only yaks, or neither. While NO_3^- and NH_4^+ were nearly equally available in control plots ($NO_3^-:NH_4^+ = 1.01$), the ratio of NO_3^- to NH_4^+ rose to 1.62 in warm x yak plots. In addition, the ratio of NO_3^- to NH_4^+ was significantly higher under the snow treatment in the summer of 2011 (no snow = 1.02; snow = 1.44), whereas snow did not have a significant effect on NO_3^- to NH_4^+ ratios in 2010 (snow x year: $F_{1,431} = 8.46$, $p = 0.004$).

3.3.3 Vegetation composition and production

The plant community in the experiment is dominated by a single species of dwarf sedge, *Kobresia pygmaea*, which covers approximately 39% of the ground surface in control plots (Fig. 3.6). Other graminoids are much less abundant, accounting for only about 3% of the ground cover on average. These include other sedges (*Kobresia* and *Carex* species), as well as several grasses (*Poa*, *Stipa*, and *Trisetum* species). Forbs comprise an additional 11% of ground cover on average.

Of the 27 forb species present in the experiment, the most common are *Potentilla saundersiana* Royle, *Astragalus rigidulus*, *Leontopodium pusillum*, *Potentilla bifurca* Linnaues, and *Androsace tapete* Maximowicz. The single species of shrub, *Potentilla fruticosa*, covers about 2% of the ground surface. The remaining area is covered by moss, lichen crusts, bare soil, stones, and plant litter.

Warming and grazing treatments had the strongest effects on vegetation cover, although their impacts differed among functional groups. Overall, due to *K. pygmaea*'s dominance, the treatments that affected *K. pygmaea* tended to translate into community-level effects. Warming had a significant, negative effect on total plant cover, *K. pygmaea*, and forbs (Fig. 3.7a, b, c), with a significantly larger effect in drier years. Snow had a significant, positive effect on forbs and total plant cover, but it could not mitigate the effect of warming on total cover in 2010, the driest year (Fig. 3.7d). In contrast, snow had a significant, negative effect on shrub cover. Yaks significantly increased total plant cover relative to un-grazed and warmed plots, but total cover was significantly lower with both yaks and warming together than with warming alone (Fig. 3.7a). This significant warm x yak interaction for the whole community was likely due to the reductions in *K. pygmaea* and forbs with warming, coupled with significant reductions in other graminoids and shrubs with grazing (Fig. 3.7e, f).

In addition to affecting plant cover, warming and grazing treatments also tended to have the most significant effects on plant height across species, whereas snow additions only affected *K. pygmaea* height (Table 3.5). *K. pygmaea* was significantly shorter with snow than in control plots, although this negative effect was cancelled out when the plots were also warmed. Most forbs were too prostrate to measure their height, including *Astragalus rigidulus*, the cushion plant *Androsace tapete*, and others. Among those that were measurable, there were no significant treatment effects on the height of *Leontopodium pusillum*, but *Potentilla saundersiana* and *P. bifurca* both grew significantly taller with warming and shorter with yak grazing. For *P. bifurca* the positive effects of warming and negative effects of grazing cancelled out when both warming and grazing were present. Graminoids tended to follow a similar pattern, with significant increases in height with warming for three species and decreases with yaks for all species, except the two other *Kobresia* species (*K. humilis* (C. A. Meyer ex Trautvetter) Sergievskaja and *K. schoenoides* (C. A. Meyer) Steudel) were unaffected by grazing. Finally, there was also a significant warm x yak interaction for the height of the shrub, *P. fruticosa*. Under warming, shrub heights increased, but this effect was reversed when yaks were also present[4].

Changes in aboveground net primary production (ANPP) in response to the treatments follow from the treatment effects on cover and height (Table 3.6). *K. pygmaea* ANPP decreased by 29% with warming but recovered to nearly un-warmed levels when snow was also added (Fig. 3.8a). There was a weaker interaction between warming and grazing, in which *K. pygmaea* production was higher with yak grazing than in control (adj. $p < 0.10$), warmed (adj. $p < 0.05$), and warm x yak plots (adj. $p < 0.01$; Fig. 3.8b). As a group, forbs also responded most to warming, decreasing by 13% on average. This significant, negative warming effect also held for the two focal forb species, *A. rigidulus* and *L. pusillum*. If cushion plants (*Androsace tapete*, *Androsace yargongensis* Petitmengin, *Arenaria bryophylla* Fernald) are removed from the forb group because of their unique growth form and lack of response to any treatments, the remaining forb ANPP also decreases with grazing, though the effect is weaker than for warming (yak: $F_{1,49} = 3.46$, $p = 0.07$). All other non-*K.-pygmaea* graminoids as a group accounted for only 6.0 g m^{-2} ANPP on average, and this decreased by 63% when yaks were present. For *C. moorcroftii*, a focal graminoid species,

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[4] Note that values differ slightly from those reported in chapter 4, due to the inclusion of snow treatment plots here but not in chapter 4.

ANPP increased under warming relative to control plots, but this effect was canceled out by yak grazing. Similarly, shrub ANPP increased significantly under warming, but this effect was also mitigated by grazing (see chapter 4 for more details)[1].

While *K. pygmaea* and forbs decreased in response to warming but increased or changed little in response to grazing, other graminoids and shrubs exhibited the opposite pattern. As a result, neither warming alone nor grazing alone caused total ANPP to diverge significantly from the controls (81.0 g m^{-2}), but the combined effect of warming and grazing led to a significant reduction in ANPP (69.2 g m^{-2}) relative to plots that were only warmed or only grazed (warm x yak: $F_{1,49} = 6.43$, $p = 0.01$; Fig. 3.8b). Although the snow treatment didn't cause significant responses in any functional groups as a whole, its ability to mitigate losses in *K. pygmaea* production under warming also caused it to buffer against warming-induced losses in total plant production (warm x snow: $F_{1,49} = 10.34$, $p = 0.002$; Fig. 3.8a). However, snow additions alone did not cause an increase in total ANPP relative to control plots (adj. $p = 0.57$).

3.3.4 Vegetation production responses to soil resources

Thus far, we have seen that the warming treatment raises air and soil temperatures, lowers soil moisture, and reduces total vegetation production through its negative effects on *K. pygmaea* and forb growth. Snow mitigates each of these warming effects (except for forb production) and may also play a role in increasing inorganic nitrogen availability. Yaks have the strongest effect on increasing inorganic nitrogen supply rates in the soil, and yak grazing also increases *K. pygmaea* production in the absence of warming. Other graminoids and shrubs tend to follow an opposing pattern by growing more in response to warming and less under grazing. Therefore, given these treatment effects on soil resources and plant growth, and that *K. pygmaea* grows more under the yak treatment, this could indicate that it experiences compensatory growth in response to grazing, or it may be primarily nitrogen-limited. *K. pygmaea* and forbs may be vulnerable to higher temperatures and/or water-limited, whereas graminoids and shrubs may be temperature-limited and/or less sensitive to lower soil moisture levels. Alternatively, graminoids and shrubs may simply be less grazing tolerant and/or do better under conditions that reduce competition from the dominant species.

The penalized regression analyses reveal that changes in plant cover can mainly be attributed to changes in soil microclimate, and to a lesser extent, inorganic nitrogen availability. *K. pygmaea* and forb cover both increased with higher soil moisture but were reduced by higher soil temperatures (Table 3.7). Conversely, soil moisture was not selected as having a significant effect on graminoids, and the yak treatment covariate was split so that the final model showed that graminoids only respond positively to soil temperature and nitrogen when there is no yak grazing (Table 3.7). The main effects for both soil temperature and nitrogen were shrunk to zero, while their interaction remained in the model. This indicates that in the absence of grazing, graminoid cover increases more strongly in response to higher soil nitrogen availability when soil temperatures are also higher. When yaks are present, the model estimates that graminoid cover is 1.4% (the back-transformed model intercept) and is not dependent on temperature and nitrogen. Presumably, the direct effects of grazing prevent graminoids from increasing in response to soil resources. (Please refer to Chapter 4 for results about increased shrub growth in response to warming when soil moisture is sufficient and grazing is excluded.) Overall, total plant cover, which is composed primarily of *K. pygmaea* and forbs, is best predicted by soil moisture and temperature, while nitrogen availability does not appear to play a significant role in driving changes in cover at the community level (Table 3.7). Therefore, the warming and snow treatments' effects on plant cover can mostly be explained by their effects on soil microclimate conditions.

3.3.5 Vegetation stoichiometry responses to soil resources

Generally, if N is not limiting to plant production, then at higher levels of N availability, it will accumulate in leaf tissue rather than promoting additional growth (Körner, 2003; Shaver et al., 1998). Therefore, C:N ratios in plant tissue serve not only as a metric of how leaf quality will affect nutrient cycling in the ecosystem, but also as an indication of whether nitrogen appears to be limiting to plant growth under different climatic conditions and land uses. Leaf tissue C:N ratios in August, 2012 differed among the five focal species, with significantly lower ratios in *A. rigidulus* (a legume) than all other species, followed by *K. pygmaea*, which was also significantly lower than *C. moorcroftii*, *L. pusillum*, and *P. fruticosa* (species: $F_{4,262} = 257.21, p < 0.0001$). With yak grazing that added significantly more N to the soil, leaf N concentrations increased significantly ($p < 0.05$) in all of the focal species except *L. pusillum* (yak: $F_{1,45.4} = 2.93, p = 0.09$). As a result, leaf C:N ratios were significantly lower with yaks for *K. pygmaea*, *C. moorcroftii*, *A. rigidulus*, and *P. fruticosa* in August, 2012 (Fig. 3.9a), suggesting that with moderate levels of grazing, N is likely not a limiting resource for these species under ambient climate conditions.

However, under the simulated climate change treatments, species' leaf C:N ratios tended to respond in the same direction as their changes in biomass production. The graminoid and shrub focal species that grew significantly more under warming (in the absence of yaks), also exhibited increases in their leaf C:N under warming, although this increase was only statistically significant for the shrub, *P. fruticosa* (warm: $F_{1,46} = 9.03, p = 0.004$). Although the increase in C:N was not significant for the graminoid, *C. moorcroftii* (warm: $F_{1,52} = 0.76, p = 0.39$), its trend toward a dilution of leaf-level nitrogen under warming corresponds well to the regression results that indicate graminoids require more available soil nitrogen in order to increase their production in response to higher soil temperatures.

Warming had the opposite effect on *K. pygmaea* sampled in August, causing significantly lower production and leaf C:N across all years, but these effects were canceled out in warmed plots that also received snow additions (warm x snow: $F_{1,204} = 6.68, p = 0.01$; Fig. 3.9b). In *K. pygmaea* sampled in early July, 2011, snow significantly increased leaf C:N (snow: $F_{1,20.2} = 6.18, p = 0.02$), but this effect did not persist until the August sampling date that year (Fig. 3.9). Snow addition also caused a significant increase in *A. rigidulus* leaf C:N (snow: $F_{1,50.1} = 6.06, p = 0.02$), although I did not detect any effects of snow on *A. rigidulus* production. Altogether, these shifts in leaf stoichiometry under the climate change treatments are consistent with the idea that nitrogen could eventually become limiting to production in species that are able to increase their growth in response to higher temperatures and/or water availability, and removing grazers could exacerbate this trend.

3.3.6 Stoichiometric and isotopic indicators of nutrient cycling

C:N ratios in senesced leaves can serve as an indicator of how conservatively plants are cycling N (Vitousek, 1982). If N is limiting in the ecosystem, plants may resorb it more efficiently from their leaf tissue before senescence, thereby reducing their need to compete with other plants and microbes for uptake of new N when they resume growth during the following growing season. C:N in standing dead *K. pygmaea* leaf tissue increased significantly in response to snow additions (snow: $F_{1,23} = 12.02, p = 0.002$), even though during the August measurements before senescence, there was no effect of snow on *K. pygmaea* leaf C:N (Fig. 3.9c).

Natural abundance N isotopes in leaf tissue can also provide insight into the sources of N used by plants. When N is limiting to plant growth, foliar $\delta^{15}N$ should reflect sources of $\delta^{15}N$ in the soil (Högberg, 1997). More depleted $\delta^{15}N$ signatures (represented by lower values), can be indicative of N limitation in the ecosystem and a more closed N cycle because processes by which N is lost from the system discriminate against ^{15}N, leading to enrichment (Högberg, 1997; Swap et al., 2004). Inter- and intra-specific differences in plant rooting depth, mycorrhizal associations, internal fractionations, and preferred forms of N also affect foliar $\delta^{15}N$ signatures (Högberg, 1997; Makarov et al., 2008; Miller and Bowman, 2002; Nadelhoffer et al., 1996). Uptake of NO_3^- causes greater depletion of foliar $\delta^{15}N$ than does uptake of NH_4^+, which in turn causes more depletion than uptake of organic N. Senesced *K. pygmaea* tissue that grew during 2011 was more depleted than live *L. pusillum* leaf tissue collected in August, 2012 (species: $F_{1,29.6} = 145.32$, $p < 0.0001$). Foliar $\delta^{15}N$ in senesced *K. pygmaea* was significantly more depleted under the snow treatment (snow: $F_{1,21} = 25.13$, $p < 0.0001$; Fig. 3.10a). The only statistically significant treatment effect for *L. pusillum* that was also beyond the analytical error range of the instrument indicated that foliar $\delta^{15}N$ was more depleted in snow than in warm x yak plots (adj. $p = 0.01$; Fig. 3.10b).

The isotopic signature of carbon in leaf tissue can serve as an indicator of plants' intrinsic water use efficiency (WUE) at the time that the carbon was assimilated. Plants with higher WUE will have less negative $\delta^{13}C$ signatures because they are discriminating less against heavier ^{13}C isotopes in order to use less water per unit of carbon gained (Ehleringer and Cooper, 1988; Farquhar and Richards, 1984). The five focal species differed in their $\delta^{13}C$ signatures in August, 2012 (species: $F_{4,268} = 103.15$, $p < 0.0001$), with significantly more negative $\delta^{13}C$ in *L. pusillum*, a shallow-rooted forb, followed by *A. rigidulus*, a deep-rooted forb, and then no significant differences among the less-negative *C. moorcroftii* (deep-rooted graminoid), *P. fruticosa* (deep-rooted shrub), and *K. pygmaea* (shallow-rooted graminoid). Under warming, *K. pygmaea* $\delta^{13}C$ values were less negative in 2009, but they were significantly more negative for *K. pygmaea* in July, 2011 and August 2012, as well as for *L. pusillum* in 2012 (Fig. 3.11a-c). The opposite pattern occurred for snow treatments, with less negative $\delta^{13}C$ in *K. pygmaea* in July and August, 2011 and for *P. fruticosa* in August, 2012 in snow addition plots (Fig. 3.11d-f). However, although I was able to detect statistically significant treatment differences, the only differences outside the analytical error range of the instrument were that *L. pusillum* $\delta^{13}C$ was significantly more negative than in all other species, and un-warmed *A. rigidulus* $\delta^{13}C$ was significantly more negative than un-warmed *K. pygmaea* $\delta^{13}C$ in 2012.

3.3.7 Ecosystem CO_2 fluxes

Daily net ecosystem production (NEP), integrated over 24-hour sampling periods throughout the growing season, showed both intra- and inter-annual patterns. The ecosystem usually did not become a net CO_2 sink on a daily basis until July, around the start of the monsoon, although positive GPP fluxes on the first sampling date each year indicated that plant growth had already started by early June. The exception to this was in 2011, a wet year, in which the ecosystem began to act as a net CO_2 sink approximately a month earlier (Fig 3.12). When comparing the three years (2010-2012) for which I had measurements throughout most of the growing season, NEP measurements were also significantly lower on average in 2010 (year: $F_{2,257} = 10.67$, $p < 0.0001$). This may have been due to 2010 being the driest summer of the experiment, with the lowest plant cover. Another possible explanation is that I did not have a sampling date in late August that year, which could have skewed the results.

The experimental climate and grazing manipulations also altered the carbon sink strength of the alpine meadow ecosystem (Table 3.8). Warming significantly lowered net CO_2 uptake across all years and sampling dates (warm: $F_{1,257} = 18.29$, $p < 0.0001$), while snow additions increased CO_2 uptake, though to a lesser extent (snow: $F_{1,257} = 3.67$, $p = 0.06$). There was also a significant interaction between snow additions and yak grazing across years and sampling dates, in which plots with both snow and yaks had significantly higher net daily CO_2 uptake on average than plots with yak grazing alone (snow x yak: $F_{1,257} = 7.27$, $p = 0.008$). Yak grazing tended to lower NEP within each year, except in 2011, when yaks significantly increased net CO_2 uptake relative to un-grazed plots (Table 3.8).

The effects of the warming and snow treatments on ecosystem CO_2 fluxes tended to change over the course of the growing season. In some years, the negative effects of warming on NEP were alleviated later in the growing season, after the start of the monsoon (Fig. 3.12a). Midday GPP and ER measurements across years indicate that this reduction in net CO_2 uptake with warming appears to be driven primarily by reductions in GPP rather than by increases in ER from June through August (Fig. 3.13a). The reverse can be seen with snow additions, which increase net CO_2 uptake early in the growing season (Fig. 3.12b), corresponding with higher rates of midday GPP in June and July in plots that received snow (Fig. 3.13b).

However, attempting to detect treatment effects on midday GPP and ER across years may obscure interannual differences caused by different climatic conditions each year, which would reduce the significance of treatment differences within each month (Fig. 3.13). Since the ecosystem appeared to respond more strongly to the treatments in wetter years, I also examine diurnal patterns of GPP and ER on each sampling date in 2011 (Fig. 3.14). Treatment effects on fluxes tended to be stronger during the day than at night. In June, the warming treatment dampened the magnitude of CO_2 efflux and uptake, while the snow treatment primarily increased rates of GPP. In August and September, in contrast, both GPP and ER increased with warming and decreased in snow treatment plots, in spite of high soil moisture during this period. These patterns led to little net difference in NEP between warmed and un-warmed plots but lower NEP in snow-addition plots during the peak of the growing season.

3.4 Discussion

3.4.1 Climate

The alpine meadow ecosystem at Namtso, central Tibet typically experiences higher water limitation on average than the more frequently studied, mesic alpine meadows in eastern Tibet. These water deficits could become exacerbated by climate warming, particularly in more arid alpine regions (Calanca et al., 2006), with cascading effects on nutrient cycling and primary production (Augustine and McNaughton, 2006; Berdanier and Klein, 2011). The experimental warming manipulations not only increased air and soil temperatures, but also significantly lowered soil moisture. The addition of spring snow somewhat alleviated this drying effect and could be especially important as a means to mitigate drought conditions during the soil dry-down period preceding the start of the monsoon (Sloat et al., 2015). Yak grazing had little effect on microclimate and did not appear to aridify the soil as in other grazed ecosystems (Veldhuis et al., 2014), likely due in part to the alpine meadows' trampling-resistant turfs and coarse soil textures (Körner, 2003; Miehe et al., 2008).

3.4.2 Nitrogen cycling

Most of the total nitrogen in the soil was stored in the top 10 cm, where plant roots are also most abundant. Low soil C:N ratios (< 18:1 in all treatments) indicate that microbes in these meadow soils should be carbon-limited and therefore mineralizing more N than they are immobilizing (Sinsabaugh et al., 2013), thus increasing the ecosystem's capacity to support plant production and perhaps compensatory growth in response to herbivory (Augustine and McNaughton, 2006; Bardgett and Wardle, 2003). Increases in total soil N with the snow treatment indicate that leaching of soluble N with increased spring precipitation, even at the high volumes of snow that I added, is likely less of a concern here than in other alpine ecosystems with winter snowpack (Edwards et al., 2007). The warming treatment also drove increases in soil C and N, leading to significantly higher soil C:N ratios, but only in warmed plots that were un-grazed. With warming alone, there may have been increased production of fine roots and/or accumulation of litter (Bjork et al., 2007), whereas there was removal of litter by yaks and reduced above- and perhaps belowground production with warming and grazing together. Since I did not remove organic matter smaller than 2 mm in diameter from the soil cores, these treatment-driven differences in belowground organic matter may be partly responsible for these differences in bulk soil C and N concentrations in upper soil layers.

Net rates of inorganic N supply rates in the alpine meadow during the growing season were comparable to those reported in other alpine and arctic tundra sites (Berdanier and Klein, 2011; Jespersen, 2013; Kelley and Epstein, 2009; Martinsen et al., 2012). I also found that inorganic soil N increased during the non-growing season period. During this measurement period soils remained frozen from mid-October to early March, when they began experiencing daily freeze-thaw cycles until the end of April (data not shown). Although microbial communities can maintain activity in frozen soils, it is likely that much of the increase in NO_3^- measured over winter may have occurred in a pulse during the freeze-thaw period before the start of the growing season (Fahnestock et al., 1998; Mikan et al., 2002; Wang et al., 2014).

Although yaks did not have a significant effect on total soil N concentrations, they nearly doubled inorganic N supply on an annual basis, similar to the rate of increase in N mineralization observed with large herbivore grazing in a temperate grassland (Frank and Groffman, 1998) and much higher than increases reported for another alpine ecosystem with sheep grazing (Martinsen et al., 2012). Although higher concentrations of NO_3^- in soil could be susceptible to leaching and denitrification, I did not find evidence to support this. This could perhaps be due to a microbial community with a higher abundance of mineralizers and nitrifiers and lower abundance of denitrifiers with grazing (Yang et al., 2013) or to a fungal-dominated microbial community under extensive grazing practices, which should reduce N leaching (de Vries et al., 2012). Furthermore, additional soil moisture from snow treatments appeared to be an important factor for mineralizing and/or mobilizing inorganic N under the yak treatment in 2010, the driest year of the experiment.

The relative abundance of NO_3^- and NH_4^+ in alpine soils is correlated with soil moisture and temperature, with warmer and drier conditions tending to favor nitrification and higher NO_3^- availability, while NH_4^+ tends to increase with higher soil moisture (Fisk et al., 1998; Makarov et al., 2008; Miller and Bowman, 2002). However, I found that NO_3^- abundance increased relative to NH_4^+ both in response to the snow additions in 2011, the wettest and coolest year, as well as in warm x yak plots, which were significantly warmer and drier than un-warmed plots. An increase in inorganic N concentrations in the top 10 cm of soil in response to warming and sheep grazing also occurred in an alpine meadow ecosystem in eastern Tibet (Rui et al., 2011). In addition to the promoting effects of higher soil temperatures on rates of nitrification under the warm x yak treatment, lower production and thereby reduced competition by plants for N may have also allowed nitrifiers to compete better for NH_4^+ to convert to NO_3^-, which was then also taken up at lower rates due to lower plant growth under this treatment. Microbial and plant competition for N may have been further affected by shifts in plant species composition (Moreau et al., 2015) and increases in lichen crusts (Jespersen, 2013) in response to the climate and grazing manipulations.

Natural abundance N isotopes in senesced *K. pygmaea* leaf tissue revealed that the snow treatment significantly depleted $\delta^{15}N$ signatures, which could be an indicator of a more closed N cycle with the addition of water to the ecosystem. In the summer of 2011, when this leaf tissue was produced, I found that NO_3^- was also more abundant than NH_4^+ in snow treatment plots, and $\delta^{15}N$ in NO_3^- is more depleted than in NH_4^+ (Högberg, 1997). Increased rates of NO_3^- uptake by *K. pygmaea* could therefore explain the depletion of its foliar $\delta^{15}N$ in the snow treatment. Availability of NO_3^- relative to NH_4^+ also increased preceding the start of the 2011 growing season, and so if *K. pygmaea* was advancing its phenology in response to snow, this could have allowed it to take up more NO_3^- than plants in plots without snow, thus depleting its $\delta^{15}N$ signature.

L. pusillum leaf tissue collected in August, 2012 had more enriched $\delta^{15}N$ than the *K. pygmaea* litter from vegetation that grew during the summer of 2011. Although both species have similarly shallow rooting depths, this difference in isotopic signature could arise if *L. pusillum* preferentially takes up more enriched forms of N, but there is little evidence to support this explanation. An alternative explanation is that there were differences in the sources of N available each year. Since 2012 was a warmer, drier summer than 2011, higher rates of volatilization and denitrification could have left relatively more enriched N in the soil in 2012. Furthermore, the only significant treatment difference for *L. pusillum* was depletion of foliar $\delta^{15}N$ in the snow treatment relative to the warm x yak treatment, and this difference, too, could be explained by increased uptake of enriched sources of N if warming drives increased volatilization of ammonia from yak urine and dung (Ball and Ryden, 1984; Mulvaney et al., 2008). Although these interpretations of two species' natural abundance N isotopes are speculative, they suggest that the N cycle could become more closed with the addition of spring snow and perhaps more open to N losses under warmer conditions and with direct N inputs from livestock.

In addition to the direct effects of climate and herbivores on N cycling, their indirect effects on foliar nutrient concentrations will also affect the quality of litter inputs to decomposition processes, which will in turn affect N availability in the ecosystem over longer time scales (Cornelissen et al., 2007; Cornwell et al., 2008; Grime et al., 1996). Although shifts in species composition will likely have a larger effect on litter decomposability at the ecosystem level than will intra-specific changes in leaf C:N ratios (Cornelissen et al., 2007; Cornwell et al., 2008), plants' nutrient resorption efficiency before senescence remains an important factor for explaining intra-specific differences in nutrient cycling (Eckstein et al., 1999). While other studies in tundra ecosystems have found lower C:N in litter in response to fertilization (Soudzilovskaia et al., 2007) or higher C:N in response to warming and water addition (Welker et al., 1997), I found that snow addition was the only treatment that affected *K. pygmaea* litter C:N. Furthermore, C:N in senesced leaves was higher in snow plots in spite of there being no significant treatment differences in live tissue sampled in August, before senescence. This change in leaf stoichiometry was driven by higher N resorption efficiency in snow plots, with 74.5% of N resorbed before senescence, relative to 71.5% of N resorbed in plots without snow. These values are at the high end of the range of N resorption values reported for alpine graminoids and forbs, which range from 40-75% in a Colorado alpine ecosystem (Bowman et al., 1995).

If *K. pygmaea* senesces earlier with snow additions, as the GPP measurements suggest, then this phenological shift could perhaps also affect their ability to resorb N more efficiently before the end of the summer. Several deciduous tree species have shown the opposite pattern, with lower N resorption before senescence in leaves that senesced earlier or more gradually over a longer period of time (del Arco et al., 1991; Killingbeck et al., 1990), but this does not preclude the possibility that an alpine sedge could differ in its nutrient resorption strategies. Alternatively, since I harvested the litter in the following spring, these higher C:N ratios with snow could also be an unintentional artifact of the treatment itself if the addition of snow drove higher rates of N volatilization or leaching from the standing dead tissue before I harvested it. However, the $\delta^{15}N$ signatures from litter collected in snow plots were also significantly more depleted, which is the opposite of what I would expect if N losses from litter after senescence was driving this treatment effect (Högberg, 1997). Overall, litter isotope signatures and C:N stoichiometry indicate that N is cycled more tightly when soil moisture is higher.

3.4.3 Vegetation composition, production, and quality

K. pygmaea cover and production responded more positively to the yak treatment than did any other species or functional group, as expected for a dominant species that is well-adapted to grazing (McNaughton, 1979; Miehe et al., 2009, 2014). Yaks' inhibiting effect on other species could be due not only to the direct effects of yaks on these species, but could perhaps also be caused by indirect, competitive effects from *K. pygmaea*'s increased dominance in response to grazing. *K. pygmaea*'s ability to respond positively to yak grazing could indicate that *K. pygmaea* is N-limited and thus benefitted from the higher availability of inorganic N in yak-grazed plots. However, inorganic N supply rate was not a significant predictor of *K. pygmaea* cover, and I found that N became more concentrated in *K. pygmaea* leaf tissue with yak grazing, which indicates that N availability is not the primary factor limiting *K. pygmaea* growth. An important caveat to these relationships among vegetation and inorganic N is that alpine sedges are also capable of using organic N (Raab et al., 1999), and this is not accounted for in my measurements of N supply rates. In addition to *K. pygmaea*'s ability to take up organic N directly (Xu et al., 2004), it also has mycorrhizal relationships (Gai et al., 2006) that could further enhance its ability to access organic N indirectly. Furthermore, other nutrients, such as phosphorus, may be more limiting than N or co-limiting to plant production in this N-rich system (Wang et al., 2015).

These results provide evidence that *K. pygmaea* and forbs are likely primarily limited or co-limited by water availability in this system, due to the positive effects of soil moisture, snow additions, and wetter years on their growth. Interestingly, snow did not increase *K. pygmaea* or forb production relative to control plots in the absence of warming, which could indicate that under ambient, un-warmed climate conditions, some other factor that I did not measure, such as phosphorous, could be limiting their ability to respond to higher levels of soil moisture. However, under simulated future climate change scenarios, *K. pygmaea*'s reduced production under warming but recovery when snow was also added suggest that it is vulnerable to soil drying, likely due in part to its shallow rooting depth that prevents it from accessing deeper soil water during dry periods (Hu et al. 2013). Therefore, unlike predictions from temperate and tropical systems (Augustine and McNaughton, 1998; Coughenour, 1985; Grime, 1977; McNaughton, 1984; Veldhuis et al., 2014), grazing-tolerant traits do not appear to confer drought-tolerance in this alpine context. However, the idea that grazing-tolerant traits may converge with cold-tolerant traits does seem to be supported for this species, which is well-adapted to historically low temperatures and does not appear to profit from warming. With future warming and potential livestock reductions, *K. pygmaea* could therefore lose its competitive advantage over other species.

As predicted, the dominance of *K. pygmaea* caused treatments that affected this species to drive responses at the community level as well. The primary exception to this pattern was that *K. pygmaea* production decreased in response to warming, while other graminoids and shrubs were able to increase their production under warming if yaks were excluded, which helped compensate for the loss of *K. pygmaea*. Non-*K.-pygmaea* graminoids' ANPP had a positive relationship with soil temperature when they also had sufficient soil nitrogen and weren't being consumed by yaks. Their increased foliar C:N with warming provides additional evidence that these species may require more nitrogen in order to be able to respond positively to higher temperatures, as has been found for graminoids exposed to warming manipulations in other tundra ecosystems (Shaver et al. 1998, Bowman et al. 1995). The deep-rooted, focal graminoid species that increased its height and ANPP with warming, *C. moorcroftii*, is also more prevalent in the nearby alpine steppe communities, which are more arid than the alpine meadows at Namtso (Hopping, personal observation). These results suggest that alpine meadows could shift toward a grassier and/or woodier state under future climate warming and grazing removals, although lower nitrogen inputs without large herbivores could attenuate the magnitude of this shift in community composition.

In addition to being resilient to herbivory, *K. pygmaea* was also one of the most nutritious of the five focal species, with only *A. rigidulus*, a legume, having lower (i.e., more palatable) foliar C:N ratios under ambient conditions. Each of the focal species' foliar C:N ratios decreased with the yak treatment, regardless of whether they were actually grazed by yaks. This indicates that with higher N availability in yak treatment plots, N began to concentrate in leaf tissue rather than promoting additional growth, and so it was therefore likely not the primary factor limiting production. However, foliar C:N increased in response to treatments that drove higher rates of production. Snow additions increased C:N in *A. rigidulus* and early-season *K. pygmaea,* although for the latter, this effect did not persist until the end of the growing season. This suggests that *K. pygmaea* may have accelerated its growth earlier in the season in response to higher soil moisture from snow, corresponding to the period when GPP fluxes were also higher in snow treatment plots.

Warming increased both ANPP and foliar C:N in *C. moorcroftii* and *P. fruticosa*. Yet, since livestock prefer not to graze shrubs, this decrease in leaf tissue quality in *P. fruticosa* is likely to have larger consequences for the recalcitrance of its litter for decomposition than for its palatability as forage. Conversely, warming decreased foliar C:N in *K. pygmaea*, likely due to its lower growth in response to warming and consequent accumulation of N in leaves. This finding contradicts results from a study in an alpine meadow ecosystem that has lower MAP than Namtso but is underlain by permafrost, which found that *K. pygmaea* foliar C:N increased in response to warming (Yang et al., 2011). These opposing responses underscore how additional soil moisture provided through permafrost thaw may initially mediate *K. pygmaea*'s ability to maintain higher levels of productivity with climate warming in different regions of the Plateau. While decreased C:N under warming should improve the quality of *K. pygmaea* as forage and as substrate for decomposition in more arid alpine meadows, the declining quantity of *K. pygmaea* production and replacement by lower quality graminoid and shrub species will likely outweigh the potential benefits of lower foliar C:N in *K. pygmaea* under future climate warming. Furthermore, although the significant increase in *K. pygmaea* leaf N concentrations suggests that *K. pygmaea* could increase its water use efficiency under warming, I did not find other lines of evidence to support this from measurements of foliar $\delta^{13}C$ and ecosystem CO_2 fluxes.

3.4.4 Carbon cycling

Overall, I did not find strong differences in foliar $\delta^{13}C$ among species or treatments, although *L. pusillum*, a hirsute, shallow-rooted forb, maintained significantly lower $\delta^{13}C$ values than other species. A lack of response in $\delta^{13}C$ values to differing levels of soil moisture has also been found in other alpine plants, which suggests that a factor other than water availability is likely regulating stomatal conductance (Berdanier and Klein, 2011). Indeed, the trend toward higher $\delta^{13}C$ in response to snow treatments and lower $\delta^{13}C$ in response to warming treatments was the opposite of what would be expected if $\delta^{13}C$ signatures were driven primarily by mean growing season soil moisture. One alternative explanation is that alpine plants exposed to high levels of solar radiation, as in Tibet, may keep their stomata open to maintain photosynthesis and thereby reduce radiation damage, even when soil moisture is low, thus decoupling $\delta^{13}C$ values from plant water status (Körner, 2003). A second explanation is that higher foliar N concentrations can increase plant WUE, which would lead to higher $\delta^{13}C$ signatures. For example, two forbs species from a moist alpine meadow in Colorado increased their WUE when they received additions of both water and nitrogen (Bowman et al., 1995). However, the focal species that increased WUE in response to snow additions (*K. pygmaea* in July and August, 2011, *P. fruticosa* in August, 2012) did not have correspondingly higher foliar N concentrations.

There may also be a phenological explanation for the slight climate treatment effects on WUE, with plants advancing or delaying their growth in response to water availability. If plants delay their growth under warming and then assimilate the majority of their carbon during the monsoon, when water is less limiting across all treatments, then this could explain why some species with access to less soil moisture over the course of the entire summer exhibited lower WUE, contrary to findings from soil moisture gradient studies (Ehleringer and Cooper, 1988; Luo et al., 2009). Conversely, if plants are advancing their growth in response to spring snow additions and accumulating more biomass before the start of the monsoon, they may have relatively higher water demands to support photosynthesis during the dry-down period (either to maintain their carbon balance or to prevent radiation damage), thus driving them to maintain higher WUE, as I found for *K. pygmaea* and *P. fruticosa*. Soil moisture is increasingly recognized as a critical phenological control globally (Forkel et al., 2015), as well as at a regional scale on the Tibetan Plateau, where pre-growing-season precipitation appears to be a more important trigger for the start of plant growth in more arid regions, such as central Tibet (Shen et al., 2015). The idea that plants may be shifting the timing of their growth in response to the climate treatments is also supported by findings that *K. pygmaea* delays reproductive phenology in response to warming and advances reproductive phenology in response to spring snow additions in central Tibet (Dorji et al., 2013).

I found that ecosystem CO_2 fluxes served not only as a measure of how C is being cycled in response to the climate and grazing manipulations that alter resource availability and vegetation production, but also that measurements of GPP provide additional evidence for shifts in plant phenology under altered climate conditions. The ecosystem became a net CO_2 sink around the start of the monsoon each year, but growing season NEP was highest in the wettest year, due to both an earlier transition to CO_2 uptake outweighing CO_2 efflux, as well as to higher rates of NEP at the peak of the growing season. Furthermore, each summer the ecosystem shifted to acting as a net CO_2 sink earlier with snow additions but later with warming, and these patterns were driven more strongly by changes in rates of GPP than ER. Reductions in GPP in response to warming were likely driven by reductions in *K. pygmaea* ANPP and, since it comprises the majority of the biomass at the community level. These decreases in production and CO_2 uptake were somewhat alleviated by increased precipitation in the wettest year, similar to other tundra and high-elevation ecosystems in which CO_2 flux responses to warmer temperatures or dry years are mediated by other limiting resources, such as insufficient soil moisture or nutrients to support production (Jones et al., 1998; Saleska et al., 1999; Sloat et al., 2015; Väisänen et al., 2014). However, I did not find a consistent interaction between snow and warming for CO_2 fluxes, even though addition of snow counterbalanced the reductions in *K. pygmaea* and total ANPP under warming.

While the large reductions in net CO_2 uptake under warming are likely to have the largest impact overall on the carbon sink strength of this alpine meadow ecosystem, increases in early spring snow may also have important consequences for the timing of when the alpine meadows sequester carbon and how they respond to grazing. In other alpine ecosystems, delayed snowmelt can reduce the length of the growing season, and thereby cumulative plant production, by delaying the timing of plant green-up (Berdanier and Klein, 2011; Choler, 2015). In central Tibet, however, I found that late spring snow additions appeared to advance both plant production and senescence. My measurements of CO_2 fluxes were not consistently late enough to capture the full seasonal cycle from green-up to brown-down in order to be able to quantify the change in length of the growing season in response to snow, but in every year of the measurements, the initial increase in NEP with snow additions switched to a decrease in NEP by August. Lower rates of ER but especially of GPP in snow plots in August and September show that this reduction in NEP later in the growing season was caused by reduced vegetation activity, rather than by higher rates of CO_2 efflux. In addition, the snow treatment interacted significantly with yak grazing. As in other tundra ecosystems in which large herbivores lower rates of CO_2 uptake (Cahoon et al., 2012; Metcalfe and Olofsson, 2015; Wohlfahrt et al., 2008), yak grazing tended to reduce rates of NEP. However, NEP increased with yak grazing in the wettest year, 2011, as well as when snow was also added to yak-grazed plots. This suggests that only when water is sufficient, either through the addition of spring snow or via a wetter summer, can yak grazing increase NEP, consistent with findings for plant production in other grazed systems (Augustine and McNaughton, 2006).

3.5 Conclusion

Alpine meadows in this region of central Tibetan are nitrogen-rich ecosystems with plant communities dominated by *Kobresia pygmaea*, a grazing- and cold-adapted species. I found that ecosystem functioning in these alpine meadows is generally maintained by yak grazing but is vulnerable to climate warming, due in large part to *K. pygmaea*'s sensitivity to soil drying. As predicted, yak grazing maintained the dominance of *K. pygmaea* and accelerated nitrogen cycling, particularly at higher levels of soil moisture. If herd reduction policies continue to remove livestock from this system, this will likely have cascading effects on how nitrogen is cycled and made available to vegetation and microbes, as well as for plant community composition. Climate warming reduced soil moisture, *K. pygmaea* production, and net CO_2 uptake but promoted the growth of other graminoids and shrubs when yaks were not present. The interactive effects of grazing and warming led to a reduction in both grazing-intolerant and warming-intolerant species, which lowered total ANPP and allowed nitrogen to accumulate in the soil, at least in the short term. Increased spring snow, which is projected to occur with climate change in this region, may alleviate warming-induced water limitation and increase nitrogen availability in dry years. The pulse of soil moisture provided by snow additions also appeared to advance vegetation green-up, as well as senescence. However, while increased snowfall under future climate conditions may counterbalance some of the undesirable effects of warming and make the system more able to respond positively to yak grazing, it should also be noted that large snowstorms in this region can be detrimental to pastoralists' herds (Miller, 2000; Yeh et al., 2013), so additional snow may come at a tangible cost to local livelihoods and human well-being. In conclusion, I found that yak grazing exerts controls over species composition and that water, more than temperature or nitrogen, is an important factor limiting to production and carbon sequestration in these central Tibetan alpine meadows. In the future, however, interacting climate and land use changes will have cascading effects on how these ecosystems function and the services they provide.

3.6 Tables

Table 3.1. Means (± SD) for measurements related to snow addition treatments. Snow water equivalent (SWE) is calculated as snow addition depth (0.5 m) multiplied by snow density. Fresh snowfall depth equivalents are calculated using SWE from the snow additions, multiplied by the mean density of fresh snowfall in this region for May, 2006-2009 (0.23 g ml^{-1}). Fresh snow density and mean annual precipitation (MAP) data are from the Nam Co research station (NAMORS).

Year	Snow added	Snow duration (days)	Snow density (g ml^{-1})	SWE (mm)	Fresh snow depth equivalent (m)	MAP (mm)	Proportion of MAP added as snow (%)
2009	April 26-May 3	8 (1.5)	0.60 (0.03)	301.3 (13.7)	1.32 (0.06)	374.3	80.5
2010	April 27-May 4	9 (1.6)	0.65 (0.03)	325.0 (14.1)	1.42 (0.06)	570.8	56.9
2011	April 26-28	11 (1.1)	0.59 (0.06)	297.4 (29.9)	1.30 (0.13)	568.8	52.3
2012	May 13-16	7 (1.4)	0.45 (0.04)	224.4 (22.0)	0.98 (0.10)	444.2	50.5
2013	May 2-4	7 (1.3)	0.49 (0.04)	246.6 (21.9)	1.08 (0.10)	488.2	50.5

Table 3.2. Mean microclimate conditions under the different experiment treatments for air temperature (June 1 - August 25) and soil moisture and temperature (May 11 - August 25), corresponding to periods when all sensors were installed in all plots for all years. Warming was significant for air temperature in all years ($p < 0.0001$), and warming, snow, or the warm x snow interaction were significant for soil moisture and soil temperature in all years ($p < 0.05$) except for soil moisture in 2011 (warm x snow: $p = 0.09$). Lowercase letters represent significant treatment differences within each year at $p < 0.05$.

	2010	2011	2012	2013
Air temperature (^{0}C)				
Control	8.91 ^{b}	7.13 ^{b}	8.80 ^{b}	8.35 ^{b}
Warm	10.25 ^{a}	8.33 ^{a}	9.87 ^{a}	9.49 ^{a}
Soil temperature (^{0}C)				
Control	10.44 ^{c}	10.00 ^{c}	11.19 ^{bc}	10.67 ^{c}
Snow	10.25 ^{c}	10.04 ^{c}	10.65 ^{c}	10.52 ^{c}
Warm	12.41 ^{a}	11.41 ^{a}	12.35 ^{a}	12.25 ^{a}
Warm x Snow	11.66 ^{b}	10.98 ^{b}	11.58 ^{b}	11.46 ^{b}
Soil moisture (m m^{-3})				
Control	0.11 ^{a}	0.18 ^{a}	0.13 ^{ab}	0.12 ^{b}
Snow	0.11 ^{a}	0.17 ^{ab}	0.14 ^{a}	0.15 ^{a}
Warm	0.06 ^{b}	0.14 ^{b}	0.11 ^{b}	0.10 ^{b}
Warm x Snow	0.09 ^{a}	0.16 ^{ab}	0.13 ^{ab}	0.13 ^{ab}

Table 3.3. Soil profile nitrogen, carbon, and texture for the experiment, outside of treatment plots.

Depth (cm)	N g kg^{-1}	C g kg^{-1}	C:N	Sand (%)	Clay (%)	Silt (%)	Texture
0-5	3.05	42.73	14.03	66.09	13.34	20.57	Sandy loam
5-10	1.52	15.92	10.51	78.69	10.31	11.00	Sandy loam
10-20	1.12	10.22	9.17	79.78	9.27	10.95	Loamy fine sand
20-30	1.06	8.96	8.46	79.49	9.05	11.46	Loamy fine sand
30-40	0.86	7.52	8.75	79.37	8.99	11.65	Loamy fine sand
40-50	0.71	6.15	8.70	80.57	9.07	10.36	Loamy fine sand
50-60	0.30	1.65	5.58	84.65	7.81	7.54	Loamy fine sand
60-70	0.26	1.34	5.19	85.10	7.80	7.10	Loamy fine sand
70-80	0.22	1.05	4.89	88.69	5.53	5.78	Fine sand

Table 3.4. Mean (±SE) total carbon and nitrogen concentrations and C:N ratio in the top 10 cm of soil for significant fixed effects. Treatments or years with different lowercase letters are significantly different at $p < 0.05$.

Effect	C g kg^{-1}	N g kg^{-1}	C:N
Year			
2009	43.35 (6.30) ^{c}	2.70 (0.25) ^{b}	15.63 (0.70) ^{b}
2010	49.99 (6.20) ^{bc}	3.13 (0.24) ^{a}	15.49 (0.69) ^{b}
2011	56.53 (6.20) ^{ab}	3.15 (0.24) ^{a}	17.69 (0.69) ^{a}
2012	60.37 (6.20) ^{a}	3.44 (0.24) ^{a}	17.08 (0.69) ^{a}
Warm x Yak			
Control	50.39 (6.22) ^{b}	3.01 (0.24) ^{b}	16.39 (0.69) ^{ab}
Yak	52.71 (6.21) ^{ab}	3.15 (0.24) ^{ab}	16.22 (0.69) ^{ab}
Warm	60.04 (6.21) ^{a}	3.36 (0.24) ^{a}	17.28 (0.69) ^{a}
Warm x Yak	47.11 (6.22) ^{b}	2.90 (0.24) ^{b}	15.99 (0.69) ^{b}

Table 3.5. Mean vegetation heights (mm) for significant treatment effects. Within each species, treatments that are not different at $p < 0.05$ share lowercase letters. F statistics for fixed treatment effects are shown below each set of treatments, and p-values are indicated by † ($p < 0.10$), * ($p < 0.05$), ** ($p < 0.01$), *** ($p < 0.001$). When warming and grazing effects are considered without their interaction term for *P. saundersiana*, yak grazing causes it to be significantly shorter than the control ($F_{1, 49} = 7.39$, $p = 0.009$), and warming causes it to be significantly taller than the control ($F_{1, 49} = 6.43$, $p = 0.01$). (C = control, Y = yak, W = warm, S = snow).

	Kobresia pygmaea	*Carex moorcroftii*	*Leontopodium pusillum*	*Potentilla saundersiana*	*Potentilla bifurca*	*Potentilla fruticosa*
C		26.6^{b}	7.5	6.9^{ab}	13.9^{b}	20.6^{b}
Y		21.1^{b}		5.8^{b}	9.8^{c}	17.6^{b}
W		34.4^{a}		7.8^{a}	19.2^{a}	32.1^{a}
W x Y		24.5^{b}		6.8^{ab}	10.3^{c}	17.7^{b}
F					7.54 ***	32.16 ***
C	17.8^{a}					
S	14.4^{b}					
W	16.3^{ab}					
W x S	17.0^{ab}					
F	12.17 ***					

Table 3.6. Mean August, 2012 ANPP ($g\ m^{-2}$) for all significant treatment effects by functional group and the five focal species. Due to *K. pygmaea*'s strong dominance, it is not included as part of the "other graminoids," while all other focal species are also included as part of their functional group totals. Within each group or species, adjusted p-values are reflected by lowercase letters, with treatments that are not different at $p < 0.05$ sharing the same letter. When warming and grazing effects are considered without their interaction term for *A. rigidulus*, yak grazing causes a significant increase and warming causes a significant decrease in its production. The interaction term is not shown when only one treatment had a significant effect. (C = control, Y = yak, W = warm, S = snow).

	Graminoids			Forbs			Shrub
	K. pygmaea	Other graminoids	*C. moorcroftii*	All Forbs	*L. pusillum*	*A. rigidulus*	*P. fruticosa*
C	62.75^{ab}	6.00^{a}	0.21^{b}	9.80^{a}	1.28^{a}	0.87^{a}	2.14^{b}
Y	70.77^{a}	2.23^{b}	0.42^{ab}			1.48^{a}	3.03^{ab}
W	60.81^{ab}		1.11^{a}	7.63^{b}	0.69^{b}	0.35^{b}	8.00^{a}
W x Y	56.22^{b}		0.19^{ab}			0.35^{ab}	3.60^{ab}
F	3.53 †	15.67 ***	7.25 **	4.98 *			4.47 *
C	71.64^{a}						
S	61.87^{ab}						
W	51.31^{b}						
W x S	65.72^{a}						
F	13.00 ***						

Table 3.7. Regression coefficients for growing season soil microclimate and nitrogen parameters selected as the best predictors of proportional plant cover. The soil temperature and nitrogen interaction only applies to graminoids when there is no yak grazing. Available N is the sum of NO_3^--N and NH_4^+-N supply rates each summer. Forb and graminoid cover data were arcsine-square-root-transformed.

Cover type	Intercept	Soil moisture (m^3/m^3 VWC)	Soil temp (^oC)	Available N (µg N 10 cm^{-2})	Soil temp x Available N	R^2
K. pygmaea	0.82	0.56	- 0.05	--	--	0.36
Forbs	0.45	0.31	- 0.02	--	--	0.30
Graminoids	0.12	--	--	--	0.003	0.13
Total plants	0.98	1.04	- 0.05	--	--	0.49

Table 3.8. Treatment and temporal effects on daily integrated net ecosystem production throughout the growing seasons from 2010-2012 and on one sampling date in 2013. Test statistics (*F*) are shown, and significant effects are indicated by *** ($P < 0.001$), ** ($P < 0.01$), * ($P < 0.05$), † ($P < 0.10$).

Effect	2010	2011	2012	2013
Warm	8.52 **	2.45	31.2 ***	7.82 *
Snow	3.13 †	0.75	6.08 *	4.39 †
Warm x Snow	1.12	12.04 ***	2.5	0.01
Yak	0.99	4.85 *	1.03	9.37 **
Warm x Yak	0.08	0.05	0.16	0.3
Snow x Yak	2.58	0.01	8.45 **	0.56
Warm x Snow x Yak	0.38	7.98 ** [a]	0.26	0.38
Day of year	37.42 ***	48.31 ***	80.02 ***	--
Warm x Day of year	4.00 *	2.52 *	2.79 *	--
Snow x Day of year	1.40	5.21 **	7.02 ***	--
Yak x Day of year	1.78	2.03	2.27 †	--

[a] The post-hoc comparisons indicate that the only significant differences were that NEP was lower in warm x snow and warm x snow x yak plots than in snow x yak plots. However, this difference may be partly due to no measurements being made in snow x yak plots on the last two sampling dates in 2011.

3.7 Figures

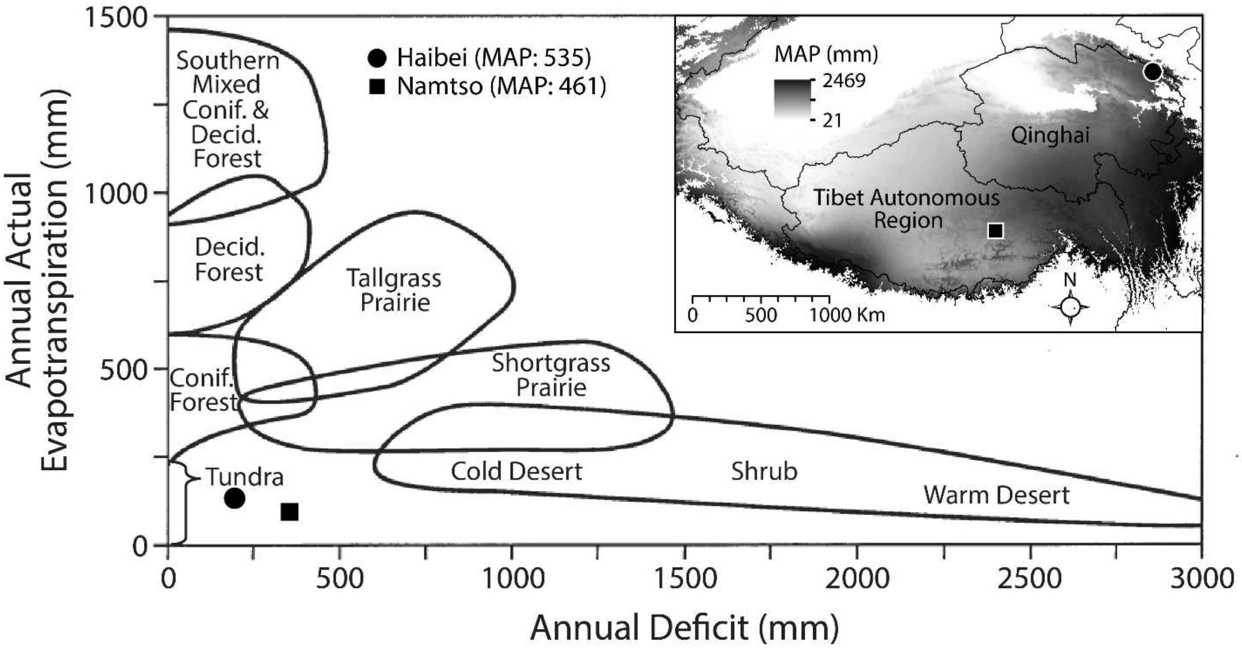

Figure 3.1. Mean annual evapotranspiration and water deficit for alpine meadows at Namtso and Haibei from 2000-2014 relative to other biomes. The inset map of the Tibetan Plateau shows mean annual precipitation (MAP) for elevations higher than 3000 m and the locations of Namtso and Haibei. The biome figure is redrawn with permission from Stephenson (1990). Data for Namtso and Haibei are from the MODIS evapotranspiration product for 49 km^2 surrounding the research sites for years 2000-2014 (ORNL DAAC 2014).

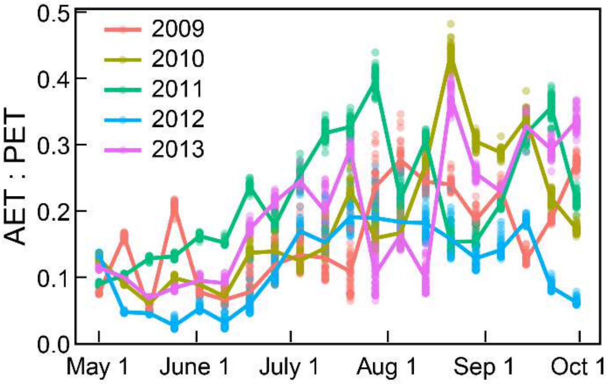

Figure 3.2. Ratio of actual evapotranspiration (AET) to potential evapotranspiration (PET) for 49 km^2 surrounding the experiment. Each point represents a 1-km^2 pixel from the MODIS Evapotranspiration product (ORNL DAAC 2014). Lines pass through means of the 49 pixels for each 8-day composite.

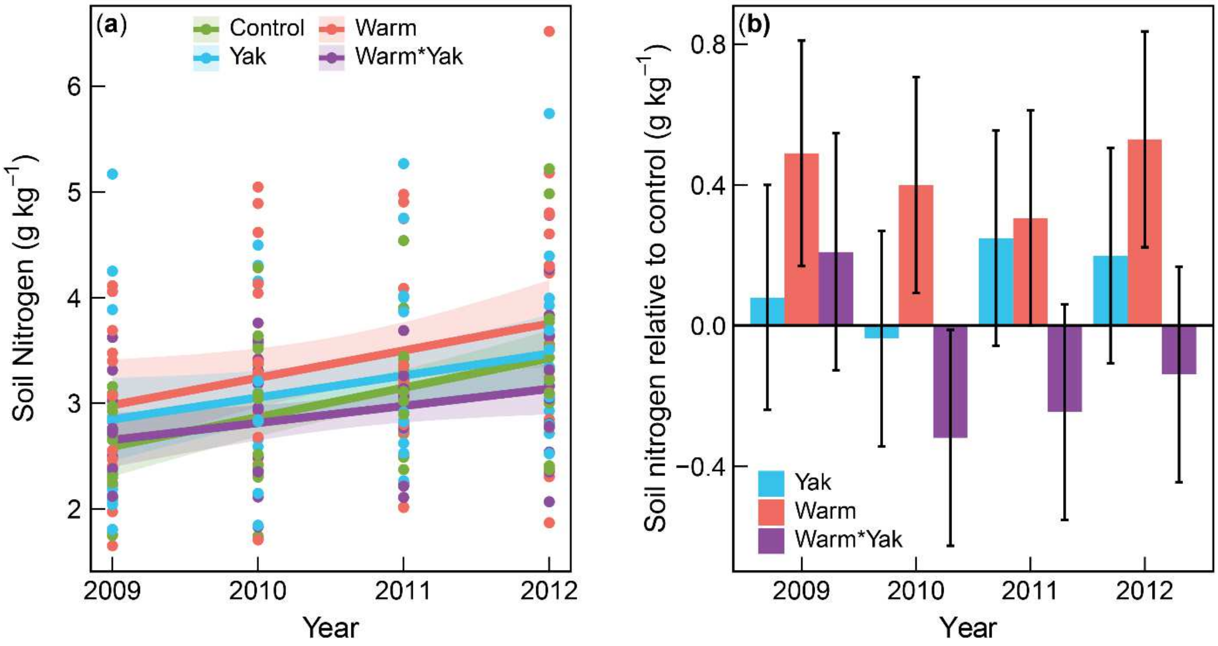

Figure 3.3. Soil nitrogen concentrations with 95% confidence intervals for warming and grazing treatments from 2009-2012 (a). Mean (± SE) soil nitrogen concentrations in treatments relative to controls (b).

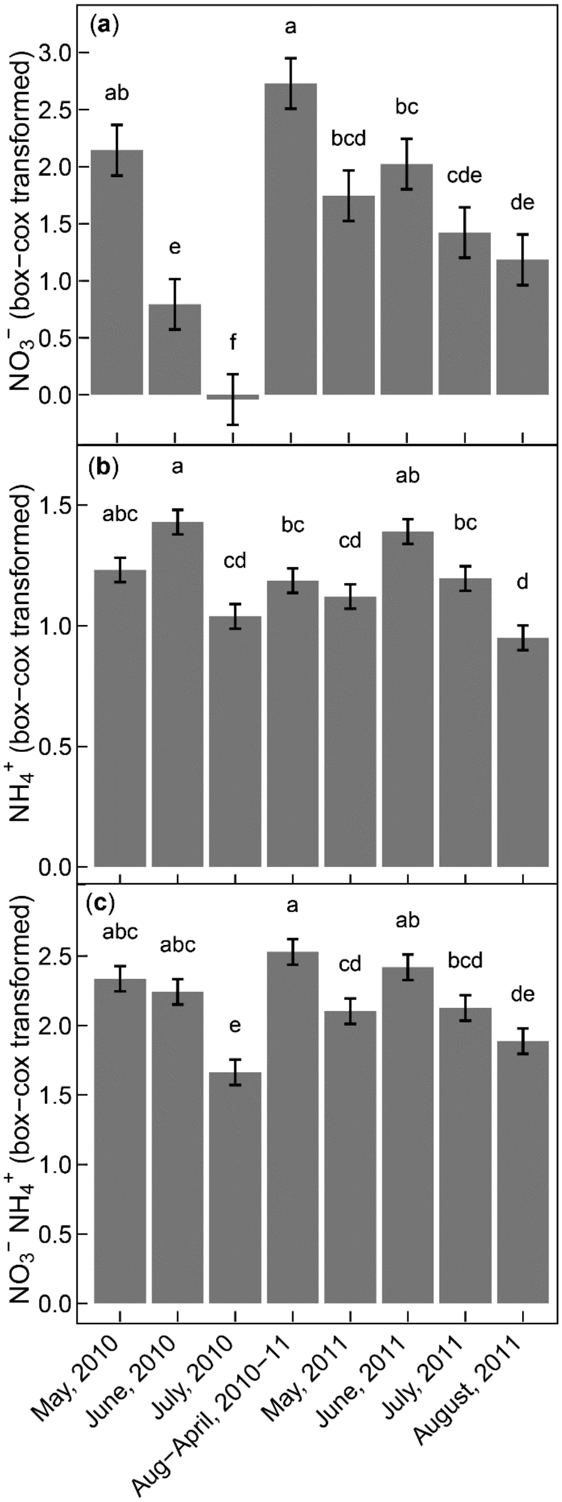

Figure 3.4. Mean (± SE) inorganic soil nitrogen supply rates from NO_3^- (a), NH_4^+ (b), and their sum (c) averaged across all treatments for each sampling period. Data were box-cox transformed to see temporal patterns without the skew caused by high N levels in yak treatment plots. Bars with different letters above them are significantly different at $P < 0.05$.

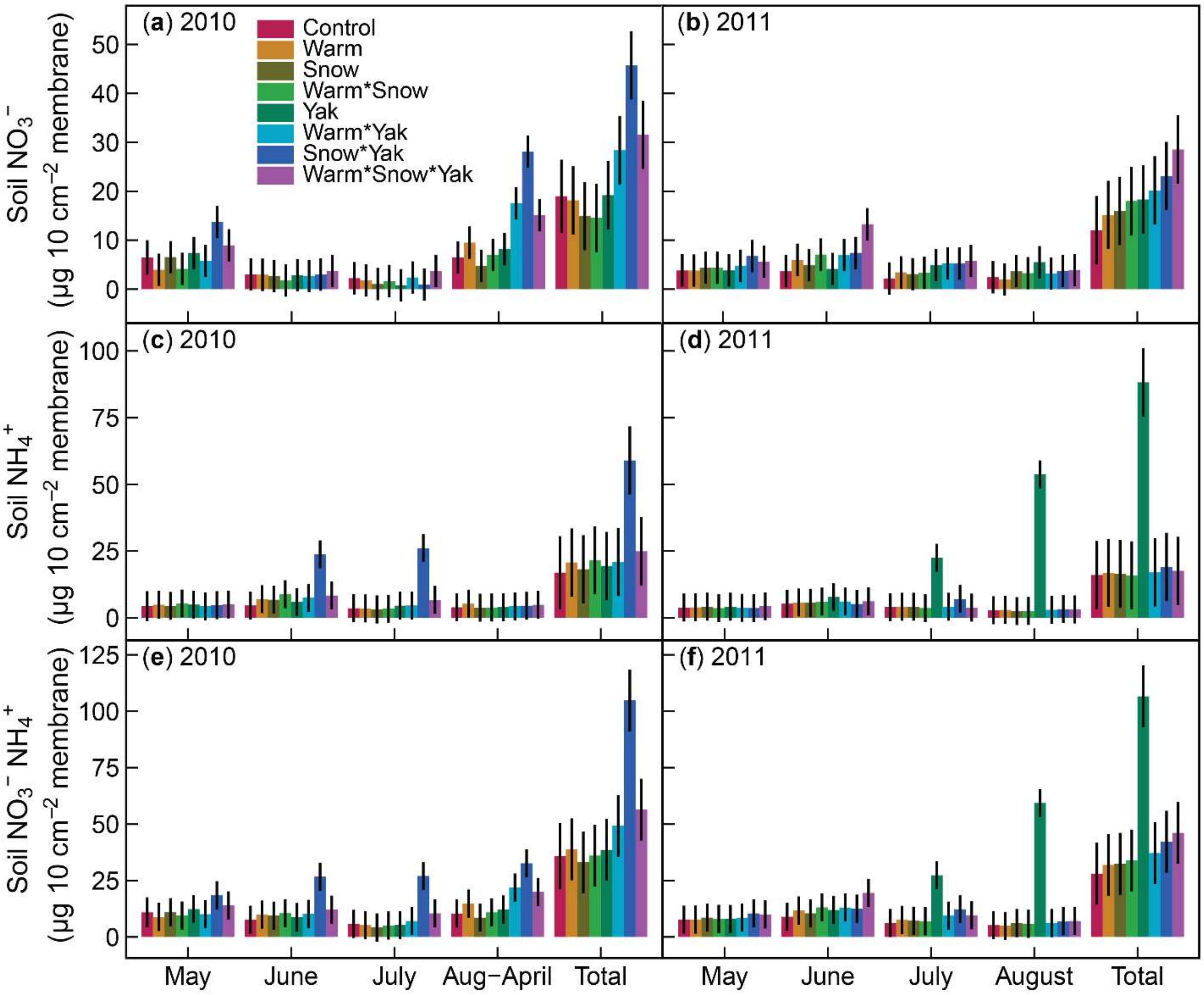

Figure 3.5. Mean (± SE) inorganic nitrogen supply rates in the top 10 cm of soil, measured with PRS probes as NO_3^- (a, b), NH_4^+ (c, d), and their sum (e, f). In 2010, probes were buried from August through the following April, so the total sum represents annual N availability from May through April, whereas in 2011 the total sum represents the growing season from May through August. Yak grazing occurred for the following durations in each nitrogen sampling period: May, 2010 – 0 days; June, 2010 – 1 day; July, 2010 – 3 days; August, 2010 – 2 days; May, 2011 – 0 days; June, 2011 – 3 days; July, 2011 – 6 days; August, 2011 – 3 days.

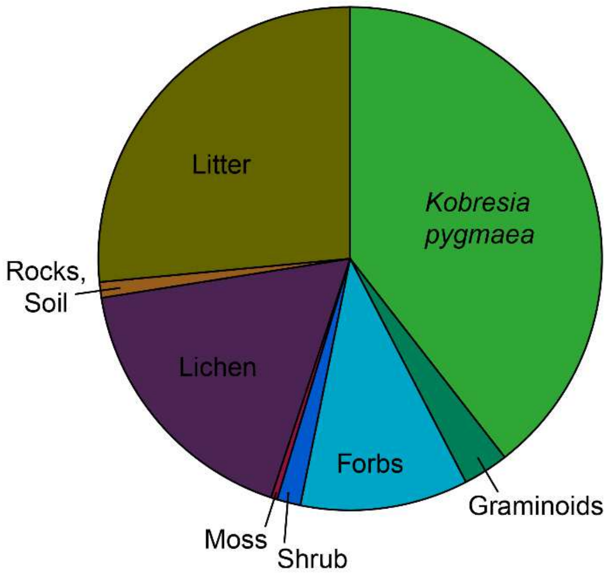

Figure 3.6. Mean areal cover in control plots across years.

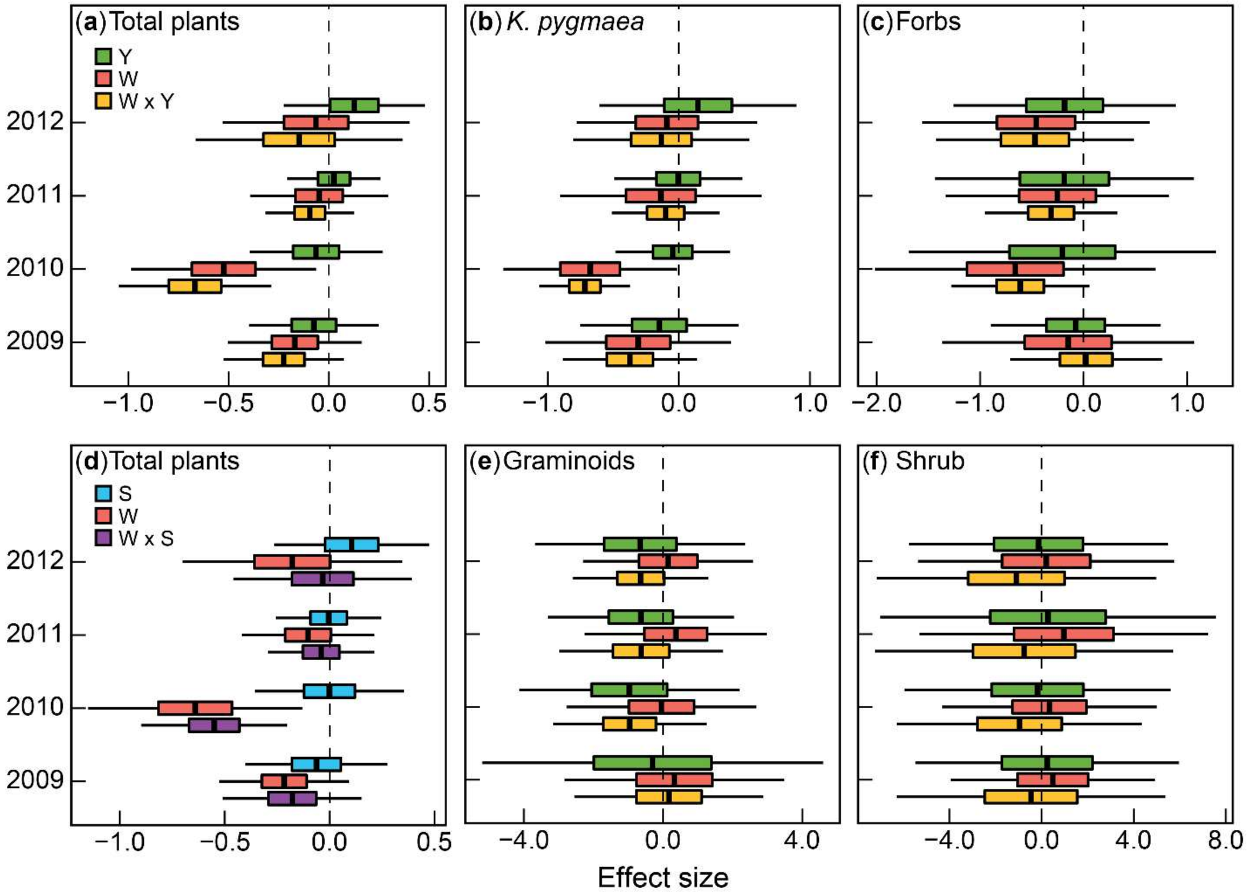

Figure 3.7. Log-response ratios of plant cover in treatments relative to control plots each year from 2009-2012. Positive values indicate increases in plant cover and negative values indicate decreases in cover relative to the control. Effect sizes for warm x graze treatment interactions are shown for total plant cover (a), *K. pygmaea* (b), forbs (c), other graminoids (e), and the shrub, *Potentilla fruticosa* (f), and the warm x snow interaction is shown for total plant cover (d). Heavy black lines are descriptive treatment means, colored boxes span from 25th to 75th quartiles, and whiskers encompass 95% of the data points for each treatment.

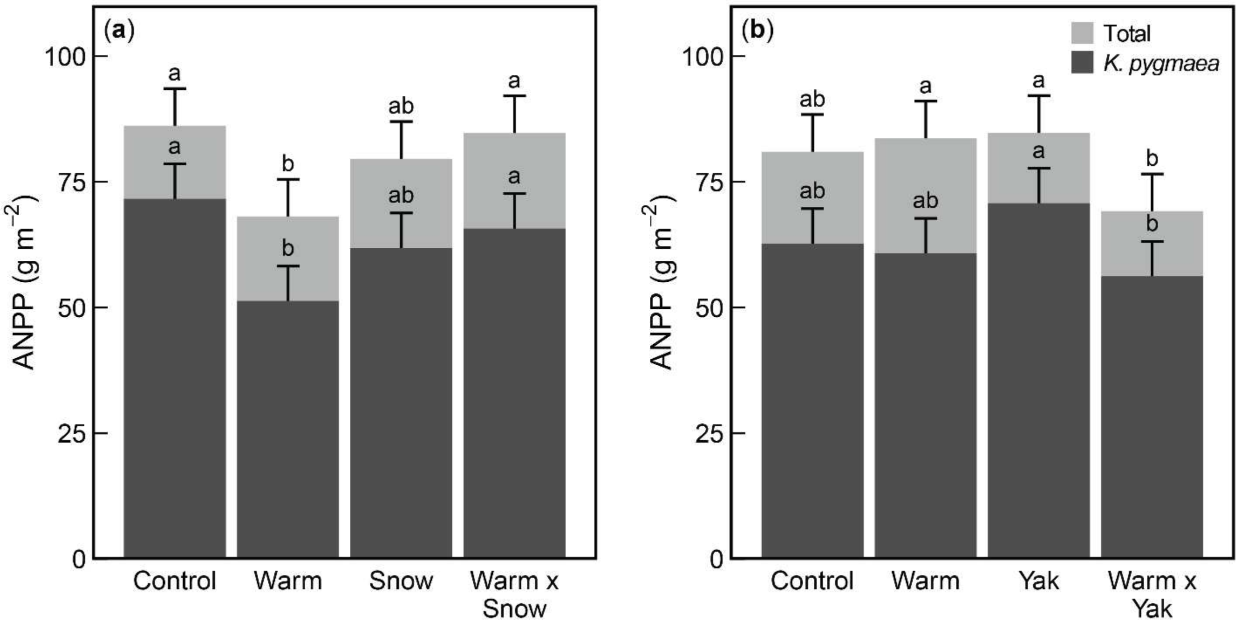

Figure 3.8. Mean (±SE) total and *Kobresia pygmaea* ANPP under warming x snow (a) and warming x yak (b) treatments. Lowercase letters indicate significant treatment differences at $p < 0.05$ for total ANPP and for *K. pygmaea* ANPP.

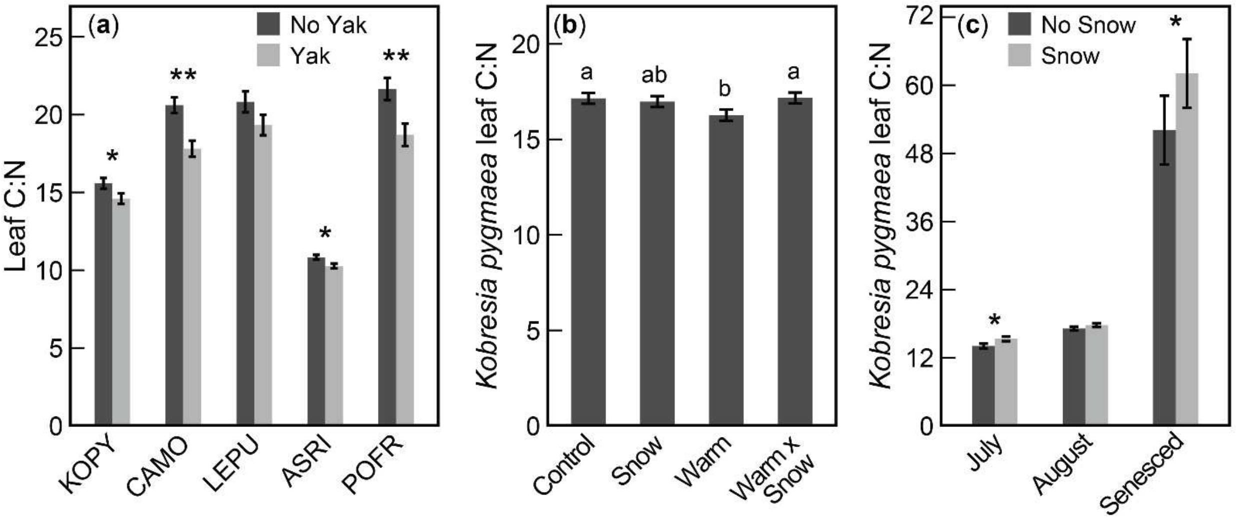

Figure 3.9. Mean (± SE) leaf tissue C:N for focal species in August, 2012 (a), *K. pygmaea* averaged across years for August, 2009-2012 (b), and *K. pygmaea* from sampling dates during and after the 2011 growing season (c). Significant treatment differences are indicated by * ($p < 0.01$), ** ($p < 0.001$) or by different lower-case letters ($p < 0.05$). Four-letter species abbreviations are for the sedges *Kobresia pygmaea* and *Carex moorcroftii*, the forbs *Leontopodium pusillum* and *Astragalus rigidulus*, and the shrub *Potentilla fruticosa*.

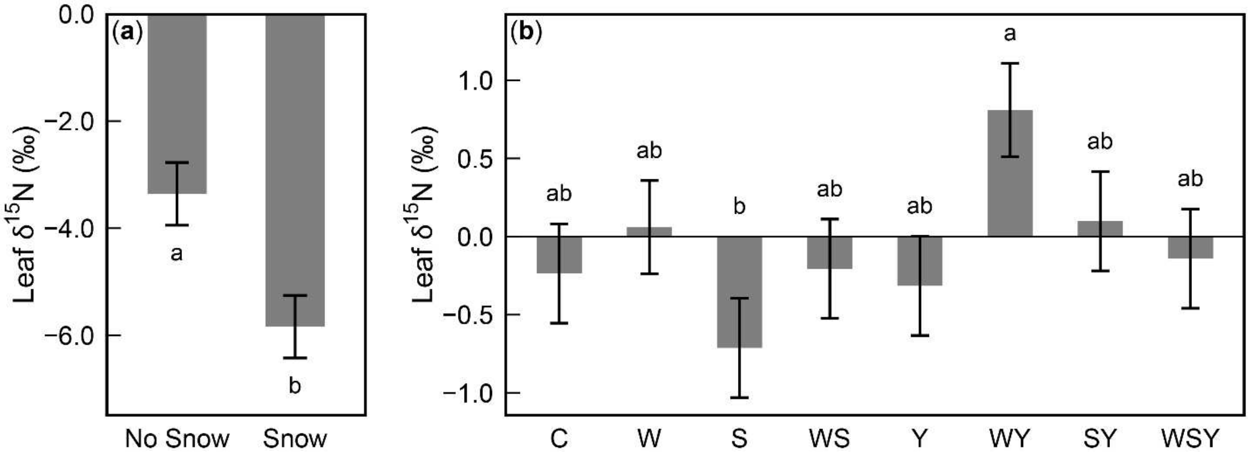

Figure 3.10. Mean (± SE) leaf δ^{15}N in senesced *K. pygmaea* leaf tissue that grew in 2011 (a) and *L. pusillum* tissue from August, 2012 (b). Treatments with different lowercase letters are significantly different at $p < 0.05$. (Treatment abbreviations: "C" = control, "W" = warm, "S" = snow, "Y" = yak)

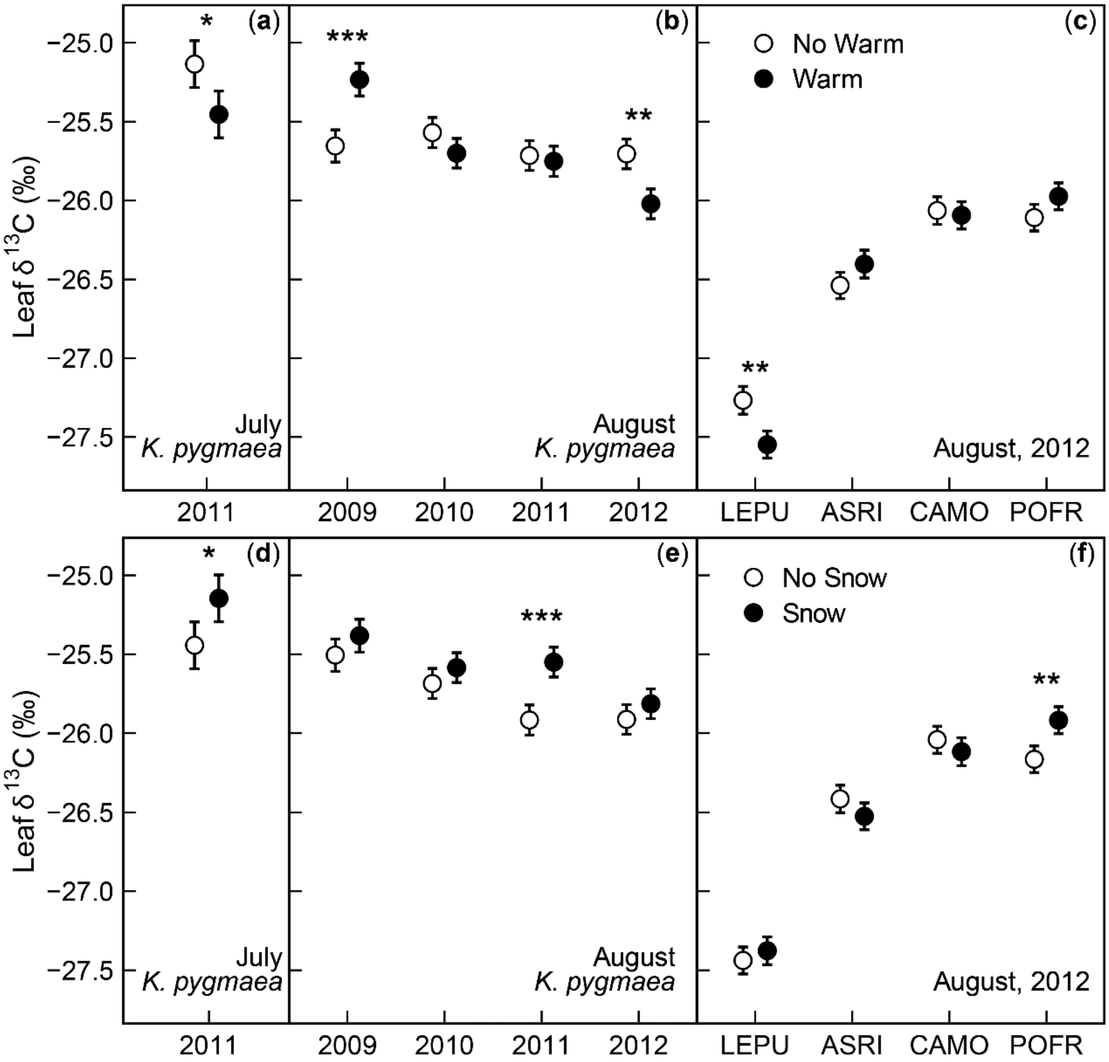

Figure 3.11. Mean (± SE) leaf tissue δ^{13}C from warming (a-c) and snow addition (d-f) treatments. *Kobresia pygmaea* was sampled in July, 2011 (a, d) and in August, 2009-2012 (b, e). *Leontopodium pusillum* (LEPU), *Astragalus rigidulus* (ASRI), *Carex moorcroftii* (CAMO), and *Potentilla fruticosa* (POFR) were also sampled in August, 2012 (c, f). Significant treatment differences within a sampling period and species are indicated by * ($p < 0.10$), ** ($p < 0.05$), *** ($p < 0.01$).

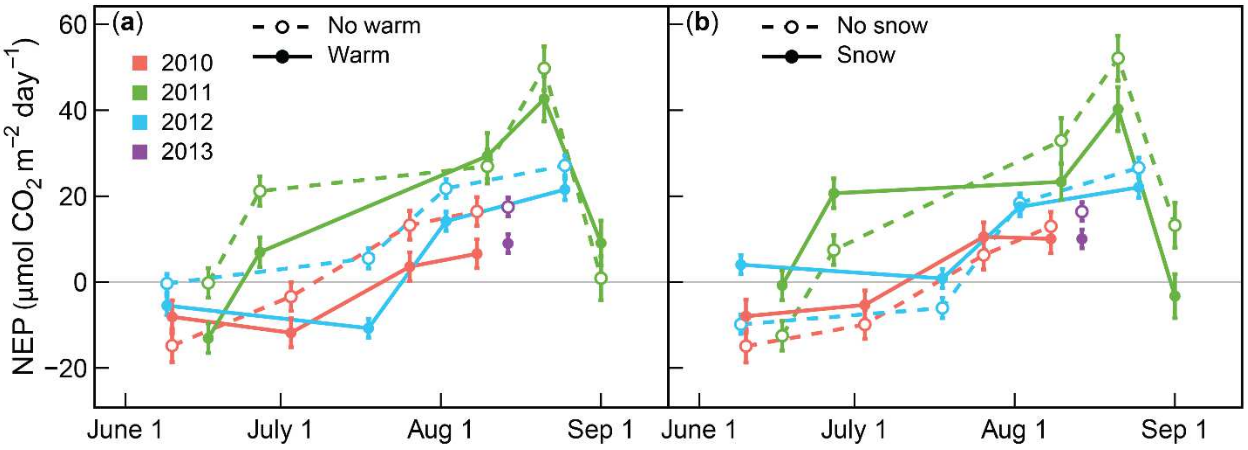

Figure 3.12. Mean (± SE) net primary production (NEP) integrated over 24-hour sampling periods under warming (a) and snow (b) treatments each year. There was only one August sampling date in 2013. Positive values represent net CO_2 uptake, and negative values represent net CO_2 efflux.

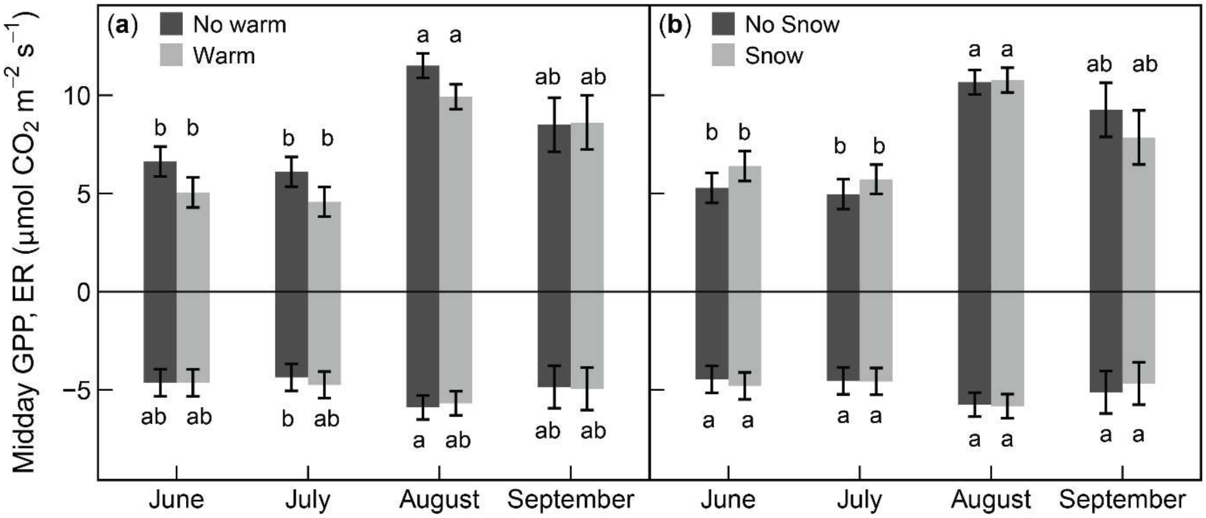

Figure 3.13. Mean (± SE) midday ecosystem CO_2 fluxes (measured from 11:00-15:00) averaged by month across years 2010-2013. Gross primary production (GPP) values are positive and ecosystem respiration (ER) is negative. Months that share lowercase letters are not significantly different ($p < 0.05$). Although there were no significant differences for warming (a) or snow (b) treatments within each month, warming significantly lowered GPP overall ($F_{1,270} = 3.94, p < 0.05$). There were no significant treatment effects on ER.

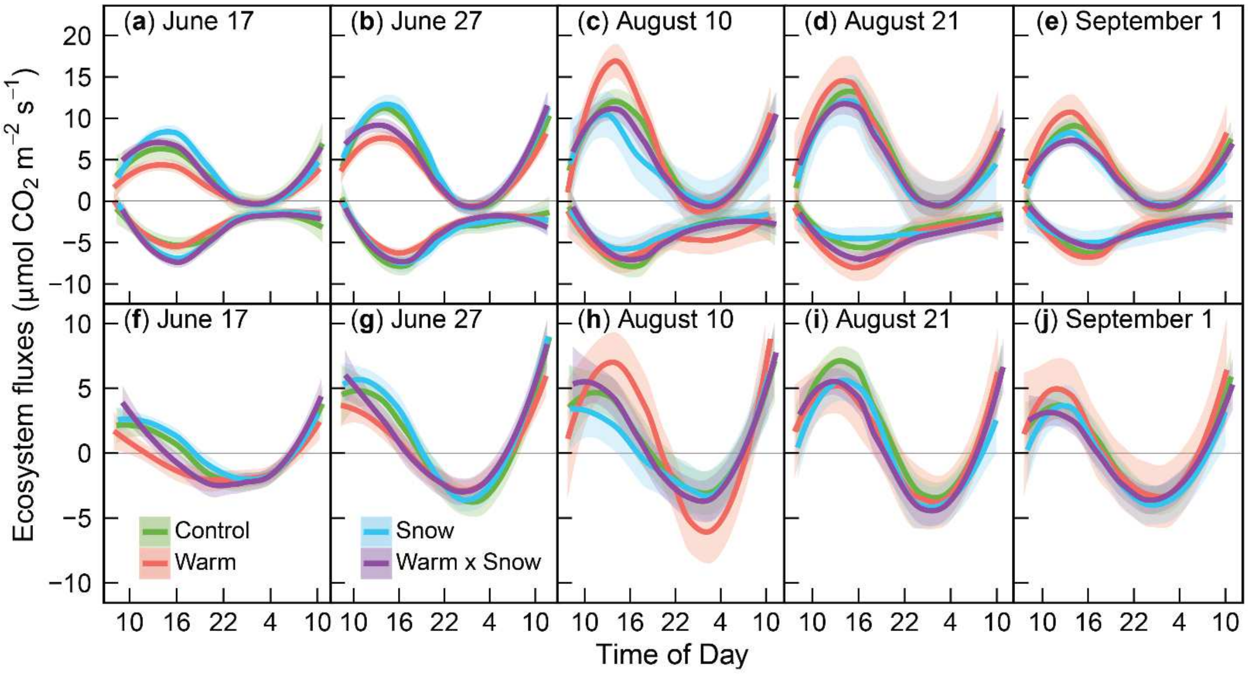

Figure 3.14. Diurnal pattern of GPP (positive) and ER (negative) fluxes (a-e) and their net balance (NEP; f-j) throughout the 2011 growing season. Lines and shaded bands represent means and 95% confidence intervals, respectively, with loess smoothing. Time of day spans a 24-hour period from 10:00 to 10:00, China Standard Time.

Chapter 4

Experimental and observational evidence of warming and grazing impacts on ecosystem services: Implications for carbon sequestration and forage production on the Tibetan Plateau[5]

"Without grassland, no livestock. Without livestock, no life."

- Tibetan pastoralist, age 25

4.1 Introduction

Global change is altering ecosystems at an unprecedented rate, with consequences for their ability to continue providing the services on which humans depend (Christensen et al., 2013; MEA, 2005). Yet in spite of the need for a comprehensive understanding of how ecosystem structure and function will respond to global change, its multiple, interacting factors often produce nonlinear and surprising ecological effects that can be challenging to predict, particularly from past conditions or short-term observations alone (Chapin et al., 1995; Coreau et al., 2009; Shaver et al., 2000; Smith et al., 2009; Zhou et al., 2008). Furthermore, although climate and land use change are two of the global change factors with the most dramatic effects on ecosystems globally (Vitousek, 1994), the relative importance of these drivers and the ways in which they interact will differ across regions (Sala et al., 2000). Thus, to understand current ecological changes and to extrapolate about their future trajectories will require an approach that considers interacting global change drivers in specific systems, while also integrating across temporal, spatial, and ecological scales (Luo et al., 2011; Smith et al., 2009). Here, I combine experimental and observational methods to examine how alpine meadows on the Tibetan Plateau will respond to the ongoing

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[5] This chapter will be submitted for publication with my co-authors Tsechoe Dorji and Julia A. Klein.

pressures of climate warming and changing pastoral land management policies, and what this will mean for these ecosystems' provision of locally and globally important ecosystem services.

While some ecosystem processes will respond quickly to global change drivers, other effects on ecosystem functioning will take longer to emerge. This temporal complexity arises, in part, because some processes will be affected directly by climate and land use changes, while others will be the product of indirect effects (Farrer et al., 2015) and cascades of ecological responses (Shaver et al., 2000; Wookey et al., 2009). Initially, rapid changes in physiology and metabolism will affect "fast" variables, such as rates of photosynthesis and respiration (Shaver et al., 2000; Smith et al., 2009). Species-reordering will occur as some individuals begin to out-compete others under the new conditions, and over longer timescales, local extinctions and immigration of new species will further change the ecosystem structure (O'Connor et al., 2012; Smith et al., 2009; Williams et al., 2007). These shifts will in turn affect production, microclimate, microbial composition, and litter quality, all of which will affect rates of decomposition and nutrient cycling (Cornelissen et al., 2007; Cornwell et al., 2008; Hobbie, 1996; Klein et al., 2007; Shaver et al., 2000; Yang et al., 2013). The implications of these cascading effects for the ongoing provision of ecosystem services are also difficult to anticipate from short-term observations if ecosystems cross unforeseen thresholds, irretrievably losing their previous functioning (Folke et al., 2004). Alternatively, ecosystem functions that were lost initially, such as carbon sequestration, may be recovered as the community shifts to a new composition better suited to the new environmental conditions (Chapin and Shaver, 1996; Saleska et al., 2002; Smith et al., 2009).

Predicting ecosystem responses to global change will therefore require mixed methods approaches that can capture both shorter- and longer-term processes (Dunne et al., 2004; Fukami and Wardle, 2005; Wookey, 2008). Ecological experiments are useful in their ability to determine causal relationships, but they are usually confined to short timeframes, have unintended artifacts, and are limited in their ability to manipulate only a few factors. Observational studies that make use of environmental gradients that mirror expected conditions under global change, such as latitudinal or elevational gradients that create a natural range of temperatures or soil moistures (Gottfried et al., 2012; Walker, 2000), can provide insight into the structure and function of established communities under these varying conditions. However, gradient studies may also be limited in their ability to predict future ecosystem functioning if, for example, there are co-varying abiotic factors along the gradient (Walker, 2000) or interspecific interactions (Brooker et al., 2007) that confound extrapolation from extant communities to those that will emerge under novel future conditions. When combined, experimental and observational approaches can mitigate each other's weaknesses to give more robust insight into ecosystem responses to global change (Dunne et al., 2004; Fukami and Wardle, 2005; Wookey, 2008). Interpretation of results will be simplest when responses to experiment treatments match the magnitude and direction of responses along the environmental gradient as expected (Dunne et al., 2004). Yet discrepancies between treatment and gradient effects (Elmendorf et al., 2015) can also suggest unforeseen responses, including tipping points that may not be reached in shorter-term experiments (Luo et al., 2011).

Alpine ecosystems on the Tibetan Plateau are particularly sensitive to the impacts of global change (Chen et al., 2013), and widespread reports of degradation (Harris, 2010; Yundannima, 2012) indicate that some areas may already be crossing environmental tipping points that will affect their ability to provide valuable ecosystem services (Wen et al., 2013). Tibet's alpine meadows make up the largest alpine ecosystem in the world[6] and are characterized by strong dominance of a grazing-adapted species of dwarf sedge, *Kobresia pygmaea* (Miehe et al., 2008).

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[6] Alpine meadows account for approximately 42% of the entire Plateau (Zhang et al. 2007) and 0.9% of the total area of the world's grasslands (Miehe et al. 2008; White et al. 2000)

These meadows provide locally important ecosystem services by supplying forage for wildlife and livestock (Klein et al., 2008; Miehe et al., 2009). They also provide a globally important service by acting as a net carbon sink (Kato et al., 2006). Alpine meadows contain the largest carbon pools of any ecosystem type on the Tibetan Plateau (Zhang et al., 2007) and of any grassland type in China (Ni, 2002), accounting for approximately 26% of the carbon stored in China's grassland soils and 1-2% of carbon stored in grassland soils globally (Ni, 2002; White et al., 2000; Yang et al., 2008). In intact alpine meadows, livestock grazing has been found to increase the allocation of resources to belowground production, causing these meadows to become a stronger carbon sink under traditional management practices (Gao et al., 2007; Hafner et al., 2012; Shi et al., 2013).

While some research has shown no decline in the carbon sink strength of these meadows over the past several decades (Yang et al., 2009a), others report that degradation is driving them to have net carbon losses at a regional scale (Xie et al., 2007) due to changing climate (Wang et al., 2002; Zhang et al., 2007) or overgrazing (Chang et al., 2014). Alpine meadows that have transitioned into a degraded state, marked by lower primary production and dominance of crustose lichens and blue-green algae, exhibit lower rates of carbon fluxes to the atmosphere and smaller soil organic carbon pools (Babel et al., 2014; Unteregelsbacher et al., 2011). However, if alpine meadows eventually shift to more of a shrub meadow state in response to climate warming, as predicted by studies from Tibet and across the tundra biome (Brandt et al., 2013; Büntgen et al., 2015; Elmendorf et al., 2012b; Walker et al., 2006), then there is evidence that more woody plant production could lead to higher rates of carbon sequestration, thus regaining the Plateau's carbon sink strength potential (Fu et al., 2009; Klein, 2003; Sweet et al., 2015; Yashiro et al., 2010; Zhao et al., 2006), though at the cost of palatable forage production (Klein et al., 2007).

Although consensus about the drivers of degradation in these alpine meadows has not been reached in the scientific literature (Harris, 2010; c.f. Klein et al., 2007; Wang et al., 2012), policies tend to focus on overgrazing as its primary cause (Bauer and Nyima, 2010). As a result, pasture management reforms are effectively reducing livestock stocking rates and mobility (Bauer and Nyima, 2010; Klein et al., 2011), thus inducing a shift in land use by modifying or eliminating livestock grazing. At the same time, climate warming on the Tibetan Plateau to date has been significant (Wang et al., 2008) and is projected to continue increasing at rates above the global mean (Christensen et al., 2013). It is therefore necessary to develop a better understanding of how changing climate and land management practices are interacting to affect Tibet's alpine meadow ecosystems in the short term as well as over longer timescales, during which slower ecological processes, such as carbon storage, will be affected.

In this study I combine experimental and observational approaches to understand the effects of climate warming and livestock grazing and its removal on Tibetan alpine meadows. First, I test whether short-term responses to experimental climate and grazing manipulations suggest a trajectory of community composition change consistent with other healthy, degraded, and shrub meadow communities already established around the landscape. Second, I examine the ability of these different communities to provide two key ecosystem services, forage production and carbon sequestration, to examine the implications of these community shifts for ecosystem functioning under future climate and grazing scenarios.

4.2 Methods

4.2.1 Study area

I conducted this study in the summer pastures of an administrative village in Namtso Township, in the Tibet Autonomous Region of China (Fig. 4.1). The study region covers an area of about 360 km^2. Its elevation ranges from approximately 4575-5600 m a.s.l., with a mean of 4900 m a.s.l., and the experiment is located at 4875 m a.s.l. (30.72 ^oN, 91.05 ^oE). Alpine meadows are the dominant plant community (Fig. 4.2a,g), with wetlands, shrub meadows (Fig. 4.2b), and alpine steppe also present across the landscape. The region experiences a monsoon climate, with over 80% of the precipitation falling during the May-September growing season. The mean annual precipitation is 461 mm, and the mean annual temperature is -0.49 ^oC, as measured by a nearby weather station from 2006-2013 (NAMORS). The Tibetan Plateau has already experienced significant warming of 0.36 ^oC per decade since 1961 (Wang et al., 2008). Yet summer and annual mean temperatures are projected to continuing rising over the next century at a higher rate than the global mean, with an additional increase of 2.5 ^oC in the summer and 2.6 ^oC annually by 2100 (50th percentile of projections from 42 CMIP5 global models; (Christensen et al., 2013).

This area has long been used by local pastoralists as summer grazing pastures. Livestock numbers have decreased nearly linearly since 2005, when limits on the number of livestock per capita were first imposed (Hopping et al. in review). In 2005 there were 39,933 livestock for 227 households (1358 people), and by 2012 there were 25,475 livestock for 320 households (1529 people), according to local administrative census data. As the total number of livestock decreased, the aggregate herd composition shifted toward a larger proportion of yaks, although sheep remain the most abundant (2005: 21% yak, 67% sheep, 12% goats, 0.68% horses; 2012: 33% yaks, 58% sheep, 8% goats, 0.84% horses). Pastoralists still move their herds daily (Dorji et al., 2014), although they report that their mobility has decreased due to recently fenced administrative boundaries and wetlands (Hopping et al. in review).

4.2.2 Experiment

I set up a climate change and grazing experiment at Namtso in 2009 with four fully crossed factors: simulated climate warming, spring snow additions, controlled yak grazing, and pika exclusion (Dorji et al., 2013; Hu et al., 2013). The warming, snow, and yak manipulations are applied to five 1 m^2 subplots within a single plot approximately 8 m in diameter. The different subplots allow us to make destructive measurements in some areas while leaving others unharmed for repeated vegetation measurements. Pikas are excluded over larger areas, and the other factors are nested within the pika exclosures (see Hu et al. (2013) for a visualization of the layout). However, since I was unable to exclude pikas effectively throughout the experiment, I treat the potential effects of my attempts to exclude them only as a random factor in analyses, thus yielding a randomized block design with 8 replicates of each of the remaining 8 treatments. With this study, I focus only on the independent and interactive effects of climate warming and yak grazing, since these factors are also occurring naturally in the region, thus allowing us to directly compare causal effects in the experiment with observations around the landscape. This leaves us with four treatments (Control, Warm, Yak, Warm x Yak) with 8 replicates (n=32).

To simulate climate warming, I installed conical, open top chambers made of Sun-Lite HP fiberglass (Solar Components Corporation, Manchester, New Hampshire, USA; Hollister and Webber, 2000; Marion, 1996; Marion et al., 1997). The chamber bases are 1.5 m in diameter, and they are elevated to 5 cm above the ground to allow air flow and pika entry. The chambers passively warm the plots during each growing season (May 24 or earlier to August 24 or later)[7]. I remove them during the remainder of the year to prevent damage and to avoid the confounding effects of ambient snow capture or exclusion.

To test the effects of yak grazing, I brought yaks at intervals throughout the growing season to graze at offtake rates similar to ambient grazing conditions in the region. To control the amount and location of yak grazing in the experiment, local herders brought their yaks and tethered them to stakes in the center of each grazing plot for approximately 7 hours per day for 3-day periods throughout the summer. I repeated these grazing periods 3 to 4 times each summer, except grazing occurred once in 2009 when I were establishing the experiment and once in 2013, due to limited labor availability. The radius of the ropes allowed the yaks to reach all subplots within a grazing plot, but not into adjacent plots. I removed warming chambers on grazing plots when yaks were present. Herders collected dung from the plots under the same conditions that they collect it from around the landscape to use as fuel.

I estimated grazing offtake by yaks and differentiated it from pika grazing by quantifying the area and height of grazed patches before and after yaks were brought to the plots. I used these measurements to calculate a volume of vegetation removed by yaks, and then I applied an off-plot biomass regression to convert the volume into an estimate of biomass removed (Harte and Shaw, 1995; Klein et al., 2007). I repeated these measurements throughout the growing season around the landscape, outside of the experiment, to verify that the rates of offtake in the grazing treatment were simulating local conditions of offtake in healthy alpine meadows.

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[7] 2010: DOY 133-236 (May 13 – August 24); 2011: 133-246 (May 13 – September 3), 2012: 144-239 (May 24 – August 27), 2013: 142-243 (May 22 – August 31)

4.2.3 Landscape plot selection

Near the peak of the growing season, from August 16-24, 2013, I selected 51 plots (n=17 healthy meadow, 16 degraded meadow, 18 shrub meadow) throughout the summer pastures of the administrative village in which the experiment is also located (Fig. 4.1). Healthy meadow and shrub meadow sites were selected based on their visual appearance at a distance (Fig. 4.2a,b) and by asking local herders to direct us toward shrub meadow areas. These shrub meadows are composed of prostrate shrubs (*Potentilla fruticosa*, Fig. 4.2e) that are mixed with other alpine meadow graminoids and forbs, thus making them relatively inconspicuous on the landscape (Fig. 4.2h). In this region *P. fruticosa* does not form dense, erect stands as it does in other, more productive areas of the Plateau (e.g., Klein, 2003). Degraded meadows (Fig. 4.2c) were selected a priori based on evidence from satellite images that their productivity had declined in the previous two decades relative to other meadow areas. This ensured that I would capture areas that had recently undergone some degree of degradation from a relatively healthier meadow state, rather than merely capturing areas that were always less productive and thus might not be indicative of degradation as a process, per se. All sampling plots in degraded and healthy meadows were located in areas with similar vegetation for at least 60 meters in all directions to ensure that these points would be representative of 2 pixels in the Landsat images. However, it tended to be difficult to find areas of shrub meadow that were this expansive, and most have fallen within 30 m^2, or one pixel.

To locate degraded areas, I identified vegetation changes using Landsat TM satellite images from September 14, 1991 and September 15, 2009, which I downloaded from the USGS Earth Explorer portal (http://earthexplorer.usgs.gov/). These dates were selected because they were two of the only Landsat images available in the archive that were mostly cloud-free, collected on nearly the same date, during or after the peak of the growing season but before its end, and spanning as long of a time period as possible. The 1991 image was from NASA's Tri-Decadal Global Landsat Orthorectified data, so I georectified the 2009 image to the 1991 image (root mean square error < 0.5 pixel) using ERDAS IMAGINE (v. 13.0, ERDAS, Inc., Norcross, GA, USA). To correct for atmospheric conditions, I applied NASA's LEDAPS tool to the 2009 image (Masek et al., 2006) and used dark object subtraction (Song et al., 2001) for the 1991 image because it lacked the metadata necessary to be processed by LEDAPS. Using ArcMap (v. 10.1, ESRI, Redlands, California, USA), I clipped out all un-vegetated surfaces, alpine steppe, and wetlands to obtain an approximation of the total meadow area in the administrative village for both images. Next I applied the Tasseled Cap (TC) algorithm to derive indices of brightness, greenness, and wetness (Crist and Cicone, 1984). I took the difference in each TC index between 1991 and 2009, re-stacked them, and visually inspected the resulting changes to locate areas where meadow vegetation had declined in greenness and increased in brightness relative to other meadow areas as an indicator of declining vegetation cover and productivity. These degraded meadow sites were located in the field using an eTrex GPS (accuracy < 3 m; Garmin, Inc., Olathe, Kansas, USA). I avoided sampling in areas that had become less productive due to intensive and localized land uses, such as livestock bedding areas and vehicle tracks.

4.2.4 Data collection

4.2.4.1 Microclimate

In the experiment, I measured air temperature (+10 cm), soil temperature (-10 cm), and soil moisture (-10 cm) every 15 minutes in every treatment plot throughout the growing season, using Decagon ECT air temperature sensors with radiation shields, EC-TM and 5TM soil sensors, and

EM50 loggers (Decagon Devices, Inc., Pullman, Washington, USA). The soil sensors integrated across the top 10 cm belowground. Within each plot, the sensors were permanently located in the center of one subplot adjacent to the subplot for measuring plant species composition and ecosystem functioning. I calibrated the EC-TM and 5TM soil sensors to field soils and applied these calibrations to all dielectric moisture data to obtain volumetric soil water content.

In the landscape plots, I made micrometeorological measurements at the time of CO_2 flux and species composition measurements. I measured soil temperature with a digital thermometer (JM-624, Jinming Corp., Tianjin, China) and volumetric soil moisture with a portable soil moisture sensor (-6 cm; Delta-T Devices, Cambridge, UK). For 19 of the 51 plots (distributed across the three plant community types) I was unable to use the soil moisture probe and collected soil cores instead, from which I obtained gravimetric water content measurements that I converted to volumetric water content.

4.2.4.2 Vegetation

I measured vegetation species composition in mid-August, near the peak of the growing season, using point-intercept and areal cover methods (Bonham, 1989). In the experiment I used a 0.75 x 0.75 m quadrat divided into 400 squares that I placed on permanent pegs to ensure that the same area within each treatment plot was sampled every year. First I visually estimated the areal cover of all species and other non-vegetation cover types in the 400 squares, with estimates at a spatial resolution down to 1/6 of a square (2010-2012). Then I recorded the species intercepted by a pin at 100 points in the quadrat and recorded multiple species on the few occasions when the pin intercepted taller vegetation overhanging shorter vegetation (2010-2013). I didn’t have permanent plots established around the landscape, so for these measurements I recorded the species intercepted at 60 points in the quadrat, at the same spatial resolution as in the experiment, within a 0.50 x 0.50 m area corresponding to the exact area enclosed by the chamber used for CO_2 flux measurements.

To monitor shrub aboveground primary production (ANPP) in the experiment, I used a non-destructive sampling method modified from Klein et al. (2007) and Harte and Shaw (1995). In addition to the areal cover measurements for *P. fruticosa*, I also measured the height of 5-10 *P. fruticosa* stems in each plot. Then I made the same measurements off-plot, but for these I also clipped all new *P. fruticosa* growth from that year, distinguishable by its not-yet woody stems. I oven-dried and weighed the harvested biomass and used it to construct a linear regression against the area covered by *P. fruticosa* in each off-plot quadrat. The R^2 values were > 0.90 for this relationship every year. I applied this regression to the areal cover of *P. fruticosa* in each treatment plot and multiplied the resulting biomass estimate by the proportion of the *P. fruticosa* height in that plot relative to the height of *P. fruticosa* in the destructively harvested plots to obtain final estimates of shrub ANPP. In 2013 I only collected point-intercept data and therefore don't have biomass estimates for this year.

4.2.4.3 Ecosystem CO_2 fluxes

To understand the effects of warming, grazing, and different plant community structures on carbon cycling, I measured net ecosystem production (NEP) and ecosystem respiration (ER), from which I also derived gross primary production (GPP), in the experiment and landscape plots. In the experiment, I measured CO_2 fluxes on August 14, 2103, from 11:00-15:00 in the same subplots in which I also measured species composition and yak grazing offtake, with three replicates per Control, Yak, Warm, and Warm x Yak treatments (n=12). In warmed plots, I placed the ecosystem CO_2 chamber directly inside the open top warming chambers. For the landscape CO_2 flux measurements, I sampled between 10:00 to 17:00 from August 16-24, 2013. I stratified the order of measurements in healthy, degraded, and shrub meadows within each day and across the 9-day sampling period to eliminate potential biases in light levels, weather conditions, and phenological changes. I measured CO_2 fluxes in each plot before making other microclimate, vegetation, or soil measurements to avoid creating any disturbances to the fluxes. I present midday values as an indicator of these ecosystems' functioning near the peak of the growing season (Shaver et al., 1998).

For CO_2 flux measurements I used a LI-6400 portable photosynthesis system (LI-COR Inc., Lincoln, Nebraska, USA) attached to a custom ecosystem chamber (0.50 x 0.50 x 0.25 m), as described in Hu et al. (2013) and modified from Saleska et al. (1999) and Vourlitis et al. (1993). I moved the ecosystem chamber and a portable base between plots, rather than installing permanent bases that would disrupt the soil and vegetation. For each measurement I ensured that the chamber orientation was always the same to prevent the infrared gas analyzer from shading the plot. I created a closed chamber volume by sealing the base to the ground with a plastic skirt weighted by a heavy chain. Air inside the ecosystem chamber was mixed with two small fans, and a tube vented to the outside to prevent pressure build-up. The pressure sensor in the LI-6400 was calibrated to lower air pressures (57.42 kPa) to accommodate the atmospheric conditions of this high-elevation study area. A thermocouple and quantum sensor attached to the LI-6400 measured air temperature and photosynthetically active radiation (PAR) in the chamber throughout each flux measurement.

To estimate NEP, I made three consecutive measurements at ambient light conditions in each plot. Following the NEP measurements, I covered the ecosystem chamber with an opaque shroud to block all light and stop photosynthesis, thus giving us an estimate of ER. First I recorded ambient CO_2 concentrations for each plot by setting the chamber on its side beside the plot. Next I placed the chamber on the base, allowed conditions to stabilize for 20 seconds, and then logged the CO_2 concentration inside the chamber every two seconds for 60 seconds (Saleska et al., 1999; Street et al., 2007). After allowing the chamber to vent until it regained ambient CO_2 concentrations, I repeated the measurement. I then used the sequence of CO_2 fluxes across the 60-s period to calculate a single flux value at ambient CO_2 concentration, as described in more detail below.

4.2.4.4 Soil resources

From 2009-2012, I collected 10-cm-deep soil cores from each experiment plot in August to measure their carbon (C) and nitrogen (N) resources. In 2013, after completing the CO_2 measurements in the landscape plots, I collected two 10-cm-deep soil cores in each plot to estimate soil bulk density and C and N content. I sieved all soil cores with a 2-mm sieve, removed roots and stones > 2 mm, and oven-dried them all at 110 ^{0}C for 24 hours. I did not find carbonates when I tested the soils with HCl. For the cores used to measure total soil C and N, I ground the soil to a fine powder and analyzed subsamples on a LECO Tru-Spec CN analyzer (LECO Corp., St. Joseph, MI, USA).

4.2.5 Data analysis

4.2.5.1 Climate

I calculated mean daily values for the 15-minute micrometerological data from the experiment plots. For yearly growing season averages, I took the mean of these daily values from

May 25 through August 25 in each plot. This captured most of the growing season and the entire duration of the warming treatment each year.

To understand how climate conditions during the experiment compared to conditions at this site over a longer timescale, I downloaded Standardized Precipitation-Evapotranspiration Index (SPEI) data for the 0.5 degree lat/long grid cell centered over the experiment (Beguería and Vicente-Serrano, 2014; Vicente-Serrano et al., 2010). The SPEI dataset is an indicator of drought that is calculated by subtracting potential evapotranspiration from precipitation. It has been shown to be highly correlated with vegetation growth (Vicente-Serrano et al., 2013), thus making it a more comprehensive indicator of relevant climate conditions than if I examined single climate factors in isolation. I used the SPEI's 3-month timescale to calculate the percentile ranks of June-August SPEI for the four years of the experiment relative to June-August conditions since 1961.

4.2.5.2 Vegetation communities

I assessed interannual changes in the vegetation composition of the experiment treatments and their relationship to the composition of the landscape communities by examining their locations in multivariate ordination space (McCune and Grace, 2002; Minchin, 1987). To enhance my ability to detect relationships among the vegetation communities, I eliminated 15 species from the point intercept data that were present in fewer than 5% of all plots in all years (n=159 plots, and most eliminated species were intercepted only once or twice; (McCune and Grace, 2002)). I calculated the relative cover of the remaining species for each plot and computed a Bray-Curtis dissimilarity matrix for these relativized data (Bray and Curtis, 1957; McCune and Grace, 2002). Then I performed nonmetric multidimensional scaling (NMDS; Kruskal, 1964) with different random starting configurations and Procrustes analysis to identify convergent solutions that minimized the root mean squared error. For the NMDS, I used the metaMDS function in the vegan package (Oksanen et al., 2013) in R (2015).

Within the NMDS, I examined how environmental gradients mapped onto the plant communities, the species that contributed significantly to the location of the plots in the ordination, and the average location of the experiment treatments each year. I calculated environmental gradients separately for the landscape and experiment plots. For the landscape gradients, I used soil moisture and temperature, elevation, and total proportional vegetation cover for each plot at the time that I sampled CO_2 fluxes. For the experiment gradients, I used average growing season soil moisture and temperature and total proportional vegetation cover each year. I did not use elevation as a variable for the experiment because all experiment plots are located at roughly the same elevation. I transformed all environmental gradient data to z-scores and used the envfit function in the vegan package (Oksanen et al., 2013) to fit them as vectors onto the NMDS. I also used envfit to fit vectors for the 23 plant species and 5 other cover types (litter, lichen, soil, rock, and dead *K. pygmaea*) to the ordination. To determine the significance of correlations between plots' overall species composition with environmental gradients and with individual species, I used a permutation test in envfit with 1000 permutations.

To further examine the environmental conditions among the landscape types and the experiment treatments, I used Pearson correlation coefficients to identify correlations among the environmental conditions. However, I included all environmental gradients in the NMDS regardless of whether they were correlated with each other because they do not influence the placement of the species composition plots in the ordination. I also tested how the treatments affected species composition along each axis of the NMDS to interpret how composition changed in the experiment relative to environmental conditions and to plant communities around the landscape. For the landscape types I used ANOVAs, and for the experiment I used mixed linear models, with year as a repeated measure and the Tukey-Kramer adjustment for multiple comparisons. I performed all univariate analyses in SAS (v. 9.3, Cary, North Carolina, USA).

If certain cover types are indicative of different landscape communities, then identifying these indicators in both the landscape and experiment plots can serve as an additional link between the experimental and observational aspects of the study. Species are considered strong indicators of a landscape type or experiment treatment if a high proportion of a species falls within one of those groups, in addition to a high proportion of plots within that group containing a high abundance of that species (Dufrêne and Legendre, 1997). Therefore, sets of indicator species that emerge under the experiment treatments in the short term may be harbingers of the type of plant communities likely to increase or develop over the longer term if the ecosystem continues to be exposed to these climate and grazing regimes. For this analysis, I analyzed the proportional cover data with the multipatt function in R (De Caceres and Legendre, 2009).

I selected a subset of the plant species or other cover types that emerged as significant indicators of the landscape or experiment communities, and which also comprised a large proportion of the total cover. In addition, I also examined differences in the cover of all graminoid species as an indication of forage availability for livestock. I arcsine-square-root transformed proportional cover data that were not normally distributed. In the experiment, I tested for significant treatment effects on species' and functional groups' areal cover (measured 2010-2012) with mixed models that had year as a repeated measure and the Tukey-Kramer adjustment for repeated measures. For the landscape communities I tested for differences using ANOVAs. I considered differences significant at $\alpha < 0.05$ (SAS).

Relative success of the only shrub species present in the study (*Potentilla fruticosa*) in some treatments relative to others could indicate an eventual shift toward shrub meadow composition over longer timescales, given certain climate and grazing conditions. Therefore, I used mixed linear models to test the experiment treatment effects on metrics of *P. fruticosa* production from 2010-2012, with year as a repeated measure. I normalized *P. fruticosa* ANPP with a square-root transformation. Then I regressed *P. fruticosa* height, percent cover, and ANPP against average growing season soil moisture, soil temperature, and air temperature in the experiment. Although the microclimate variables were correlated, their variance inflation factors for multicollinearity were < 5, so I retained them in the full models.

4.2.5.3 CO_2 fluxes

I calculated fluxes by mimicking the calculations computed internally by the LI-6400's soil efflux program. To do so, I regressed measurements of CO_2 fluxes against chamber CO_2 concentrations that logged every two seconds during the 60-second measurement period. In some instances where a linear regression did not fit the data well, as indicated by a low R^2 value, I removed deviant points near the beginning or end of the measurement or the entire replicate from further analysis because this indicated a chamber leak or other problem. Then, using the resulting regression slope and intercept, I estimated the CO_2 flux at the ambient CO_2 concentration for that plot that I had recorded before starting the flux measurements. I took the mean of three replicates as the final flux value in each plot. Then I calculated GPP by subtracting ER from NEP. I represent net CO_2 uptake and GPP as positive, whereas net CO_2 efflux and ER are negative (Chapin et al., 2006).

To analyze differences in midday CO_2 fluxes among the landscape communities and experiment treatments in August, 2013, I ran ANOVAs in SAS and determined significant differences at $\alpha < 0.05$. To test for differences among experiment treatments, I used the full mixed model for the experimental design. For the landscape measurements I also ran ANCOVAs to partition the effects of soil moisture, soil temperature, plant cover, and root biomass on GPP, ER, and NEP, with landscape type as a fixed effect (Shaver et al., 1998). I included interactions between landscape type and each covariate to test for homogeneity of slopes in the different plant communities.

4.2.5.4 Soil resources

I used soil bulk density estimates to convert the C and N concentrations (g kg^{-1} soil) to g m^{-2} for the top 10 cm of soil in each landscape plot. Then I used ANOVAs to test for differences in the bulk density, root biomass, and C and N resources among the three landscape types (SAS). I did not have bulk density estimates for all experiment plots, so for these I only report C concentrations. I tested for treatment and interannual differences in the experiment using mixed models with year as a repeated measure.

4.3 Results

4.3.1 Environmental conditions

Interannual summer climate conditions throughout the duration of the experiment were highly variable relative to the long-term average. 2010 was the driest year during the experiment and the only year to experience drought conditions, according to the Standardized Precipitation-Evapotranspiration Index (SPEI; Beguería and Vicente-Serrano, 2014). It was also much drier than the long-term average, ranking only in the 15th percentile for growing season conditions from 1961-2013. Furthermore, in 2010 I observed relatively long (mean = 0.34 m) and deep (mean = 0.14 m) cracks forming in the soil in of 9 out of 16 warmed plots. In contrast, 2011 was the wettest and coolest year in the experiment and much wetter than the longer-term average (Table 4.1). The drought status in the other two years of the experiment was more intermediate (Table 4.1). During the 2010-2013 growing seasons, the warming treatment significantly increased average soil temperatures by 1.7 °C, average air temperatures by 1.3 °C, and midday (11:00-15:45) air temperatures by 3.9 °C. The effect of warming on soil moisture was more variable, depending on the amount and timing of precipitation each year (Table 4.1).

There were strong correlations among environmental conditions around the landscape and in the experiment. In the landscape plots, plant cover was positively correlated with elevation (r = 0.60, $p < 0.0001$) and negatively correlated with soil temperature (r = -0.38, $p = 0.005$). Soil temperatures decreased at higher elevations (r = -0.27, $p = 0.06$), but soil moisture was not significantly correlated with other environmental conditions around the landscape. In the experiment, soil moisture and plant cover were positively correlated with each other (r = 0.74, $p < 0.0001$), and both were negatively correlated with soil temperature (moisture and temperature: r = -0.59, $p < 0.0001$; plant cover and temperature: r = -0.55, $p < 0.0001$).

4.3.2 Plant community composition

The NMDS ordination revealed clear patterns in the species composition of the 159 plots across the landscape and experiment treatments from 2010-2013. After ten tries there were two convergent solutions to explain the variation in species composition in two dimensions, and the stress for plotting the ordination on these two axes was 0.14. Most of the variation in the original dissimilarity among plots was explained by their distances in NMDS space ($R^2 = 0.98$). Nine plant species and five un-vegetated cover types were significantly correlated with the NMDS overall and were also significant indicators for the landscape communities and experiment treatments (Table 4.2).

The first NMDS axis mostly separated shrub meadows from healthy and degraded meadows, including the experiment plots, which are located in a healthy meadow area (Fig. 4.3). For the landscape plots, this axis was also slightly negatively associated with soil moisture ($R^2 = 0.08$, $p = 0.16$), and the landscape soil moisture vector indicates that higher soil moisture is most strongly associated with healthy meadows (Fig. 4.3a). ANOVAs also revealed that healthy meadows tend to have the highest soil moisture (0.12 $m^3\ m^{-3}$ healthy vs. 0.08 $m^3\ m^{-3}$ shrub and 0.09 $m^3\ m^{-3}$ degraded; $F_{2,48} = 2.73$, $p = 0.08$). Cover types that are significant indicators of shrub communities are more positively associated with this axis, and those that are significant indicators of healthy meadows are more negatively associated with it (Table 4.1).

The second NMDS axis mostly separated healthy from degraded meadows and warmed treatment plots from un-warmed plots (Fig. 4.3). This axis was positively associated with soil temperature for both the landscape ($R^2 = 0.13$, $p = 0.03$) and experiment ($R^2 = 0.30$, $p = 0.001$) plots. It was negatively associated with elevation for the landscape ($R^2 = 0.47$, $p = 0.001$), soil moisture for the experiment ($R^2 = 0.52$, $p = 0.001$), and plant cover for both the landscape ($R^2 = 0.81$, $p = 0.001$) and experiment ($R^2 = 0.93$, $p = 0.001$). This corresponds to degraded meadows having significantly higher soil temperatures than healthy and shrub meadows (2.7 ^{o}C higher on average; $F_{2,48} = 5.50$, $p = 0.007$), being located at lower elevations (79 m lower on average; $F_{2,48} = 19.22$, $p < 0.0001$), and having lower plant cover than the other two community types (degraded = 51.5%, healthy = 83.4%, shrub = 73.8% total plant cover; $F_{2,48} = 31.85$, $p < 0.0001$; Fig. 4.3a).

Un-vegetated and dead vegetation cover types were most strongly, positively associated with this axis, and their vectors point toward degraded meadows and warmed treatment plots (Table 4.2, Fig. 4.3).

While yak grazing did not significantly shift species composition in the experiment, warming had a strong and immediate effect (Fig. 4.3b,d). In the warmest and driest year of the experiment (2010), all treatments tended to shift higher on axis 2, closer to a degraded meadow state, and in the wettest, coolest year (2011), all treatments moved lower on axis 2, closer to a healthy meadow state (year: $F_{3,87.3}$=35.36, $p < 0.0001$). However, there was also a significant year x warming interaction ($F_{3,84.7.}$ = 12.05, $p < 0.0001$), in which the warming effect along axis 2 was stronger in 2010, the driest year. Overall, the warming treatment caused the 95% confidence intervals for warmed plots to overlap with the 95% confidence interval for degraded meadows, regardless of whether yak grazing also occurred in the warmed plots (Fig. 4.3c). Across all years, the warming treatment also shifted species composition to be more positive on axis 1, closer to the shrub meadow community ($F_{1,92}$ = 14.36, p = 0.0003).

4.3.3 Focal cover types

Of the cover types that were significant indicators for the vegetation communities under the experiment treatments (Table 4.2), I selected the following for more detailed analyses: *K. pygmaea*, which is the dominant species (accounting for 71% of the total vegetation cover on average) and an indicator of healthy meadows and yak grazing (Fig. 4.2a,d,g); litter, which is an indicator of warming; and lichen crusts, which are indicators of degraded meadows and warming x yak grazing (Fig 4.2c,f,i). These three cover types comprised 62-95% of the total ground cover in the experiment plots across all years. I also chose to examine dead *K. pygmaea*, defined as *K.*

pygmaea that had grown and subsequently died during that year, as opposed to having senesced the previous year and turned to litter. Although dead *K. pygmaea* had low coverage on average, it also emerged as a significant indicator of the warming treatment.

There was a significant interaction between warming and year for *K. pygmaea*, with lower cover under warming in all years, but with the most significant intra-annual difference between warmed and un-warmed plots in 2010, the driest year (Table 4.3, Fig. 4.4a). *K. pygmaea* cover was also significantly higher across all treatments in the wettest year, 2011, and in that year the warming treatment had the smallest effect on *K. pygmaea* cover (Table 4.3, Fig. 4.4a). Lichen crusts increased significantly with warming and yak grazing, although there was significantly more lichen cover across all treatments in 2012 (Table 4.3, Fig. 4.4b). A marginally significant interaction between yak x year indicated that the increase in lichen cover with yak grazing was diminished in 2011, when vegetation was more productive (Table 4.3). Litter cover, composed mostly of senesced *K. pygmaea* from the previous year that lay flat against the ground, was highest across all treatments in 2010 (Fig. 4.4c). Yak grazing had the strongest effect on litter cover, reducing litter by 59% on average relative to un-grazed plots across all years, although litter peaked in the yak treatment in 2010 (Table 4.3, Fig. 4.4c). Litter was also significantly reduced by warming in 2011. Overall, litter cover was highest in un-grazed, un-warmed plots. Dead *K. pygmaea* increased significantly with warming, especially in 2010 (Table 4.3, Fig. 4.4a).

Although *K. pygmaea* is the primary forage species in the alpine meadows, livestock also graze other sedges and grasses. However, other graminoids are not very abundant in the three landscape types, ranging from 1.9% of the cover in healthy meadows to 6.9% and 8.4% in the degraded and shrub meadows, respectively. Degraded and shrub meadows had significantly higher cover of non-*K.-pygmaea* graminoids than the healthy meadows ($F_{2,48} = 7.93$, $p = 0.001$), but these patterns reverse if *K. pygmaea* is included. When considering all graminoids available to grazers, healthy meadows therefore have significantly higher forage potential (67% graminoid cover) than degraded (40%) and shrub meadows (27%; $F_{2,48} = 74.34$, $p < 0.0001$). These other non-*K.-pygmaea* graminoids make up a very small proportion of the vegetation in the experiment plots too, at less than 5% of the total cover. Nonetheless, the warming treatment had a stimulating effect on these other graminoids, increasing their cover by 76.4% on average ($F_{1,77} = 4.12$, $p = 0.05$). Yak grazing had an inhibitory effect on the other graminoids, decreasing their cover by 49.3% on average ($F_{1,77} = 26.42$, $p < 0.0001$). There were no significant treatment or year interactions.

The indicator species analysis revealed that *P. fruticosa* was an indicator of shrub meadows and of the warming treatment (Table 4.2, Fig. 4.2b,e,h). To further examine treatment effects on *P. fruticosa*, I performed univariate tests for metrics of shrub growth in the experiment from 2010-2012. I found that there was a significant warm x yak interaction for *P. fruticosa* height ($F_{1,70.8} = 20.55$, $p < 0.0001$), proportional cover ($F_{1,77} = 11.86$, $p < 0.0009$), and ANPP ($F_{1,77} = 17.33$, $p < 0.0001$). The warming treatment promoted shrub growth while yaks consistently suppressed it, regardless of whether the plot was also warmed (Fig. 4.5). Year was marginally significant ($F_{2,77} = 2.87$, $p = 0.06$) for *P. fruticosa* ANPP, with higher *P. fruticosa* production in 2011, the wettest year, across all treatments.

Higher soil moisture and air temperature were the most significant aspects of microclimate to explain increases in shrub growth (Table 4.4). I removed all non-significant soil temperature and interaction terms from the models. There was a significant interaction between year and air temperature for shrub ANPP, due to a significantly dampened production response to temperature in 2012 (Fig. 4.6). The relatively low explanatory power of the microclimate model for shrub height reflects the strong top-down effect of yak herbivory on vertical shrub growth. Although yaks won't eat woody stems, I observed them stripping leaves and phloem from new, upright stems, which subsequently died. If I eliminate all plots with yak grazing from the regression, then air temperature became a significant factor promoting increases in shrub height as well.

4.3.4 Ecosystem CO_2 fluxes

Midday CO_2 fluxes in the experiment (August 14, 2013) correspond well to fluxes measured around the landscape (August 16-24, 2013) when experiment treatments are paired with the landscape types toward which their plant communities are converging (yak with healthy meadows, warm with shrub meadows, and warm x yak with degraded meadows; Fig. 4.7). The relatively low sample size for the experiment flux measurements made it more difficult to detect significant treatment differences, but measurements from around the landscape indicate that the different communities also differ in their functioning. Degraded meadows have significantly lower rates of GPP than the healthy and shrub meadows, which drives them to have the lowest net CO_2 uptake (NEP; Fig. 4.7). Healthy meadows, conversely, have significantly higher rates of CO_2 uptake (GPP), along with the highest rates of efflux (ER), which causes their net CO_2 balance (NEP) to be similar to that of shrub meadows, which have intermediate GPP but low ER (Fig. 4.7). Although I only measured midday fluxes in 2013, I found a significant, linear relationship between midday flux values and net daily CO_2 balance in previous years in the experiment. Therefore, I can assume that patterns in these midday fluxes are indicative of daily trends in response to the different treatments and landscape communities.

I used ANCOVAs to partition the effects of soil moisture, temperature, plant cover, and root biomass on CO_2 fluxes around the landscape. There were no significant interactions between landscape type and any of the covariates, indicating that slopes were homogenous across healthy, degraded, and shrub meadows. Furthermore, the landscape types themselves were no longer significant when I included covariates, indicating that the communities' different microclimate and vegetation conditions explain most of the variation in their CO_2 fluxes (GPP: $R^2 = 0.56$, ER: $R^2 = 0.67$, NEP: $R^2 = 0.62$). Across all landscape types, GPP is most strongly associated with plant cover, while ER is most associated with soil temperature, followed by plant cover and then soil moisture (Table 4.5). Consequently, higher plant cover promotes higher NEP while higher soil temperature reduces NEP (Table 4.5). Root biomass also emerges as having an inhibiting effect on NEP, due to the combination of its slightly negative effect on GPP and slightly positive effect on ER. It should be noted that roots weren't partitioned into live and dead fractions, so it is possible that a greater proportion of dead biomass at higher root densities could have been serving as substrate for decomposition but not contributing directly to processes related to plant growth and carbon uptake.

4.3.5 Soil resources

Soil properties were consistently different among the three landscape community types (Table 4.6). Healthy meadow soils had significantly higher carbon and nitrogen concentrations than the degraded and shrub meadow soils. However, a higher density of roots (live and dead, > 2 mm) in the healthy meadows lowered the bulk density of the soil in those samples, which tempered the differences in their total soil carbon and nitrogen pools relative to the other meadow types on a per area basis, leading to no significant differences in total soil nitrogen (Fig. 4.8). Yet even without accounting for the carbon stored in the root pool, the healthy meadow soils had significantly higher soil carbon storage than the shrub meadows ($F_{2,48} = 5.69$, $p = 0.006$; pairwise comparison adj. $P = 0.002$) and marginally significantly more than the degraded meadows (adj. $p = 0.06$).

Although soil carbon accumulation is generally a relatively slow process, I found changes in C concentrations within the first years of the experiment. There was a significant temporal effect ($F_{3,103} = 6.75$, $p = 0.0003$), with soil C concentrations higher across all treatments in the last half of the experiment (2011-2012) relative to the first half (2009-2010; Fig. 4.9a). There was also a significant warm x yak interaction ($F_{1,103} = 6.75$, $p = 0.001$), with higher soil C concentrations in warmed, un-grazed plots across all years (Fig. 4.9b). When I collected the first soil samples in August, 2009, the treatment plots had already undergone several months of warming manipulations but had only experienced one brief exposure to controlled yak grazing. Qualitatively, there appears to have been a warming effect as early as this first summer, and although there were no significant intra-annual treatment differences in any year, by 2012 the warm treatment had diverged most from the warm x yak treatment (adj. $p = 0.17$).

4.4 Discussion

4.4.1 Shifts in community composition

I predicted that short-term vegetation responses to experimental manipulations would show trajectories of change consistent with different plant communities around the landscape. Indeed, within five years of being exposed to climate warming and yak grazing treatments, vegetation composition in the experiment plots began to converge with the composition of healthy and degraded meadows observed around the landscape. While vegetation under the yak and control treatments remained most similar to healthy meadows throughout the duration of the experiment, the warming treatments drove immediate changes in species composition, causing a transition to more of a degraded meadow state. Interannual shifts in the composition of the experiment plots in response to ambient weather conditions also showed that in warmer, drier years, even un-warmed plots more closely resembled warmed plots and degraded meadows, thus strengthening my conclusions about the degrading effects of climate warming on alpine meadow communities (Elmendorf et al., 2015). Although these treatment effects on vegetation could be transient, mounting evidence that herbaceous and tundra ecosystems' initial responses to global change factors do, in fact, tend to be sustained over longer timescales indicates that a transition from healthy to degraded meadows under climate warming is a likely scenario for this system (Clark and Tilman, 2008; Elmendorf et al., 2012a; Smith et al., 2015).

The rapid community response to warming was likely catalyzed by extremely dry conditions in 2010 that pushed the dominant species, *K. pygmaea*, beyond a physiological threshold, which in turn had cascading effects on community composition. *K. pygmaea* is a shallow-rooted species that accesses water in upper soil layers (Hu et al., 2013) and performs better in more humid environments (Miehe et al., 2011), thus making it vulnerable to the larger reduction in soil moisture with warming in an already dry year. With significant mortality of *K. pygmaea* in 2010 and lower *K. pygmaea* production under warming in all years, other species, including other graminoids and shrubs, may have been more productive not only because they were better suited to the warmer conditions, but also because they were no longer forced to compete as strongly for space and resources in the dense turf created by healthy *K. pygmaea* (Miehe et al., 2008). However, increases in these other species in the short term did not compensate for the loss of plant cover in the experiment overall, and nor did established degraded and shrub meadows communities around the landscape have as high of plant cover as healthy, *K.-pygmaea*-dominated meadows. With climate extremes projected to increase under climate change, this lack of drought-resistance for the dominant species could therefore lead to widespread changes in alpine meadow community structure (Christensen et al., 2013; Hoover et al., 2014).

Accumulation of plant litter is a common response to warming temperatures throughout the tundra biome (Elmendorf et al., 2012a, b; Klein et al., 2005), but I found that yak grazing counteracted this affect by removing a significant proportion of senesced plant material. Higher areal cover of litter across all experiment plots in 2010 was likely due to litter accumulation starting in 2009, when I established a fence around the experiment to exclude livestock but only had a few days of the controlled yak grazing treatment. This build-up of litter in 2010 was likely affected by the very low level of yak grazing (and thus biomass removal) in the experiment plots in 2009, the first year of the experiment, in combination with lower plant cover across all treatments in 2010 that otherwise may have obscured the litter. With a more robust grazing treatment in subsequent years, litter cover decreased in grazed plots. Generally, grazers reduce litter build-up indirectly by consuming standing live biomass before it senesces (Augustine and McNaughton, 2006), but I also observed that yaks consume litter directly through licking it up off of the ground. Local herders and historical accounts (Ekvall, 1968) confirm that this is common grazing behavior for yaks, particularly early in the growing season, before new plant growth is tall enough for them to bite easily. In the absence of climate warming, this litter removal effect likely increases rates of nutrient cycling (Hobbs, 1996; Yang et al., 2013) and helps maintain healthy meadow conditions. However, with die-back of *K. pygmaea* and subsequently lower plant cover in warmed plots, litter removal revealed lichen crusts forming over dead *K. pygmaea* root mats. As a result, the warm x yak interaction produced a significant increase in lichen cover, an indicator of degraded alpine meadows. In contrast, the lack of lichen crusts in un-warmed, grazed plots suggests that yak grazing alone is not directly responsible for driving a shift to this more degraded state. So while overgrazing may be responsible for contributing to lichen crust formation in some alpine meadow ecosystems (He and Richards, 2014; Unteregelsbacher et al., 2011), my results suggest that the interacting drivers of lichen dominance in degrading alpine meadows should be examined more closely, rather than assuming that overgrazing is the primary or sole cause.

Plant species composition in the experiment plots did not converge with shrub meadow composition within five years of climate and grazing manipulations, but the fourfold increase in shrub production in response to the warming treatment does suggest that alpine meadow communities could eventually transition to a woodier state under climate warming if livestock grazing is reduced or eliminated. Shrubs' release from air temperature limitation allowed them to grow above the dense *K. pygmaea* canopy, although this effect was also mediated by soil moisture availability. The importance of soil moisture for shrub growth has also been demonstrated in an alpine steppe ecosystem close to this study area, where May-June water stress is the main factor limiting annual growth of dwarf juniper shrubs (Liang et al., 2012). If *P. fruticosa* is similarly susceptible to early-growing-season moisture limitation, then shrubs' dampened ANPP response to warming in 2012 could be explained by May-June drought conditions that year (Appendix 1 for soil moisture data, SPEI data not shown; Beguería and Vicente-Serrano, 2014). This explanation is further supported by results from warming experiments in tundra ecosystems globally, which show that in sites with similar summer temperatures to ours, the promoting effects of warming on shrub growth are sustained longer in sites with wetter soil conditions (Elmendorf et al., 2012a). Therefore, the decline in responsiveness of shrub ANPP to warming in 2012 could have been a temporary response to soil moisture limitation, or it could signal that the initial warming effect will diminish if drier conditions prevail. However, the strong interaction between warming and grazing indicates that in alpine meadows around the landscape, shrubs will ultimately be unable to respond to climate warming if yaks continue to suppress their new growth. This type of interaction has also been found in other tundra systems with large grazers, where muskox counteract the effects of warming on shrub growth (Jørgensen et al., 2013; Post and Pedersen, 2008) by eating their new shoots and leaves (Forchhamer, 1995).

4.4.2 Shifts in ecosystem functioning

Loss of a dominant species from a community can have strong and cascading effects on ecosystem functioning (Smith and Knapp, 2003), and I found that reductions in the dominant species, *K. pygmaea*, did lead to declines in alpine meadows' ability to provide critical ecosystem services, such as forage for livestock and wildlife (e.g., Plateau pikas, Himalayan marmots, and Tibetan gazelles). In both the degraded meadows around the landscape and in the warming x grazing experiment plots that shifted to a community dominated by lichen crusts, the overall decrease in plant production reduced the meadows' ability to support grazers and, thereby, local herders. Alternatively, an eventual shift to a more shrub-dominated community under climate warming and reduced livestock populations would not replace the value of healthy meadows in grazers' diets either. Even though yaks eat fresh stems from low-stature shrubs interspersed among healthy meadow vegetation, shrubs are not an important source of forage for livestock, and local herders reported that yaks won't graze in shrub meadows where woody plants are already established as the dominant species. This also implies that the higher abundance of grasses in shrub meadows will not be beneficial to livestock who are disinclined to enter shrub-dominated areas, and, in fact, the grasses' establishment there is indirect evidence of lower grazing pressure in these shrub communities.

However, if other, non-*K.-pygmaea* graminoids continue to increase around the landscape in response to climate change, as seen under the warming treatment and as has been found in other tundra warming experiments (Elmendorf et al., 2012a; Walker et al., 2006), this replacement by other palatable vegetation could partially compensate for the loss of *K. pygmaea* as a source of forage. The success of other graminoids under warming also suggests an alternative pathway that the meadows could take, eventually shifting to Poaceae-dominated alpine steppe communities instead of to shrub or degraded meadows. At a regional scale, alpine meadows currently transition to alpine steppe following an aridity gradient across the Plateau, and a shift toward communities dominated by steppe graminoid species has been observed in long-term livestock exclosures (Miehe et al., 2011). Degraded or shrub meadows could therefore be an intermediate phase on the way to these more arid alpine steppe communities, perhaps particularly if grazing pressures are reduced. Alpine steppe ecosystems, although still grazed by livestock, are less productive, store less carbon (Fu et al., 2009; Ni, 2002; Wang et al., 2002), and are not as resilient to grazing as healthy alpine meadows are (Miehe et al., 2008, 2011).

In addition to their ability to provide locally important forage, Tibet's alpine meadows also serve as a globally important carbon sink (Kato et al., 2006; Ni, 2002). However, I found that this capacity to sequester carbon is unlikely to be sustained if climate warming drives a shift toward degraded meadow communities, which had the lowest rates of NEP, whereas healthy and shrub meadow NEP rates near the peak of the growing season were similar. Although healthy meadows and grazed treatment plots had the highest rates of CO_2 uptake (GPP), they also had higher rates of efflux (ER). These higher-magnitude fluxes for both uptake and efflux drove healthy meadows' net CO_2 balance to be similar to shrub meadows and warmed plots, which maintained higher rates of CO_2 uptake relative to their efflux. Higher GPP relative to ER in shrub meadows and warmed plots may have been caused in part by higher shrub production, since *P. fruticosa* has been shown to contribute more than other alpine meadow species to CO_2 uptake, due not only to its greater abundance in shrub meadow communities, but also to its higher light use efficiency than herbaceous plants, which could be particularly important during the cloudy monsoon season (Yashiro et al., 2010). The relatively lower ER in shrub meadows and warmed plots could have also been caused by lower plant cover coupled with lower soil moisture that limited microbial respiration. Although I saw pattern matching overall between experiment treatment plots and landscape plots paired on the basis of their converging species compositions, ER in plots with warming and grazing was actually more similar to healthy meadows than to degraded meadows. This may be explained by more allocation to belowground biomass under grazing (Gao et al., 2007; Shi et al., 2013), and perhaps to the presence of more dead root material after the *K. pygmaea* dieback in 2010, which could then act as substrate for decomposition. With more time, however, I would expect the lower rates of plant production under warming to lead to a reduction in the rates of both GPP and ER, thus producing flux values even closer to those observed in the degraded meadows.

Since warmer temperatures had a negative effect on August CO_2 uptake across the landscape plots, regardless of their species composition, this suggests that a shift in composition in response to climate warming is unlikely to lead to a recovery of ecosystem functioning via the establishment of a community able to sequester more CO_2 at higher temperatures. Nor did CO_2 fluxes in the different landscape types differ significantly in their sensitivity to changes in soil moisture, or per unit plant cover. Yet with only August measurements, I cannot account for the possibility that shifts in composition could also lead to increasing abundance of species with different phenological cues that could effectively lengthen the growing season by greening up earlier or senescing later. This has been observed in the Arctic, where increasing dominance of shrubs has led to earlier community green-up, thereby expanding the window of net carbon uptake by the ecosystem (Sweet et al., 2015). However, ecosystem chamber and eddy covariance measurements from a site on the eastern Tibetan Plateau indicate that healthy meadows also tend to be a stronger net carbon sink than shrub meadows on an annual basis (Fu et al., 2009; Kato et al., 2006; Li et al., 2006; Zhang et al., 2009; Zhao et al., 2006), and eddy covariance measurements from a site in central Tibet found that healthy meadows sequester more CO_2 throughout the growing season than degraded meadows, which act as net CO_2 source (Babel et al., 2014). Although these results support the conclusions that I can draw from my August CO_2 flux measurements, soil carbon storage can also serve as an indicator of plant communities' longer-term carbon sink strength.

Even without accounting for the carbon stored in healthy meadows' dense *K. pygmaea* root systems, which has been reported in other studies (Hafner et al., 2012; Ingrisch et al., 2015; Unteregelsbacher et al., 2011), healthy meadows contained the largest amounts of soil carbon per area relative to shrub and degraded meadows. I found that total soil organic carbon in healthy meadows at Namtso was higher than some values reported for alpine meadow ecosystems on other parts of the Plateau (Dong et al., 2012; Li et al., 2011a), similar to some (Klein, 2003), and lower than some (Gao et al., 2007; Hafner et al., 2012; Unteregelsbacher et al., 2011), likely due to regional differences in climate and variations in species composition within the alpine meadow vegetation classification. My finding of lower soil carbon in degraded meadows parallels a similar decrease in soil carbon storage in degraded, lichen-crust-dominated meadows on the eastern Plateau, which can be attributed to reduced vegetation production and belowground inputs in both cases (Unteregelsbacher et al., 2011). While I found that shrub meadow soils had the lowest carbon storage of the three landscape communities, Klein (2003) found that shrub meadow soils on the eastern Plateau stored more carbon than alpine meadows. This difference may be explained in part by the more productive, warmer, and more mesic conditions on the eastern Plateau that are more conducive to sustained increases in shrub growth (Elmendorf et al., 2012a), which in turn should lead to higher rates of above- and belowground production of recalcitrant litter (Cornelissen et al., 2007; Klein et al., 2007). In addition, different edaphic conditions, such as higher rock content, in the shrub meadow sites relative to healthy meadows could also reduce their carbon storage potential. Overall, this suggests that meadow degradation to a lichen-crust state will reduce ecosystem carbon storage potential across the Plateau, but carbon sink strength of shrub meadows may vary more depending on rainfall, temperature, and soil conditions.

Ultimately, sampling from different plant communities around the landscape should give us a longer-term perspective of soil carbon storage potential if changes in climate and grazing drive healthy meadows to an alternative state, but initial changes under the experiment treatments can also indicate how soil carbon pools respond to climate warming and grazing removal in the short term. Although some studies have found a significant loss of soil carbon after excluding livestock (Gao et al., 2007; Hafner et al., 2012; Shi et al., 2013), I found relatively little change between grazed and un-grazed plots without warming (Ingrisch et al., 2015). Instead, warming caused a substantial increase in soil carbon concentrations across the first four years of the experiment (in contrast to (Li et al., 2011a), while warming with yak grazing caused a reduction. This trend could be driven by lower soil moisture that causes slower decomposition under warming (Klein, 2003; Welker et al., 2004), as well as the increase in dead *K. pygmaea* biomass in response to warming, which should increase the amount of organic matter being broken down and entering the belowground carbon pool in the short term. When yaks are also present, their removal of dead and senesced biomass through licking should reduce the amount of aboveground plant material contributing to the light fraction in the soil, thus leading to the divergent response in soil carbon concentrations under warming with and without grazing. With more time, however, I would expect that the increase in soil carbon under the warming treatment would not be maintained, since the warmed plots have lower plant production and a shift in species composition away from healthy meadow communities, which appear to be most capable of storing more belowground carbon. Thus, the increase in soil carbon in response to experimental warming may be a transient effect that is not well supported by the landscape observations and which is unlikely to be sustained over longer timescales (Saleska et al., 2002). The increase in soil C across years in all treatments is more difficult to explain, and although it seems unlikely, I cannot rule out the possibility that experiment-wide changes in bulk density could have led to the higher soil C concentrations.

4.4.3 Limitations of this study

The primary limitation of this study stems from the inability to infer causal relationships from observations in plant communities around the landscape, which means that I cannot say definitively whether healthy meadows will transition to degraded or shrub communities at a landscape scale based on my findings from the experiment. For example, the patches of shrub meadow around the landscape may exist for reasons unrelated to climate and grazing, such as different edaphic conditions, which could preclude alpine meadows in this region from transitioning into shrub meadows resembling those already present around the landscape. In addition, I cannot determine if warmer and drier conditions drove a transition to degraded meadows around the landscape, or whether a reduction in plant biomass and increase in lichen crusts for other reasons led to a subsequent increase in rates of evaporation (Babel et al., 2014) and reduced water infiltration (He and Richards, 2014), thereby creating the more arid conditions that I observed in degraded meadows. However, by linking results from experiment manipulations with landscape observations, I can gain more insight into the functioning of these ecosystems than either approach could offer alone. The causal drivers that I elucidated from the experiment produce new, testable hypotheses about land cover change in the region, such as that the degraded meadow communities that already exist at slightly lower elevations around this landscape, and thereby more in the rain shadow of the Nyenchen Tanglha mountains, may have crossed a tipping point in response to rising temperatures and lower summer precipitation (Xu et al., 2008) and then remained in this less productive state.

There are also several more minor caveats affecting interpretation of my results. The relatively small effect of soil moisture on CO_2 fluxes around the landscape and its lower correlation with landscape communities' species composition could be due to measurement error associated with using a combination of volumetric and gravimetric methods to calculate soil moisture. Alternatively, measuring soil moisture at a single point in time for landscape plots, when the CO_2 fluxes were measured, may have failed to capture relevant conditions that occurred earlier in the season. However, I can again use the more comprehensive soil moisture data from the experiment to bolster conclusions about the importance of water availability in promoting plant production and *K. pygmaea*'s resilience to warming temperatures (Chapter 3).

Also, while I found significant differences in soil carbon storage when sampling to 10 cm depth, other studies found no differences in soil carbon below 15 cm (Hafner et al., 2012) or an opposing trend below 15 cm (Unteregelsbacher et al., 2011) that reduced the strong differences seen in upper soil layers due to different plant community composition (Unteregelsbacher et al., 2011) and removal of grazers (Hafner et al., 2012). In this study area, the top 10 cm of soil have

1.6 times higher carbon concentrations than from soil between 10 and 80 cm depth (see Chapter 3). This does not negate the fact that the differences I found in upper soil layers could be mitigated by deeper soil carbon storage, but it does highlight that the majority of the soil carbon is still relatively close to the surface, where it appears to be vulnerable to changes in climate, grazing, and the composition of the plant community.

4.4.4 Future trajectory of alpine meadow ecosystems

To extend the scope of my inferences about the effects of warming on alpine meadow vegetation, I can also place my results in the context of much longer-term climate fluctuations during the Holocene. A study of the fossil pollen record at Namtso (dating to 8.4 kyr before present) found that during cooler climate periods, alpine meadow vegetation expanded its range by shifting lower in elevation, whereas during warmer periods, it contracted upslope and was replaced by alpine steppe vegetation (Li et al., 2011b). Genetic data suggests that the distribution of *P. fruticosa* may have followed a similar pattern of retreating to higher and cooler regions of the Plateau during warmer periods (Shimono et al., 2010), contrary to current evidence of increasing shrub production in response to climate warming in Tibet and throughout the tundra biome (Brandt et al., 2013; Büntgen et al., 2015; Elmendorf et al., 2012a; Klein et al., 2007; Walker et al., 2006). Although there are limitations to using historic conditions to predict future vegetation responses (Adams and Woodward, 1992; Overpeck et al., 1991), this palaeological evidence is consistent with contemporary observations that healthy alpine meadows are dominant in the higher-elevation, cooler regions of my study area, and that the experimental warming treatment drives the vegetation community away from a healthy meadow composition, closer to a lower-elevation, degraded community. Together, these results from short- and long-term warming suggest that in response to projected climate change, alpine meadows will retreat to higher, cooler refugia. However, it remains to be seen whether the degrading alpine meadows at lower elevations could eventually transition to alpine steppe vegetation and whether shrub growth will continue to increase in response to warming if grazing pressure is reduced.

4.5 Conclusion

Overall, I found that linking shorter-term experiments to landscape-scale observations was a successful approach to gaining insight into the likely trajectories of change that Tibet's alpine meadows will face under ongoing climate change and policies that alter livestock management practices. I expected that in response to these drivers, shifts in plant species composition would either mitigate or exacerbate changes in ecosystem functioning (Smith et al., 2009), which would in turn affect the provision of ecosystem services. Short-term composition shifts in the experiment in response to warming and grazing treatments aligned well with established healthy and degraded meadow communities around the landscape, with some indication that a shift to shrub meadows could be possible in the longer term. The dominant species, *K. pygmaea*, plays a particularly important role in maintaining healthy meadows, and loss of *K. pygmaea* in response to warming had a cascade of effects on ecosystem structure and functioning. However, I did not find that a shift to degraded meadows under warming and grazing, nor an eventual shift to shrub meadows under warming and without grazing, is likely to mitigate the reduction of at least two locally to globally important ecosystem services currently provided by healthy meadow ecosystems. Therefore, I predict that with climate warming, whether livestock are present or not, alpine meadows will produce less palatable forage for domestic and wild herbivores and will also be less of a carbon sink. Without warming, I found that yaks maintained healthy meadow communities, which leads us to conclude that rangeland management policies targeted at reducing livestock grazing will do little to ameliorate the undesirable effects of climate warming on Tibet’s alpine meadows.

4.6 Tables

Table 4.1. Mean microclimate conditions in the un-warmed experiment treatments (control and yak) and their mean change with warming (warm and warm x yak) from May 25 to August 25 each year. The SPEI drought index reflects growing season drought status (June through August) in the years of the experiment relative to growing season conditions from 1961-2013. Low percentiles indicate drier-than-average years, and high percentiles indicate wetter-than-average years. The 2009 growing season, when the experiment started, was in the 67th percentile. Plant cover represents the total proportional cover of all vegetation each year based on point-intercept data.

		Plant Cover (%)		Air temperature (°C)		Soil temperature (°C)		Soil moisture	
Year	Drought (percentile)	Un-warmed mean	Warmed mean	Un-warmed mean	Warming effect	Un-warmed mean	Warming effect	Un-warmed mean ($m^3 m^{-3}$)	Warming effect (% change)
2010	15th	66.8	39.3	8.5	+ 1.4	10.9	+ 2.0	0.10	- 45.6
2011	95th	80.6	72.9	7.0	+ 1.2	10.4	+ 1.4	0.19	- 23.2
2012	55th	70.0	60.0	8.7	+ 1.2	11.8	+ 1.5	0.12	- 17.6
2013	82nd	71.0	58.0	8.6	+ 1.1	11.4	+ 1.7	0.13	- 19.4

Table 4.2. Cover types that are significantly correlated with the NMDS ordination of species composition and that are also significant indictors for the landscape and/or experiment treatment plots, as indicated by *** ($P < 0.001$), ** ($P < 0.01$), * ($P < 0.05$). There were no significant indicators for control treatment plots.

Plant species/ground cover	Plant type	NMDS p-value	Landscape	Experiment
Kobresia pygmaea	sedge	< 0.001	Healthy***	Yak**
Oxytropis stracheyana	forb	0.02	Healthy*	
Gentiana farreri	forb	0.03	Healthy**	
Lichen crust		< 0.001	Degraded***	Warm x Yak***
Potentilla fruticosa	shrub	< 0.001	Shrub***	Warm*
Soil		< 0.001	Shrub***	
Leontopodium pusillum	forb	< 0.001	Shrub***	Yak**
Lancea tibetica	forb	< 0.001	Shrub***	
Tristeum tibeticum	grass	< 0.001	Shrub***	
Poa litwinowiana	grass	< 0.001	Shrub**	
Potentilla bifurca	forb	< 0.001	Shrub*	
Rock		0.001	Shrub**	Warm x Yak*
dead *K. pygmaea*	sedge	< 0.001		Warm*
Litter		< 0.001		Warm*

Table 4.3. Treatment and year effects and their interactions on areal cover in the experiment from 2010-2012 (n=96). Test statistics (*F*) are shown, and significant effects are indicated by *** (*P* < 0.001), ** (*P* < 0.01), * (*P* < 0.05), † (*P* < 0.10).

Effect	df	*Kobresia pygmaea*	Lichen	Litter	dead *K. pygmaea*
Yak	1,77	0.60	42.87***	56.01***	2.23
Warm	1,77	45.29***	52.11***	5.60*	177.00***
Warm x Yak	1,77	0.03	0.06	0.57	2.75
Year	2,77	40.64***	12.02***	64.86***	122.54***
Yak x Year	2,77	0.55	3.00†	4.27**	0.17
Warm x Year	2,77	6.96**	0.38	2.68†	118.89***
Yak x Warm x Year	2,77	0.44	1.10	2.27	0.88

Table 4.4. Standardized regression coefficients for microclimate factors regressed against aspects of shrub (*P. fruticosa*) growth. Microclimate variables are averaged across the growing season. Significance is indicated by ** ($P < 0.01$), * ($P < 0.05$).

Potentilla fruticosa	Soil moisture (m^3/m^3 VWC)	Soil temperature (°C)	Air temperature (°C)	R^2
Height (mm)	0.34	n.s.	0.55	0.13
Cover (%)	0.28**	n.s.	0.25*	0.28
ANPP (g m^{-2})	0.50**	n.s.	NA	0.43

Note: NA indicates that the coefficient is not shown because of a significant interaction with year (see Fig. 4.6).

Table 4.5. ANCOVAs for the effects of landscape type and environmental covariates on CO_2 fluxes (GPP, ER, NEP). Standardized coefficients indicate whether each covariate had a promoting or inhibiting effect on each type of flux. There were no significant interactions between landscape type and covariates. Significance of covariates is indicated by *** ($P < 0.001$), ** ($P < 0.01$), * ($P < 0.05$), † ($P < 0.10$).

Model	df	GPP	ER	NEP
Landscape type	2	n.s.	n.s.	n.s.
Soil moisture	1	-0.01	0.17†	-0.14
Soil temperature	1	-0.07	0.63***	-0.54***
Plant cover	1	0.72***	0.48**	0.45**
Roots (> 2mm)	1	-0.15	0.16	-0.28*
Error	42			

Table 4.6. Mean (± SE) for soil properties in the landscape communities. Roots > 2 mm were present in the 50 cm^3 soil sample but were sieved out for bulk density, C, and N measurements. Superscript letters indicate significant differences among community types derived from ANOVA ($P < 0.05$).

Meadow type	Roots (g per sample)	Bulk density (g cm^{-3})	C conc. (g kg^{-1})	N conc. (g kg^{-1})	C:N	C pool (g m^2 -10 cm^{-1})	N pool (g m^2 -10 cm^{-1})
Healthy	1.72 $(0.13)^a$	0.34 $(0.04)^b$	78.02 $(5.42)^a$	4.19 $(0.21)^a$	17.98 $(0.55)^a$	2225.4 $(140.3)^a$	127.76 $(9.21)^a$
Shrub	0.70 $(0.12)^c$	0.65 $(0.04)^a$	24.65 $(5.27)^b$	2.03 $(0.20)^b$	12.01 $(0.54)^b$	1568.6 $(136.3)^b$	130.46 $(8.95)^a$
Degraded	1.07 $(0.13)^b$	0.64 $(0.04)^a$	29.52 $(5.59)^b$	2.30 $(0.21)^b$	12.80 $(0.57)^b$	1833.0 $(144.6)^{ab}$	142.49 $(9.49)^a$

4.7 Figures

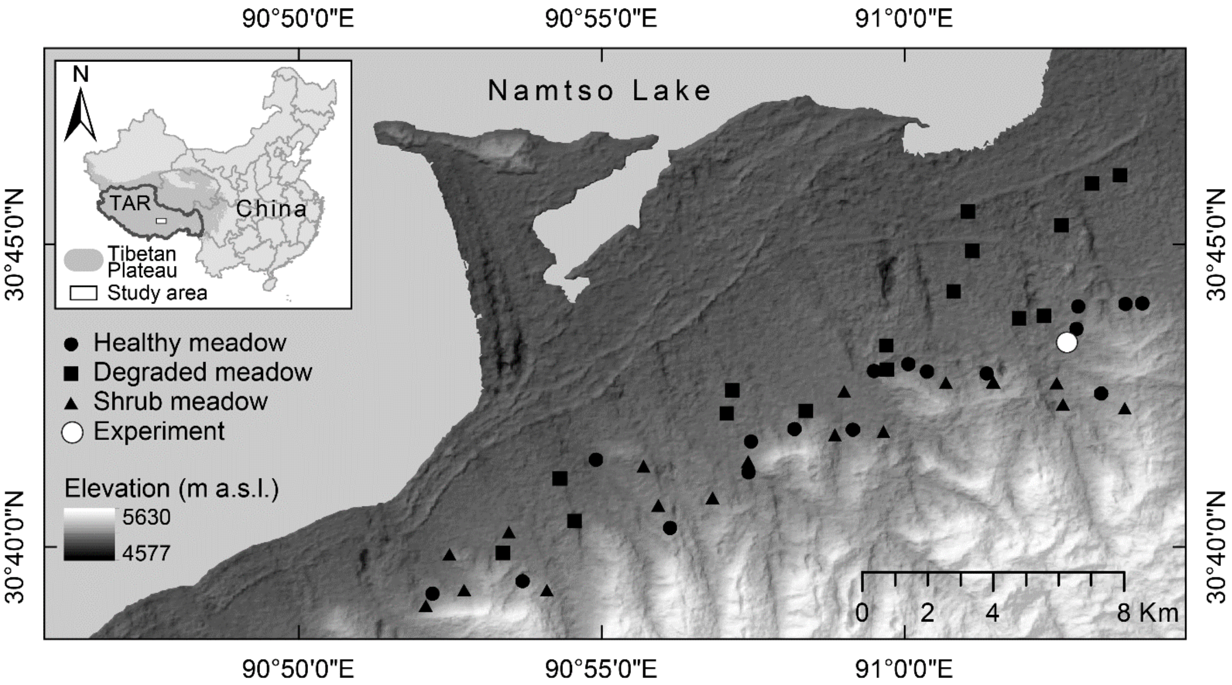

Figure 4.1. Study area with sampling plots in the Tibet Autonomous Region (TAR).

Figure 4.2. Healthy (a), shrub (b), and (c) degraded meadow communities and their respective indicator species, *Kobresia pygamaea* (d), *Potentilla fruticosa* (e), and crustose lichens (f). Healthy meadows cover large expanses of the Tibetan Plateau (g). Prostrate *P. fruticosa* shrubs are inconspicuous among other alpine meadow vegetation (h). An experiment subplot with warming and grazing treatments can be distinguished from the surrounding healthy meadow by its higher proportion of lichen coverage (a blue tag is in the center of the subplot, and stakes for the warming chamber ring its perimeter; i).

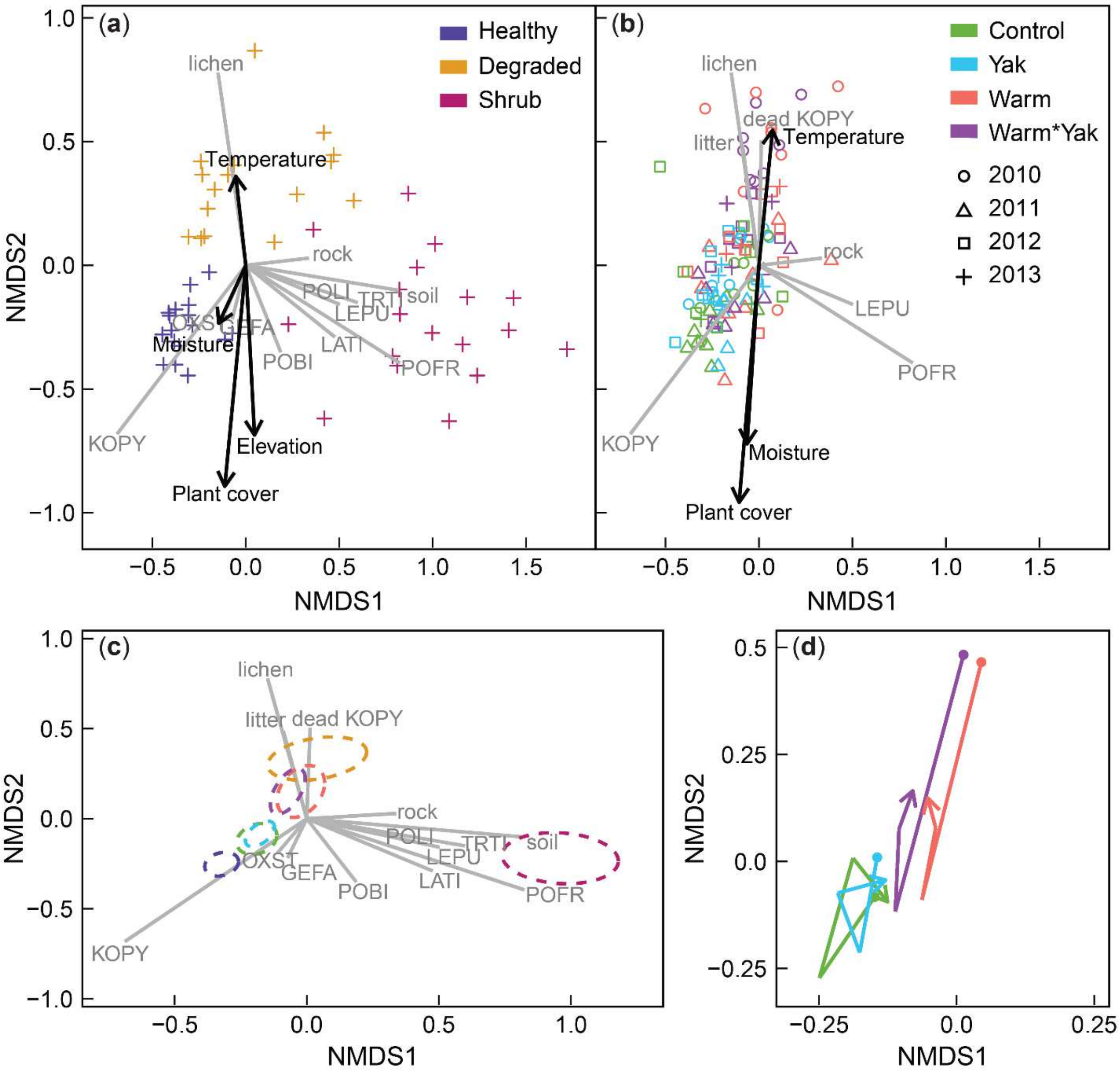

Figure 4.3. Nonmetric multidimensional scaling (NMDS) of species composition for the landscape and experiment. Each point represents a measurement plot. All plots contribute to the ordination, but only landscape plots are displayed in (a), while only experiment plots are displayed in (b). Ellipses represent 95% confidence intervals around the landscape communities in 2013 and experiment treatments from 2010-2013 (c). The average trajectory of change for the experiment treatments each year, starting with the point in 2010 and ending with the arrow head in 2013, are shown in (d). Gray vectors are for cover types that are significant for the ordination and that are also significant indicators for the landscape communities and experiment treatments ($P < 0.05$; plant species represented by 4-letter codes, but see Table 4.2 for complete names). Black arrows show environmental gradients for soil microclimate, elevation, and proportional vegetation cover based on the conditions in each plot. Vector and arrow lengths scale with the strength of their correlations to the ordination.

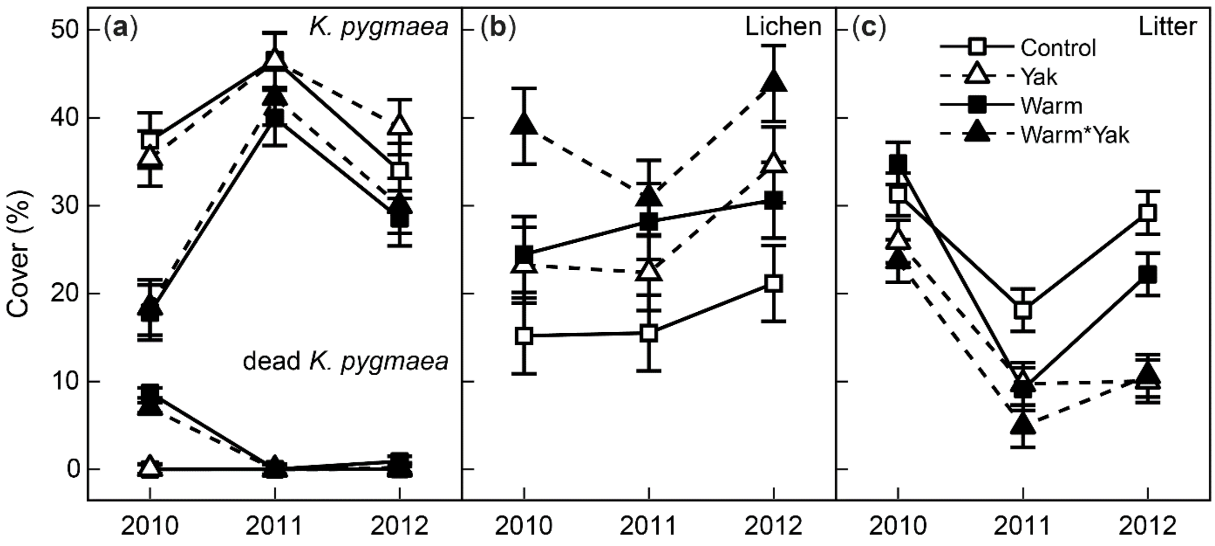

Figure 4.4. Mean percent cover (± SE) of the dominant species, *Kobresia pygmaea*, and dead *K. pygmaea* (a), lichen crusts (b), and litter (c) in the experiment from 2010-2012. N=8 for each treatment.

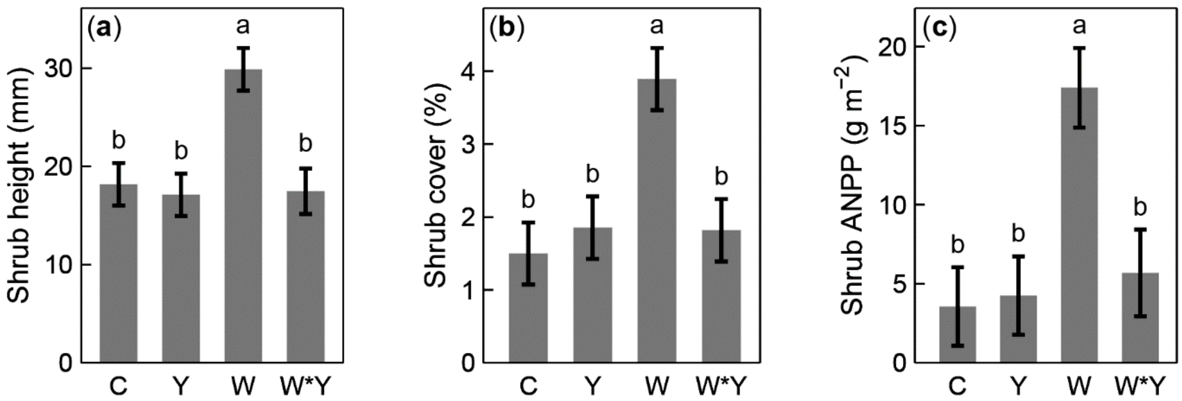

Figure 4.5. *Potentilla fruticosa* height (a), percent cover (b), and aboveground net primary production (ANPP; c) under the warming and grazing treatments from 2010-2012. There were no significant interactions between treatment and year. Error bars are ± 1 standard error. Letters above the bars indicate treatment differences that are significant at $p < 0.001$ based on comparisons of least squared means. (C = Control, Y = Yak, W = Warm, W*Y = Warm x Yak).

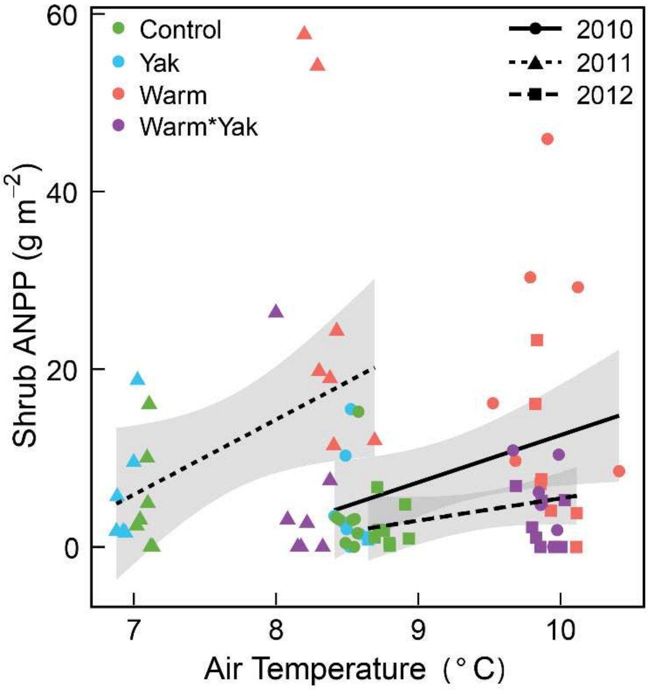

Figure 4.6. Shrub (*Potentilla fruticosa*) aboveground net primary production regressed against air temperature in the experiment treatment plots. Data were normalized and standardized for all statistical analyses, but raw data are shown here. The significant interaction between year and air temperature indicates that the positive relationship between shrub production and air temperature was weaker in 2012.

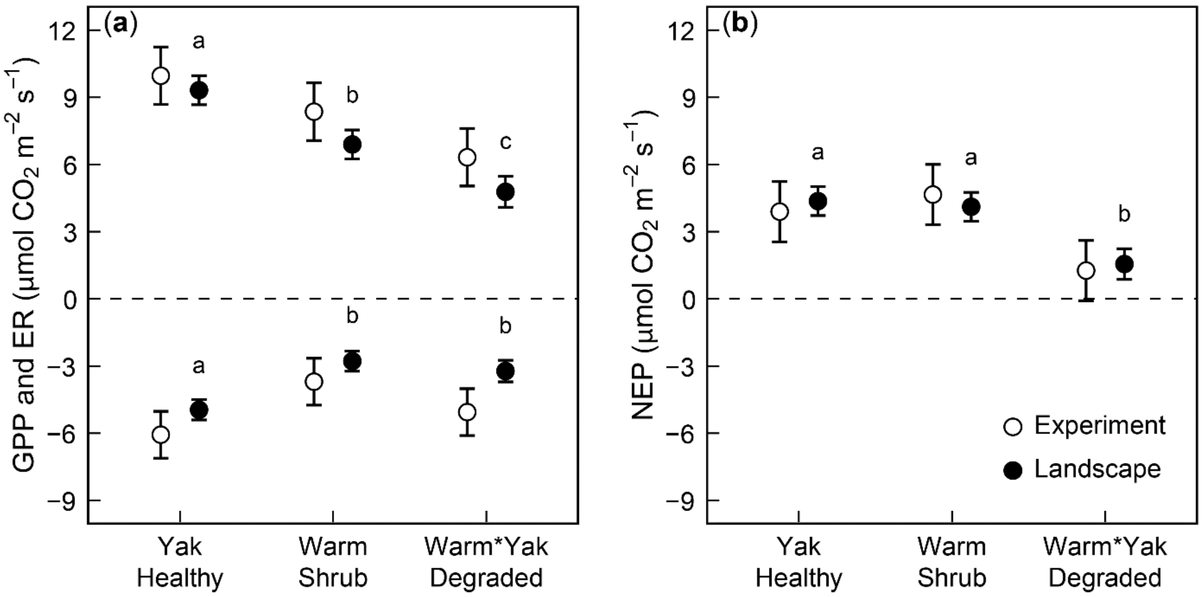

Figure 4.7. Midday CO_2 fluxes in the experiment and landscape plots, paired based on their plant species compositions. Mean (± SE) fluxes are shown for gross primary production (GPP; a), ecosystem respiration (ER; a), and net ecosystem production (NEP; b). Letters above the points represent significant differences among landscape types ($P < 0.05$). Control plots from the experiment were similar in magnitude to the Yak treatment. There were no significant differences among experiment treatments, nor between paired experiment treatments and landscape types. For GPP, the Yak and Warm treatments had significantly higher CO_2 uptake than the degraded meadows. For ER, the Yak treatment had significantly higher CO_2 efflux than the shrub and degraded meadows.

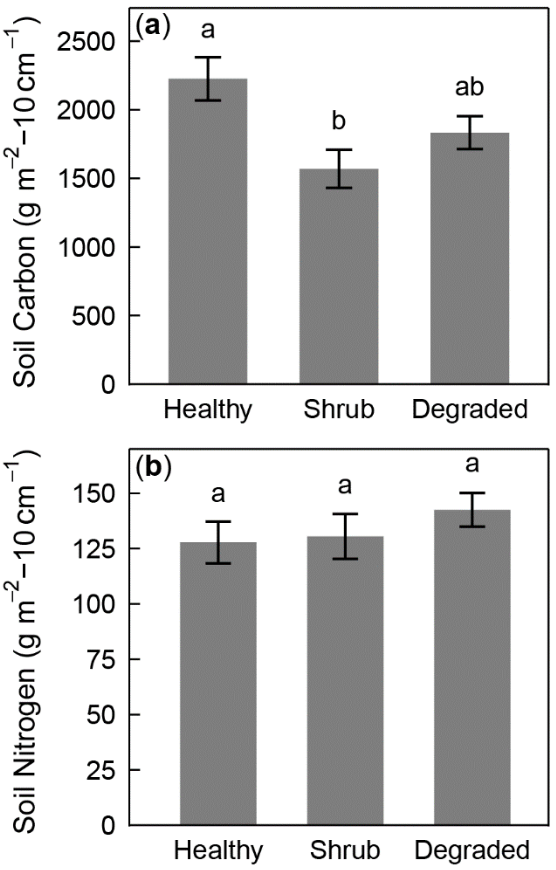

Figure 4.8. Mean (± SE) total organic soil carbon (a) and nitrogen (b) in the three landscape communities. Different letters above the bars indicate significant differences in least squared means at $p < 0.05$.

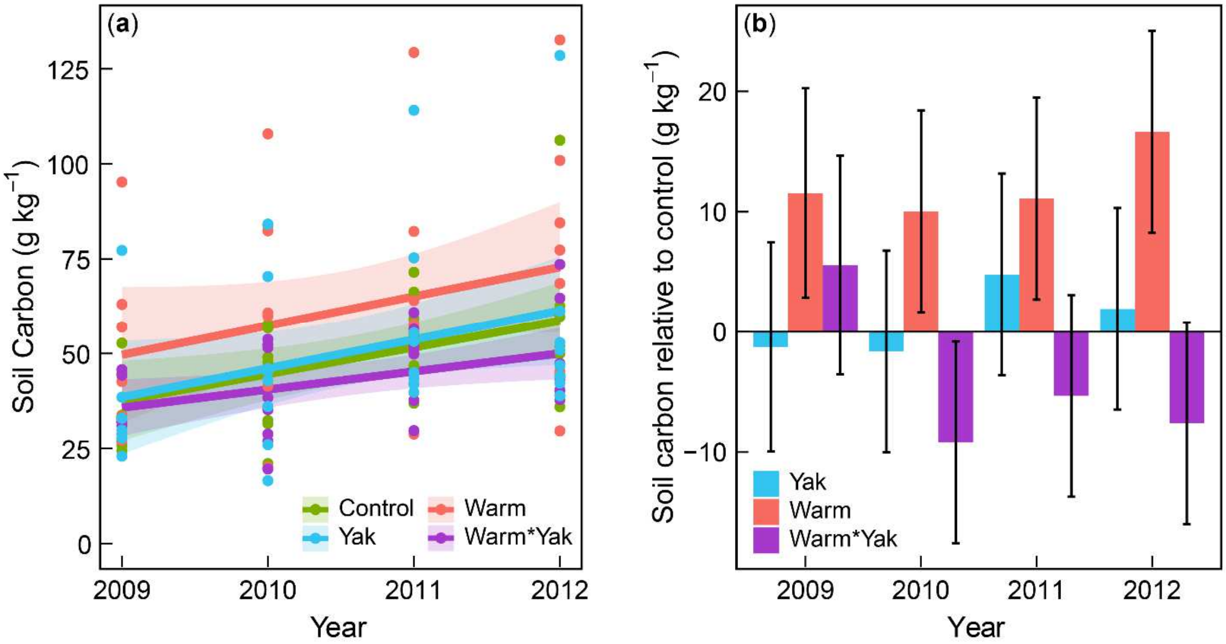

Figure 4.9. Soil carbon concentrations with 95% confidence intervals for warming and grazing treatments from 2009-2012 (a). Mean (± SE) soil carbon concentrations in treatments relative to controls (b).

Chapter 5

Conclusions

With this work I integrated local ecological knowledge with Western scientific knowledge to develop a better understanding of how alpine meadow ecosystems and pastoral livelihoods will be affected by climate and land use changes in central Tibet. To do so, I focused on three primary sets of questions regarding (1) pastoralists' knowledge of environmental change, (2) vegetation production and biogeochemical cycling in alpine meadows, and (3) longer-term trajectories of the provision of two key ecosystem services, forage production and carbon sequestration, under different climate and grazing conditions.

My interviews with pastoralists indicate that their perceptions of the environmental changes already occurring at Namtso generally fit well with a Western scientific perspective of climate change and its impacts in Tibet. They tended to have strong consensus on the changes that had the strongest impacts on their livelihoods, and in many cases they found that the forced changes in livestock management practices, such as the implementation of fences, were equally or more problematic than the effects of climate change. Some expressed concern that due to mandatory education at a boarding school and shifting social conditions, children from this village will not have the rangeland-based experiences necessary to provide them with the reservoir of LEK that was acquired by older generations. I found that the adults who appeared to be most observant of environmental changes were not necessarily those who were also regarded by their peers as being experts about traditional, more temporally stable pastoral knowledge. People tended to report that they learned about environmental changes from their own observations, and my social network analyses corroborated this finding that people seemed to be seeking out others in the community to discuss these changes primarily as a means to take action, rather than to learn from each other about the nature of the changes themselves. Herders disproportionately sought out village leaders to discuss these changes, which further highlights the interplay of power, knowledge, and the importance of strong local leadership to facilitate pastoral communities' capacity to cope with the changes they are facing.

Results from the climate change and grazing experiment confirmed herders' observations that water is likely a critical resource controlling ecological functioning in central Tibet's alpine meadows. In contrast to the widely held view that temperature and nitrogen should be the most limiting resources to support vegetation production in alpine ecosystems, I found that these alpine meadows are relatively nitrogen-rich and vulnerable to warming-induced soil drying. As expected for an ecosystem with a long evolutionary history of grazing, yak grazing maintained or even enhanced production of the dominant, grazing-tolerant species of dwarf sedge, *Kobresia pygmaea*, which in turn drove responses in production and at the community level due to its abundance under ambient climate conditions. Yaks also accelerated nitrogen cycling and improved the quality of vegetation as forage and substrate for decomposition, thereby creating positive feedbacks between grazers and plant production.

However, grazing interacted with warming to drive a reduction in both the warming-intolerant *K. pygmaea* as well as grazing-intolerant graminoids and shrubs, leading to the largest reduction in production when both yaks and warming were present. Increased spring snow mitigated some of the reductions in production under warming and also appeared to advance both green-up and senescence of vegetation that received an additional pulse of soil moisture preceding the monsoon. This change in the timing of phenology will advance the timing of when the alpine meadows act as a net carbon sink and could also provide an earlier source of forage for livestock emerging from an extended period of low forage availability each winter. However, increased snowstorms can be detrimental to livestock herds and pastoral livelihoods, so the potential benefits of additional snow for summer vegetation and carbon cycling are tempered by these other serious consequences of changing precipitation regimes. Overall, the warming treatment caused the largest decrease in net CO_2 uptake by the ecosystem, particularly by reducing GPP before the start of the monsoon each summer. This indicates that alpine meadows will likely become less of a carbon sink under future climate warming.

Yet, it is also possible that short-term responses in physiological processes, such as lower rates of photosynthesis under warming, will be counterbalanced by longer-term shifts in species composition. If the community eventually transitions to an assemblage that is better suited to the new climate and/or land use conditions, this could in turn lead to the recovery of previous ecosystem functioning. To test this idea, I paired results from the warming and grazing treatments in the experiment with observational measurements in healthy, degraded, and shrub meadows around the landscape. I found that the plant communities began to converge within five years of experimental manipulations, with yak grazing maintaining healthy meadow communities, but warming driving the species composition to become more similar to degraded meadows dominated by lichen crusts. The exponential increase in shrub production with warming and no grazing suggested that with climate warming and livestock removals, the alpine meadows could potentially shift to more of a shrub meadow state. However, neither the degraded meadows nor the shrub meadows stored as much soil carbon nor provided as much palatable vegetation as the healthy alpine meadow communities, which indicates that longer-term responses to climate warming and livestock removals are unlikely to lead to a recovery of the alpine meadows' current ability to provide critical ecosystem services, such as forage production and carbon sequestration.

Collectively, these results suggest that ecosystem functioning in Tibet's alpine meadows is maintained by grazing under ambient climate conditions, but these ecosystems will likely be particularly vulnerable to climate warming. Reductions in soil moisture under warming will have cascading effects on nutrient cycling, vegetation production, and, ultimately, the viability of pastoral livelihoods. Policies that restrict pastoralists' mobility and reduce their herd sizes will likely only constrain their ability to cope with these ecological changes but do little to reverse their undesirable effects. Therefore, my results highlight the need for more climate change adaptation efforts, rather than an emphasis on overgrazing as the primary cause of environmental change in Tibet. This leads to new questions about how to create appropriate adaptation strategies to help maintain the sustainability of Tibetan social-ecological systems facing unprecedented changes, but it is clear that these efforts could benefit from the integration of ecosystem science with the knowledge and needs of local pastoralists and leaders.

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Appendix 1

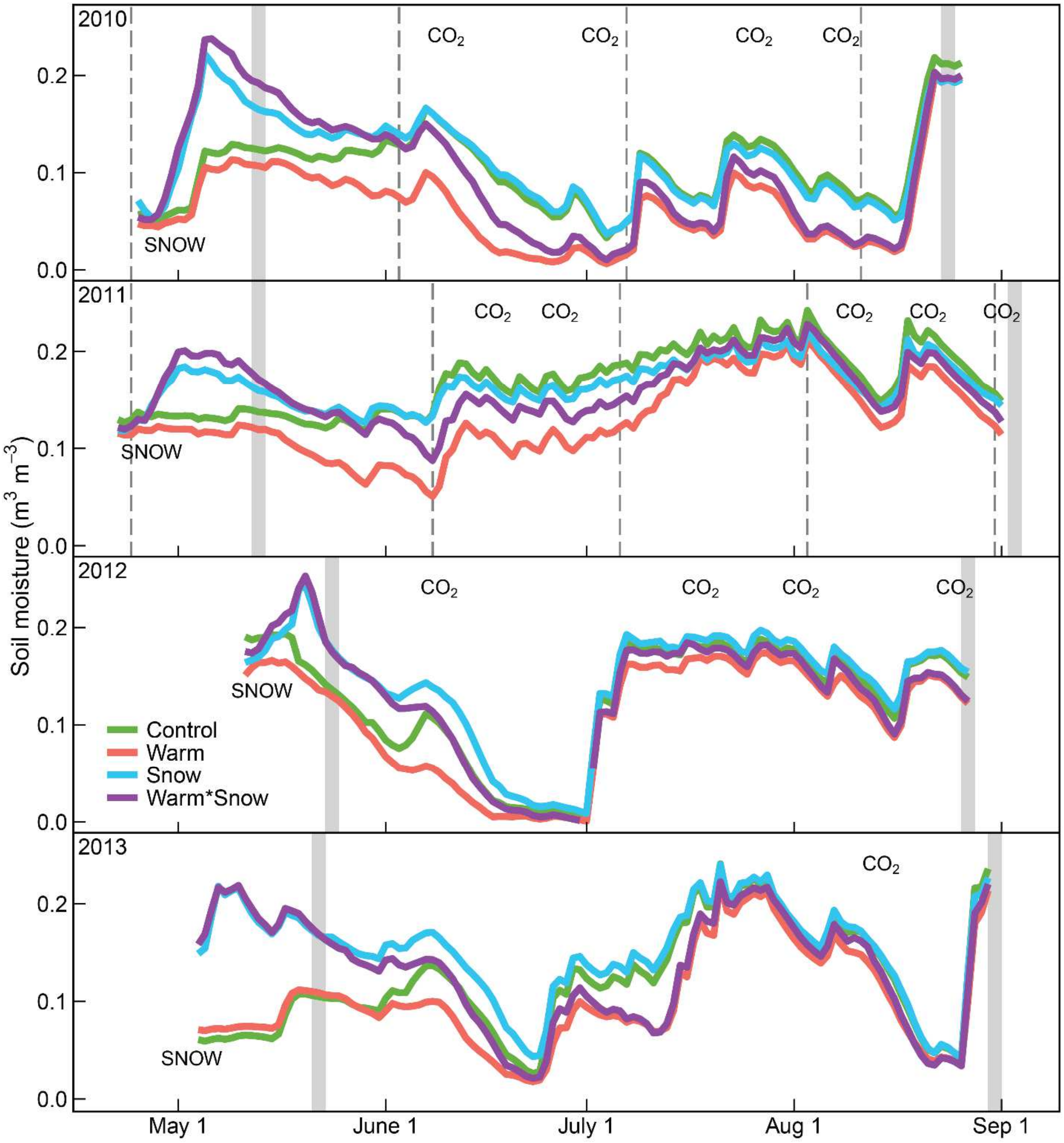

Figure A.1. Mean daily volumetric soil moisture in all experiment plots. The line for snow treatments sometimes obscures the line for control plots, and the line for warm*snow sometimes obscures the line for warm treatments when their means are nearly identical. The "SNOW" label indicates when snow additions were applied each year, and the vertical gray bars indicate when warming chambers were installed and removed each year. The dashed vertical lines indicate nitrogen probe burial dates in 2010 and 2011, and the "CO$_2$" labels indicate the days when CO$_2$ flux measurements were made each year.

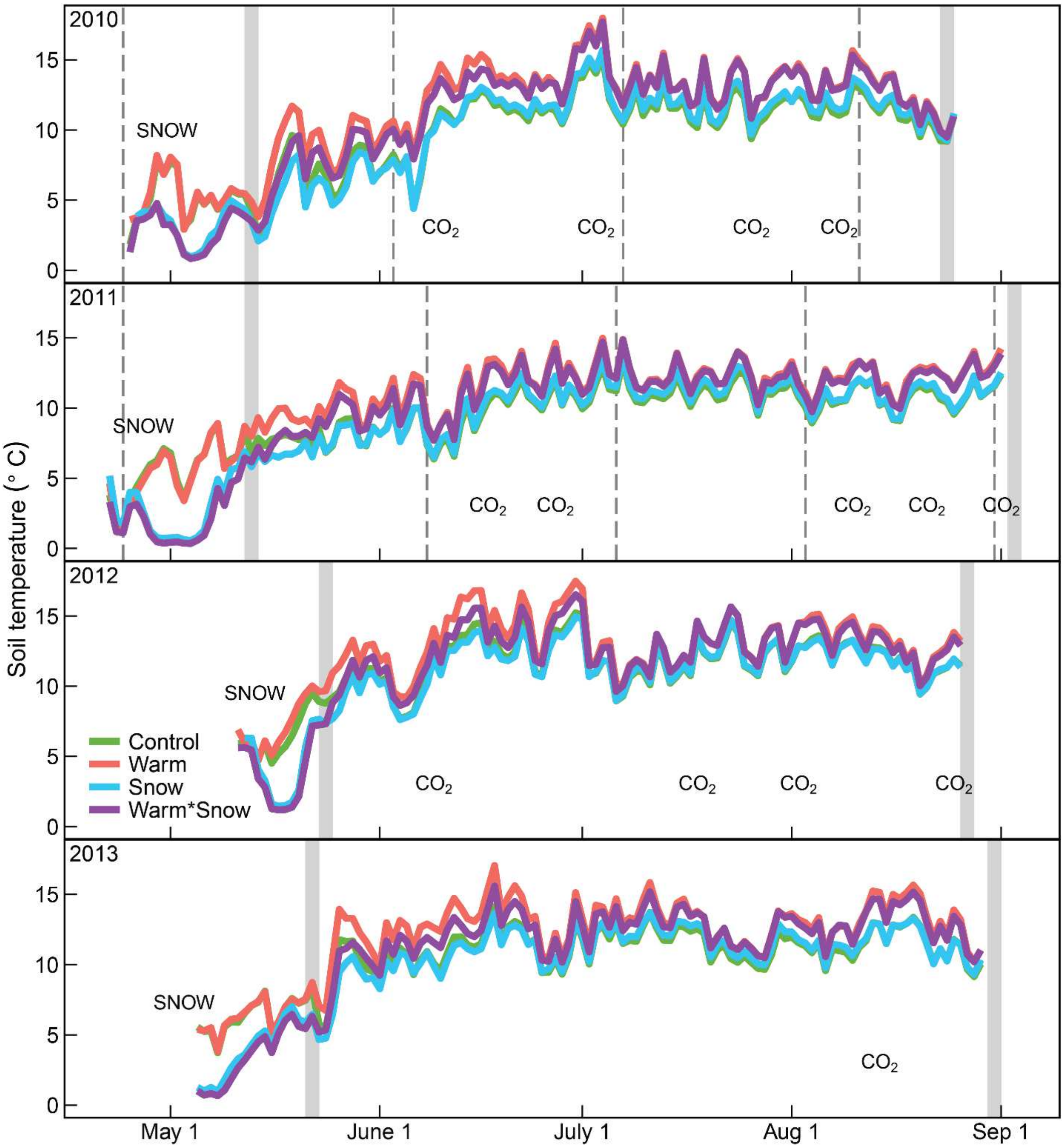

Figure A.2. Mean daily soil temperature in all experiment plots. The line for snow treatments sometimes obscures the line for control plots, and the line for warm*snow sometimes obscures the line for warm treatments when their means are nearly identical. The "SNOW" label indicates when snow additions were applied each year, and the vertical gray bars indicate when warming chambers were installed and removed each year. The dashed vertical lines indicate nitrogen probe burial dates in 2010 and 2011, and the "CO_2" labels indicate the days when CO_2 flux measurements were made each year.

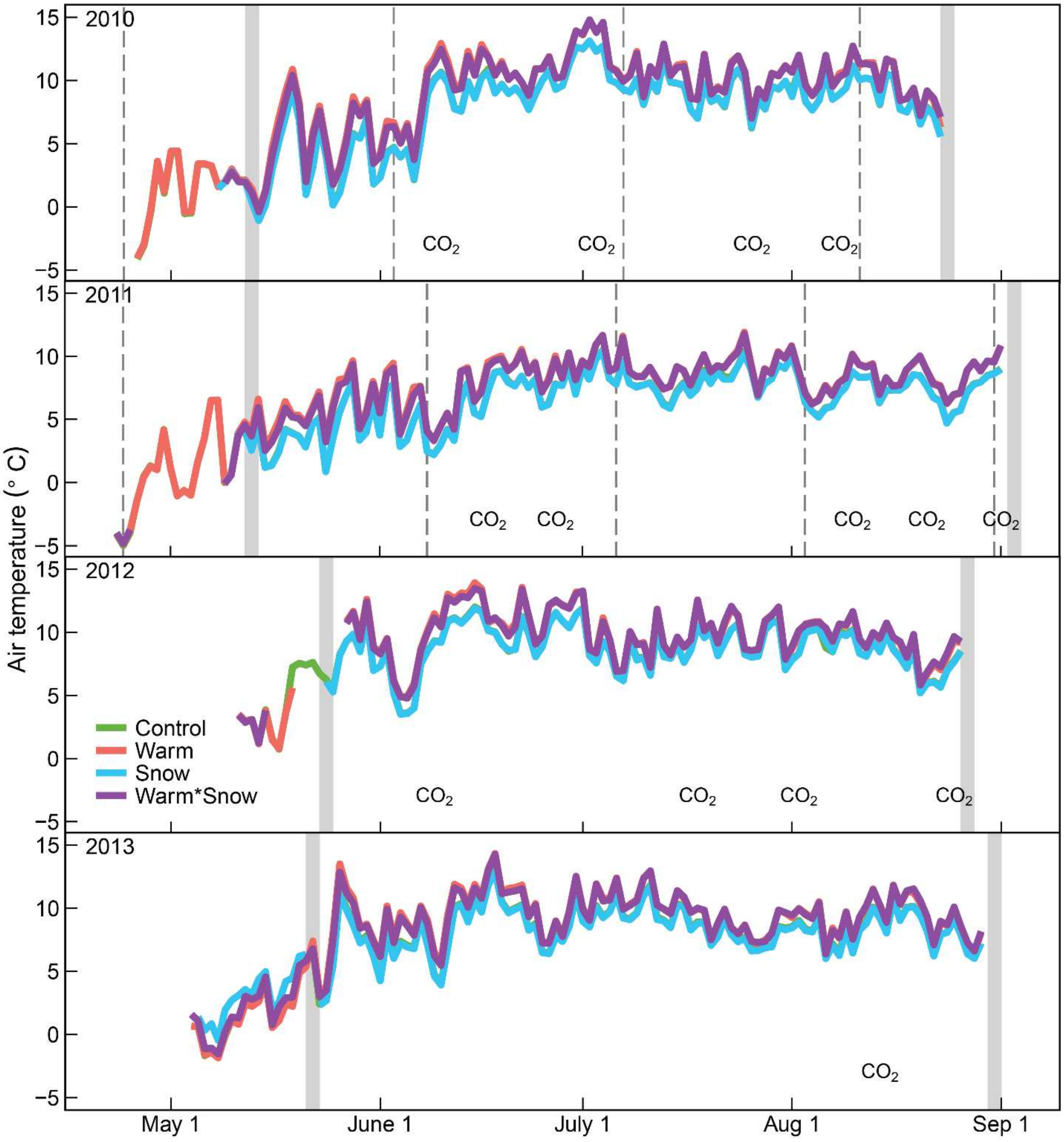

Figure A.3. Mean daily air temperature at 10 cm above the canopy in all experiment plots. The line for snow treatments obscures the line for control plots, and the line for warm*snow obscures the line for warm treatments when their means are nearly identical. Air temperature sensors couldn't be installed in plots with snow additions until the snow had melted, so snow plots are missing some early-season air temperature data. The vertical gray bars indicate when warming chambers were installed and removed each year. The dashed vertical lines indicate nitrogen probe burial dates in 2010 and 2011, and the "CO_2" labels indicate the days when CO_2 flux measurements were made each year.