CHAPTER 13

Responses of grasslands to experimental warming

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Contents

Introduction

Grasslands cover about 40.5% of the world's terrestrial area (Suttie et al., 2005) and provide important ecosystem services, such as supporting a variety of animals and plants. Climate change may have profound impacts on grasslands. Such impacts must be fully understood in order to mitigate climate change impacts and maintain grassland ecosystem functions and services throughout the world. There are dozens of manipulative experiments that have been set up in grassland ecosystems worldwide to explore how climate warming would affect them. In this chapter, we synthesize the current knowledge from these manipulative experiments. We focus on the responses of plants and microbes to experimental warming, carbon (C) and nitrogen (N) cycles as affected by experimental warming, and modeling studies on grassland ecosystems in response to warming.

Ecosystem Consequences of Soil Warming
https://doi.org/10.1016/B978-0-12-813493-1.00014-4

Responses of grassland plants to experimental warming

Global warming is influencing species and may cause extinction, including endemic species (Spurgeon, 2000; Jensen, 2004). Plants are very responsive to climate warming. Herbarium records show that flowering times of 229 plants have become progressively earlier over the past century (Primack et al., 2004). There are many ongoing manipulative experiments that have examined the effects of warming on plants in grasslands. This section reviews the responses of plants, including phenology, species composition, and community structure in response to warming.

Changes in plant phenology in response to experimental warming

Earlier phenological development is among the most common of responses of plants to warming (Hollister et al., 2005). Shifts in reproductive phenology, that is, flowering and fruiting times, have been widely observed under experimental warming conducted in grassland ecosystems. For example, in a Californian grassland dominated by annual grasses, the onset of flowering of all annual species was accelerated by 2–5 days by warming (Cleland et al., 2006). In a warming study conducted in northern Alaska, flower emergence of most plants was advanced by warming treatments (Hollister et al., 2005). Experimental warming resulted in immediate shifts in the phenology, flowering and fruiting, of plant communities at high elevations, which was mediated largely through changes in the timing of snowmelt (Price and Waser, 1998).

Shifts in the reproductive phenology of plants are often reported to be different among plant functional types and life histories. Functional groups were found to significantly affect flowering variables. For example, the phenology and duration of flowering in forbs was earlier and longer than in grasses and nitrogen-fixing legumes in both years of a 2-year warming experiment, with no differences detected between grasses and nitrogen-fixing legumes (Valencia et al., 2016). While manipulative warming significantly advanced the timing of flowering of three plant functional types (shrubs, graminoids, and forbs) in a subalpine meadow, the patterns and the explanatory microclimate factors varied across functional types and between life history traits (i.e., early- vs late-flowering species; Dunne et al., 2003). Dunne et al. (2003) found that warming usually had the strongest effect on early-flowering forbs. Shifts in timing of the earliest flowering species can be singularly explained by snowmelt date, but a combination of temperature-related microclimate factors, such as earlier snowmelt date, warmer soil temperatures, and decreased soil degree-days, is needed to explain earlier timings for other species. Similar conclusions were made by Price and Waser (1998). That is, phenological shifts were entirely explained by earlier snowmelt in the case of six early-flowering plant species, but four later flowering species responded to other factors. In another warming experiment, Wang et al. (2014) found warming advanced the first flowering date of both early spring–flowering species and midsummer-flowering species of alpine plants, however, the sensitivity of first flowering date to soil temperature change is significantly different.

Shifts in reproductive phenology can also exhibit divergent patterns for species with different phenologies. In a tallgrass prairie ecosystem in North America, experimental warming advanced the flowering and fruiting of species that flower before the peak of summer heat, but delayed flowering and fruiting for species that flower after the highest temperatures in summer (Fig. 1; Sherry et al., 2007). Conversely, in a typical alpine meadow on the Tibetan Plateau, warming was found to delay the reproductive phenology of

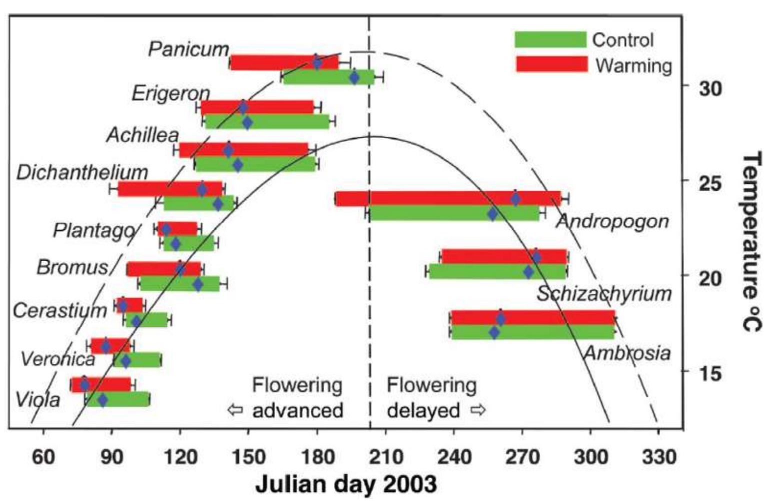

Fig. 1 Timing and duration of the entire reproductive period composed of three phases (budding, flowering, and fruiting) for the 12 species under experimental warming in a tallgrass prairie ecosystem in Oklahoma, United States. The *diamond symbols* indicate the average start date of flowering. The *dotted vertical line* indicates the peak summer temperature as defined by the maximum temperature of the regression curve. *From Sherry, R.A., Zhou, X., Gu, S., Arnone, J.A., Schimel, D.S., Verburg, P.S., Wallace, L.L., Luo, Y. 2007. Divergence of reproductive phenology under climate warming. Proc. Natl. Acad. Sci. U. S. A. 104, 198–202, © 2007 National Academy of Sciences, U.S.A.*

those early-flowering species and advance the reproductive phenology of late-flowering species, resulting in increased temporal overlap among the reproductive stages of early- and late-flowering species, which was attributed to soil moisture stress caused by warming (Zhu et al., 2016). Plants adjust their reproductive phenology in order to catch peak rainfall.

Vegetative phenology at the community level is also commonly changed by warming. Warming advanced the mean day of peak canopy greenness (Normalized Difference Vegetation Index, NDVI) by 9.3 days (Cleland et al., 2006). Warming also increased the length of the growing season in a temperate grassland in Wyoming, United States, resulting from earlier leaf emergence by the first species and later senescence by other species compared to controls (Reyes-Fox et al., 2014). However, surprisingly, the day of leaf onset of almost all plants at the four sites in northern Alaska was often found to be unresponsive to temperature increase, or that temperature was subordinate to other factors (Hollister et al., 2005). The reason for the lack of major changes in earlier phenological development in the study by Hollister et al. (2005) is that plots were only warmed in the growing season, starting treatment after snowmelt occurrence.

Cumulative effects of warming on phenology may exist, as shown in a warming study in which six Australian subalpine plants were investigated (Hoffmann et al., 2010). In some species, phenological changes caused by warming were detected within the first year of warming, whereas phenological changes in most other species occurred after 2–4 years of warming treatment. Warming effects on the phenology of plants in grasslands interact with other climate change factors (e.g., elevated CO_2, Reyes-Fox et al., 2014) or are mediated by variation in both intraannual and interannual precipitation (Zelikova et al., 2015).

Warming effects on plant species composition and community structure

Biodiversity is the basis of ecosystem functions. Climate change has long been recognized to have significant impacts on species distribution and biodiversity worldwide (Parmesan and Yohe, 2003; Root et al., 2003; Malcolm et al., 2006; Rosenzweig et al., 2008; Williams et al., 2008). The distributions of many terrestrial species have recently shifted to higher elevations and higher latitudes at an unprecedented rate as a result of climate warming and the distances moved by species are greatest in studies showing the highest levels of warming (Chen et al., 2011). A synthesis study on how experimental warming affects biodiversity revealed that experimental warming caused an 8.9% decline in species richness across ecosystems worldwide—the decline being stronger in terrestrial rather than marine ecosystems (Gruner et al., 2017). Climate warming may cause the extinction of many species in the near future in tropical regions (Williams et al., 2008) and throughout the world (Thomas et al., 2004), making studying changes in biodiversity and the relevant changes in ecosystem functions under climate warming a hot topic. Many warming experiments examined changes in plant biodiversity in grassland ecosystems. Unlike some clear patterns in phenology shifts with warming, diverse changes in plant species composition and community structure under experimental warming have been observed.

A 26%–36% decrease in species richness, caused by 4-year experimental warming, was reported in the northeastern Tibetan Plateau, with higher species losses occurring at the drier sites where N was less available (Klein et al., 2004). It was concluded that heat stress and warming-induced litter accumulation were responsible for the dramatic declines in plant species diversity. In a temperate steppe in northern China, experimental warming significantly reduced the species richness of grasses and community coverage as a result of decreased soil moisture, but it was found that species interaction could mediate the responses of functional group coverage to warming (Yang et al., 2011). However, in the same ecosystem but with two different warming manipulations, daytime warming versus nighttime warming, neither daytime nor nighttime warming significantly changed the community-level cover or the cover of dominant, subordinate, or rare species (Yang et al., 2016). Changes in species richness under warming may be strongly modulated by herbivories. For example, total species richness in a tundra meadow was found to be increased by warming but only in the presence of herbivories. When herbivores were excluded the ecosystem lost species under warming (Kaarlejarvi et al., 2017).

In some ecosystems, however, it takes a long time for community composition to respond to warming. For instance, in a tallgrass prairie ecosystem, community composition was found to be resistant to experimental warming in the first 7 years, with responses occurring in the 8th year (Shi et al., 2015a). Long-term warming manipulations may result in different plant species responses to short-term treatments. After warming for 18 years, plant diversity rebounded to initial levels compared with control plots, but with novel community composition (Zhang et al., 2017).

Impacts of climate warming on plant diversity may not be random; instead, some functional groups are more vulnerable than others. Cross and Harte (2007) found that warming decreased the aboveground biomass and flowering success of shallow-rooted forbs but increased or had no effect on the growth of tap-rooted forbs in the warming experiment conducted in a subalpine meadow in Colorado. Similar phenomena were reported in a Tibetan Plateau grassland. Deep-rooted medicinal plants were less sensitive to warming than shallow-rooted nonmedicinal plants, resulting in a 20% species loss in medicinal plants versus a 40% species loss in nonmedicinal plants under warming (Klein et al., 2008). In a warming experiment in an alpine meadow, plant species richness significantly decreased by 10% due to warming after the third year of the experiment (Wang et al., 2012) and warming significantly increased cover of graminoid and legumes, whereas it reduced cover of nonlegume forbs. In contrast, in another warming experiment also in the Tibetan Plateau, warming increased the importance value of forbs and grasses by 4.9% but decreased the importance value of sedges by 4.4% (Fig. 2, Peng et al., 2017). During 20 years of experimental manipulation in northern Alaska investigating the influence of enhanced snow depth and warmer summer temperatures, the community shifted from

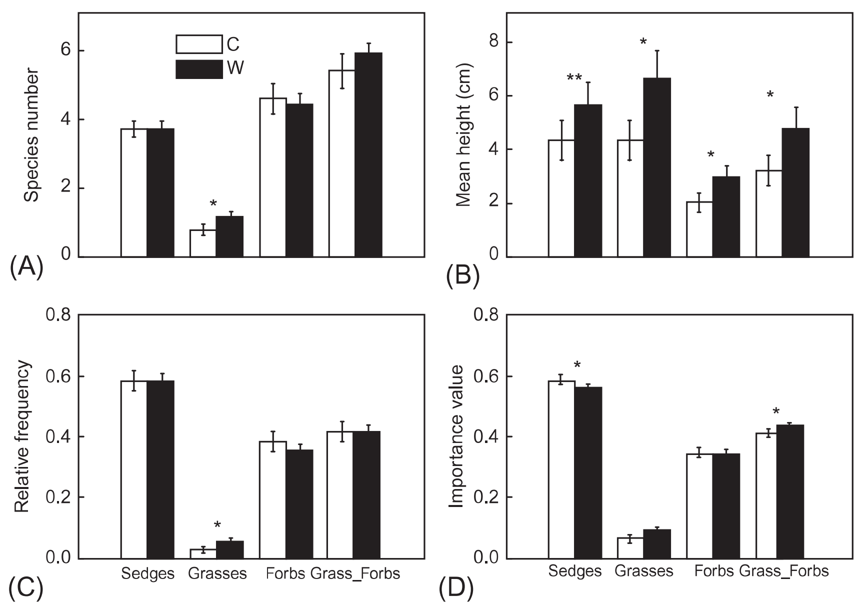

Fig. 2 Species number (A), monthly mean height (B), relative frequency (C), and importance value (D) of sedges, grasses, forbs, and a combination of grasses and forbs in warming (W) and control (C) treatments throughout 2012 and 2013. *Stars above the bars mean a statistical significance between W and C in different functional groups. From Peng, F., Xue, X., Xu, M., You, Q., Jian, G., Ma, S. 2017. Warming-induced shift towards forbs and grasses and its relation to the carbon sequestration in an alpine meadow. Environ. Res. Lett. 12, 044010, https://creativecommons.org/licenses/by/3.0/*

a wetter system dominated by the sedge *Eriophorum vaginatum* to a drier system dominated by deciduous shrubs, including *Betula nana* and *Salix pulchra* (Leffler et al., 2016).

Warming-induced changes in species diversity may serve as a major mechanism for regulating the temporal stability of ecosystem production. While changes in biodiversity explain part of the variation in temporal stability in a grassland ecosystem that was subject to 15 years of experimental warming, it was a secondary mechanism. The major contributor to the increased temporal stability in this ecosystem under warming over time was the promotion of biomass in the dominant C_4 functional group (Shi et al., 2016). In a temperate steppe in northern China, daytime warming, rather than nighttime warming, significantly reduced community temporal stability through a reduction in the abundance of dominant, stable species (Yang et al., 2017).

Another challenge facing grassland ecosystems is that climate warming may favor some invasive species expanding to new habitats and therefore introducing new environmental threats (Smith et al., 2012). The growth of three invasive species *Trifolium pratense* (legume), *Phleum pratense* (grass), and *Plantago lanceolata* (herb) in a temperate-boreal ecotone in North America were found to have increased in soils with a history of experimental warming (Thakur et al., 2014). The increased probability of seed release of invasive *Carduus nutans* by experimental warming over the growing season, combined with previously reported increases in the plant height of this species as a result of warming, was predicted to result in an increase in the population spread rate of *C. nutans* by 38% per year due to increased temperature (Teller et al., 2016). A community composition shift occurred in a 14-year warming experiment, resulting from the changes in an invasive species and three dominant species, in which negative correlations in relative abundance between the invasive species and the dominant species suggested interspecific competition (Shi et al., 2015a,b).

Warming was found to increase the species richness of both tundra and lowland plants (considered as future invasive species in tundra under a warmer climate), however, fertilization associated with stimulated mineralization under warming could cancel this positive impact (Eskelinen et al., 2017). While warming alone did not increase the cover of lowland species, the combination of warming and fertilization had a synergistic, positive impact on the cover of lowland species. In contrast, warming increased the cover of tundra species, but fertilization had negative effects on cover—opposite to the effect of fertilization on lowland species

(Eskelinen et al., 2017). Therefore in future climate conditions, with more nutrients resulting from enhanced mineralization, tundra meadow ecosystems may be under risk of invasion by lowland species.

Microbial responses to experimental warming in grassland ecosystems

The effects of climate warming on soil C storage are still uncertain (Lu et al., 2013; Crowther et al., 2016). Such uncertainty is partially due to the lack of a mechanistic understanding of the feedback between the responses of belowground microbial communities and climate warming (Zhou et al., 2012; Wieder et al., 2013). Consequently, scientists have argued that microbial mechanisms should be represented in soil C cycling models (Schimel and Schaeffer, 2012; Wieder et al., 2013; Hagerty et al., 2014). However, the current understanding of the effects of warming on microbial communities lags significantly behind that of plants. In this section, we first synthesize the common patterns of the responses of soil microbial biomass, diversity, and community structure to experimental warming through metaanalytical techniques in grasslands globally. We then attempt to link microbial biomass, diversity, and community structure to their functions.

Microbial biomass, diversity, and community structure as affected by experimental warming

Climate warming affects microbial biomass via two different mechanisms: elevated temperatures increase substrate supply from plant biomass input and soil environment temperature. Both benefit microbial growth. However, microbial biomass may negatively respond to warming because of a warming-induced decline in soil water content (Lu et al., 2013; Xu and Yuan, 2017). For example, an elevated soil temperature of 2°C increased microbial biomass by 78% in an old field tallgrass prairie located in the U.S. Great Plains (Luo et al., 2014). However, in an experiment on a south-facing slope on the Nyainqentanglha Mountains, along an altitudinal gradient (i.e., 4313, 4513, and 4693 m, respectively) in the Tibetan Plateau, 2-year elevated temperatures consistently inhibited microbial biomass across 3 alpine meadows at different altitudes (Fu et al., 2012). In order to obtain a general pattern, we performed a metaanalysis on 16 sites to examine how warming impacts grassland microbial biomass, diversity, and community structure (Table 1).

Current metaanalysis has revealed that warming grasslands stimulates significant microbial growth by 16%, despite the fact that elevated temperatures

Table 1 Locations and characteristics of grassland warming experiments

Grassland types	Location	Geographic coordinates	MAT (°C)	MAP (mm)	Warming (°C)	Response variables	References
Tallgrass prairie	Kessler's Farm Field, Laboratory, Oklahoma, United States	34°58′N, 97°31′W	16.3	967	2	Biomass, OTU, F:B	Zhang et al. (2005), Sheik et al. (2011), and Luo et al. (2014)
Temperate steppe	Jasper Ridge, Biological Preserve, Stanford, United States	37°40′N, 122°22′W	14	400	1	Biomass, F:B	Gutknecht et al. (2012)
Semiarid grassland	High Plains Grasslands Research Station, Wyoming, United States	41°11′N, 104°54′W	7.5	384	2.25	Biomass	Dijkstra et al. (2010)
Model grassland	Oak Ridge, Tennessee, United States	35°54′N, 84°20′W	15.7	1322	3	Biomass, F:B, OTU	Castro et al. (2010) and Gray et al. (2011)
Tussock grassland	Cass Field Station, New Zealand	43°2′S, 171°45′E	9	1300	3	Biomass	Graham et al. (2014)
Temperate grassland	Pontville, Tasmania, Australia	42°42′S, 147°16′E	11.6	560	2	Biomass, OTU	Hayden et al. (2012)
Alpine grassland	Beiluhe Station, Qinghai-Tibet Plateau, China	34°51′N, 92°56′E	−3.8	383	1.5	Biomass, F:B	Zhang et al. (2014)
Alpine grassland	Haibei Station, Qinghai-Tibet Plateau, China	37°30′N, 101°12′E	−1.3	501	2	OTU	Zheng et al. (2012) and Zhang et al. (2016a)

Continued

Table 1 Locations and characteristics of grassland warming experiments—cont'd

Grassland types	Location	Geographic coordinates	MAT (°C)	MAP (mm)	Warming (°C)	Response variables	References
Alpine grassland	Nagqu County and Bange County, Qinghai-Tibet Plateau, China	31°27′N, 92°1′E/ 31°23′N, 92°2′E	4/4	620/300	1.5	OTU	Zhang et al. (2016c)
Alpine grassland	Hbamers, Qinghai-Tibet Plateau, China	37°37′N, 101°12′E	−2	500	1.45	OTU	Li et al. (2016)
Alpine grassland	Dadu River, Qinghai-Tibet Plateau, China	102°21′E, 31°33′N	1.7	397	1	Biomass, F:B	Xiong et al. (2016)
Alpine grassland	Songpan County, Qinghai-Tibet Plateau, China	32°51′N, 103°33′E	2.8	718	1	Biomass, F:B	Shi et al. (2012)
Alpine grassland	Damxung Station, Qinghai-Tibet Plateau, China	30°31′N, 91°3′E	1.3	477	1	Biomass	Fu et al. (2012)
Temperate grassland	Songnen, Jilin, China	44°45′N, 123°45′E	4.9	410	1.8	Biomass, F:B	Ma et al. (2011)
Temperate steppe	Duolun County, Inner Mongolia, China	42°2′N, 116°17′E	2.1	385.5	1.79	Biomass, F:B, OTU	Shen et al. (2014) and Zhang et al. (2016b)

F:B, fungi to bacteria ratio; MAT, mean annual temperature; MAP, mean annual precipitation; OTU, bacterial operational taxonomic unit richness.

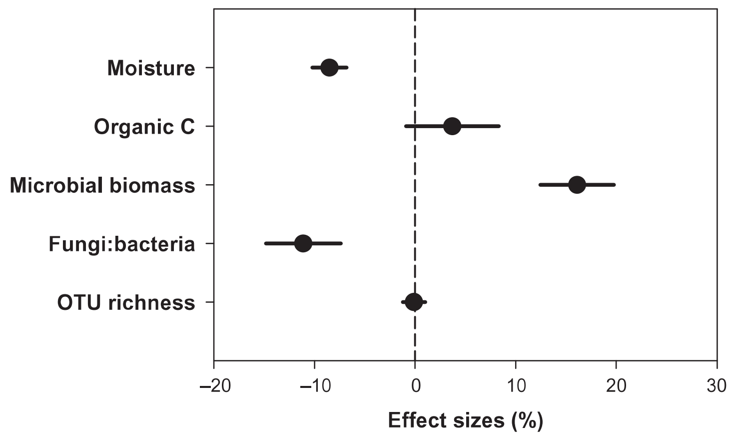

Fig. 3 Effects of experimental warming on soil moisture, soil organic carbon, and microbial biomass, diversity, and community structure.

result in a decrease in soil water content of 8% (Fig. 3). With a thick and interlinked peptidoglycan cell wall, fungi are very capability of tolerating water stress and spatially exploring water and nutrients (Schimel et al., 2007). Therefore we hypothesized that, similar to microbial biomass, experimental warming may increase the fungi to bacteria ratio (fungi:bacteria) due to the decreases in soil water content. However, results have shown that warming significantly decreased the grassland fungi:bacteria ratio by 11% (Fig. 3), suggesting that elevated temperatures shift soil microbial community compositions from fungi-dominated to bacteria-dominated. A recent global metaanalysis found that the microbial C:N biomass ratio also has a negative response to warming (Xu and Yuan, 2017). Consistent responses between the fungi:bacteria ratio and microbial C:N ratio to elevated temperatures were mainly due to significantly higher C:N biomass ratios in fungal communities than in bacterial communities (the mean C:N biomass ratio of bacteria and fungi are 5 and 15, respectively; Strickland and Rousk, 2010). One interpretation for a lower fungi:bacteria ratio under warming is that fungal growth is less inhibited by low temperatures whereas bacterial growth is less inhibited by high temperatures (Pietikäinen et al., 2005). Such a negative relationship between fungi: bacteria ratio and environmental temperature has been observed in a laboratory incubation study (Pietikäinen et al., 2005). A reduced fungi:bacteria ratio under warming is also in accordance with the findings that fungi dominate in soils during winter and spring, when the soils are covered with snow, while bacteria appear to dominate during summer under snow-free conditions (Lipson et al., 2002; Schadt et al., 2003; Pietikäinen et al., 2005). In addition, fungi were found to dominate during the decomposition of soils with low-nutrient content, because compared to bacteria, the nutrient demands and metabolic activities of fungi are relatively low (Zhou et al., 2017a,b). Previous studies showed that warming significantly increased soil N availability (Rustad et al., 2001; Dijkstra et al., 2010; Xu and Yuan, 2017), which might in turn decrease the fungi:bacteria ratio. Overall, global grassland warming experiments revealed that shifts in microbial biomass and community structure result mainly from changes in temperature rather than changes in water.

Warming had no significant effect on microbial diversity as reflected by the comparable bacterial operational taxonomic unit (OTU) richness between control and treatment (Fig. 3). The patterns of species diversity along spatial and environmental axes have been fascinating ecologists, biogeographers, evolutionary biologists, and natural historians for centuries (Schluter and Pennell, 2017). According to metabolic theory, higher environmental temperatures would increase biodiversity by accelerating biochemical reactions that control speciation rates (Allen et al., 2002). Actually, the ability of mean annual temperature to predict species richness is strongest in aboveground plants and animals, followed by soil animals (Decaëns, 2010; Tedersoo et al., 2014). However, more and more evidence supports that a scaling of the law regulating species diversity, based on thermodynamic theory derived from macroecology, in order to predict bacterial diversity has failed (Fierer and Jackson, 2006; Fierer et al., 2011; Chu et al., 2010) because the predominant drivers for bacterial diversity vary from temperature (Zhou et al., 2016) to moisture (Maestre et al., 2015), soil carbon (Delgado-Baquerizo et al., 2016), stoichiometry (Delgado-Baquerizo et al., 2017), and pH (Fierer and Jackson, 2006; Fierer et al., 2011; Chu et al., 2010). In macroecology, species richness is usually positively correlated with community biomass production (Duffy et al., 2017), but our synthesis of the grassland warming experiments suggests that bacterial diversity does not necessarily correspond to the productivity of bacterial communities.

Overall, our synthesis showed that warming not only increased total microbial biomass but also resulted in a shift of microbial community structure from fungi-dominated to bacteria-dominated (Fig. 3). However, bacterial diversity did not simultaneously increase with bacterial biomass under experimental warming. Soil bacterial communities are extremely diverse. It has been estimated that 1 g of soil contains up to 1 billion bacteria cells consisting of tens of thousands of taxa (Wagg et al., 2014). Soil is characterized by a redundancy of diversity. The relationship between microbial diversity, biomass, and function, which fundamentally differs from well-established knowledge on plants and animals, has seldom been proved (Nannipieri et al., 2003; Fierer and Jackson, 2006; Fierer et al., 2011). Generally, a reduction in any group of microbial species has little effect on the overall processes in soil because other microorganisms can quickly take on its function (Nannipieri et al., 2003).

Microbial community functions

Warming mediates the functions of microbial communities, something that is critical to sustaining grassland biomass production. It has been commonly observed that warming increases plant growth in grasslands (Zhou et al., 2012). A warming-induced increase in biomass production needs an additional supply of nutrients. Experimental warming often stimulates net N mineralization and increases soil inorganic N availability in grasslands whether the systems are water limited or not (Rustad et al., 2001; Pendall et al., 2004; Parton et al., 2007; Dijkstra et al., 2010; Bai et al., 2013; Xu and Yuan, 2017). In addition, the response magnitude of inorganic N availability to warming is much higher in the growing season than the nongrowing season when the growth rate of plants is low (Dijkstra et al., 2010). For example, in a water-limited semiarid grassland located at the High Plains Grasslands Research Station of the U.S. Department of Agriculture's Agricultural Research Service (USDA-ARS), Dijkstra et al. (2010) found that warming significantly increased the soil inorganic N pool size in midsummer (31%–63%) but only marginally increased the soil inorganic N in the nongrowing season (17%). Nitrogen is generally considered to be one of the key limiting nutrients in terrestrial ecosystems (Vitousek and Howarth, 1991; LeBauer and Treseder, 2008; Xia and Wan, 2008). A warming-induced increase in the internal production of inorganic N could stimulate plant growth and net ecosystem productivity, especially at N-limited sites (Rustad et al., 2001).

Extracellular enzymes are important because they catalyze the rate-limited steps of decomposition and nutrient cycling (Sinsabaugh, 1994). Assays for extracellular enzyme activity became a common tool for studying soil microbial responses in global change experiments (Henry, 2013). Generally, in field experiments, the potential activities of both hydrolases and oxidative enzymes either responded positively (Xu et al., 2010; Zhou et al., 2013) or did not significantly respond to warming (Bell et al., 2010; Kardol et al., 2010). Soil samples collected from warming experiments are typically analyzed for the potential activity of enzymes at a specific incubation temperature, which provides a relative measure of change in enzyme pool sizes in response to warming (Henry, 2013). However, the temperature dependence of enzyme activity in the field cannot be fully addressed because warming increases kinetic energy and thus accelerates reactions requiring enzymes (Sinsabaugh and Follstad Shah, 2012; Henry, 2013). In other words, the in situ activity of enzymes in warmed soils is actually higher than in ambient soils despite the potential activity of enzymes under warming treatments and controls being comparable.

Microbial communities regulate soil carbon balance in response to warming. A variety of individual studies and metaanalyses suggested that warming did not significantly alter grassland soil organic C storage (Zhou et al., 2012; Lu et al., 2013; Crowther et al., 2016). Scientists argued that compared with plant C pools, the large C pool in soil may conceal its smaller response to experimental warming, especially when the duration of experiments is too short to detect changes in the soil C pool (Batjes, 1996; Lu et al., 2013). However, in a warming experiment of 19 years in a tall-grass prairie ecosystem in the U.S. Great Plains, soil organic C did not exhibited any significant change as a result of warming (Courtesy with Dr. Yiqi Luo). The unchanged soil C storage in this grassland ecosystem under warming conditions is likely a result of the enhanced litter decomposition and soil respiration, which roughly offsets warming-induced increases in biomass production (Zhou et al., 2012). Microbial activities offset warming-induced increases in net primary production (NPP) through a variety of mechanisms. First, warming increases the quantity of decomposers as shown by the positive responses of microbial biomass to experimental warming (Fig. 3). Second, warming decreases the fungi: bacteria ratio (e.g., Fig. 3). A ^{13}C labelled litter decomposition experiment also provided evidence that in soils with high fungi:bacteria ratio, litter derived ^{13}C in respired CO_2 was lower and residual ^{13}C in bulk soil was higher (Malik et al., 2016). In addition, the turnover rate of fungi is slower than that of bacteria (Strickland and Rousk, 2010; Zhou et al., 2017a,b). Accelerated turnover rate can increase respiration rate per unit of microbial biomass (Hagerty et al., 2014). Warming decreased fungi:bacteria ratio, resulting in more C being released rather than stored in soils (Bailey et al., 2002; Six et al., 2006; Fierer et al., 2007; Malik et al., 2016). Third, enzymes may also contribute to faster decomposition and higher soil respiration rate under warming treatment.

Warming did not change microbial diversity, but did change microbial functions like N mineralization, extracellular enzyme activity, and C decomposition rate. Based on a long-term warming experiment in a tallgrass prairie ecosystem, Zhou et al. (2012) found that less than half the functional genes and operational taxonomic units detected overlapped between warming and control conditions, but no difference in the phylogenetic/functional gene richness and diversity was observed between warming and control plots. Overall, based on current grassland warming experiments, it seems that microbial diversity may be unnecessary for ecological functions. Moreover, in some studies, the relationships between microbial diversity and biomass and/or ecosystem functions are controversial and need further investigation.

Carbon and nitrogen cycles in response to experimental warming in grasslands

Carbon cycle

The warming experiments conducted in grassland ecosystems worldwide during the previous decades suggested that soil warming significantly affected most carbon processes, such as carbon fluxes and pools in grasslands. Overall, warming enhanced the activity of photosynthetic enzymes and photosynthetic rates, resulting in positive responses in grassland productivity. However, there still were large variations among different grasslands. For example, by applying a metaanalysis to a global data set, Lu et al. (2013) showed that the response of aboveground NPP (ANPP) in grasslands to global warming ranged from −21% to +37%. Neutral or negative responses were even observed in temperature-limited systems, like the Tibetan Plateau grasslands with an 11% decrease in ANPP (Klein et al., 2007). In addition, a metaanalysis focusing on the Tibetan Plateau also showed insignificant responses of photosynthesis rates to experimental warming (Fu et al., 2015a).

The positive effects of experimental warming on carbon input could first result from the stimulating effects of elevated temperature on a series of biochemical processes. Second, the increased N mineralization rate and soil N availability induced by warming also increased photosynthesis rate and primary productivity (Lu et al., 2013). Third, in a warmer environment, earlier leaf bud burst and delayed defoliation could prolong the growing season length and the period of carbon assimilation (Sherry et al., 2007). Fourth, warming could enhance the dominance of C_4 plants, which responded more strongly than C_3 plants to warming (Luo et al., 2009).

However, on the other hand, warming-induced changes may result in insignificant or even negative effects on carbon input. For example, the thermal acclimation of photosynthesis may adjust photosynthetic characteristics, so as to keep similar rates of carbon fixation at different growth temperatures (Way and Yamori, 2014). Some species even performed detractive adjustment, reducing photosynthesis at elevated temperatures (Way and Yamori, 2014). In most grasslands, experimental warming decreased soil moisture (Xu et al., 2013) and consequently reduced productivity. This effect may be responsible for the decreased ANPP in the Tibetan Plateau grasslands found by Klein et al. (2007), because this site received the majority of its precipitation in winter and therefore suffered warming-induced drought in the growing season. Moreover, species loss caused by climate warming (Thomas et al., 2004) may mediate the warming responses of grassland productivity (Cowles et al., 2016).

Soil warming can also accelerate processes related to carbon effluxes, such as litter decomposition and soil respiration (Lu et al., 2013). These positive effects may be derived from the increases in temperature, decomposition substrate (e.g., litterfall and root biomass), and microbial biomass (Luo and Zhou, 2006). However, opposite patterns were also reported. For example, Garten et al. (2009) found that warming-induced drought reduced soil respiration by 24% in a grassland near Oak Ridge, Tennessee, United States. Using a metaanalysis, Yue et al. (2015) found large variation in the warming effects on litter decomposition rates across 21 grasslands, resulting in an insignificant overall effect. Similarly, the synthesis by Lu et al. (2013) showed that warming had little effect on ecosystem respiration. These variations in the responses of carbon effluxes to experimental warming may reflect the complexity of the field environment in grasslands.

As for carbon pools, warming had more apparent effects on plant biomass than soil organic carbon (SOC). The metaanalysis by Lin et al. (2010) suggested that warming increased the biomass of herbaceous plants by 5%. Other metaanalyses also showed significant positive effects on both aboveground and belowground biomass at the biome scale for grasslands, due primarily to enhanced productivity (Lu et al., 2013; Fu et al., 2015b). In contrast, SOC showed little response to warming, at least during observation periods (Lu et al., 2013; Fu et al., 2015b). This could be caused by the similar responses of carbon influxes and effluxes to warming, which result in an unchanged net ecosystem exchange (NEE) and thus unchanged SOC in grasslands (Lu et al., 2013). Another reason for the unresponsiveness of SOC to warming might be the huge amounts of carbon stored in soil compared with the magnitude of NEE. At the global scale, the soil carbon pool contains more than 1000 Pg C, while the global NEE has a magnitude of 1–2 Pg C $year^{-1}$ (Luo and Zhou, 2006; Le Quéré et al., 2009). This disproportion between soil carbon pool and ecosystem NEE might make changes in SOC unobservable, especially over short-term periods.

Nitrogen cycle

Soil warming had differential effects on various nitrogen processes in grasslands as shown in results from a metaanalysis of the responses of nitrogen processes (Fig. 4). Overall, experimental warming tended to increase net N mineralization, soil inorganic N, denitrification, and leaf N concentration but had little effect on net nitrification, microbial N immobilization, and N leaching (Bai et al., 2013). The increase in N mineralization could be the direct effect of temperature on microbial activities (Melillo et al., 2002). Some studies suggested that the increment in N mineralization might be dampened by enhanced plant growth and microbial uptake in the long term (e.g., Bai et al., 2013). On the other hand, the indirect effects of warming may offset the positive responses of N mineralization by reducing soil moisture (Brzostek et al., 2012) and causing physiological acclimation in microbes (Davidson and Janssens, 2006).

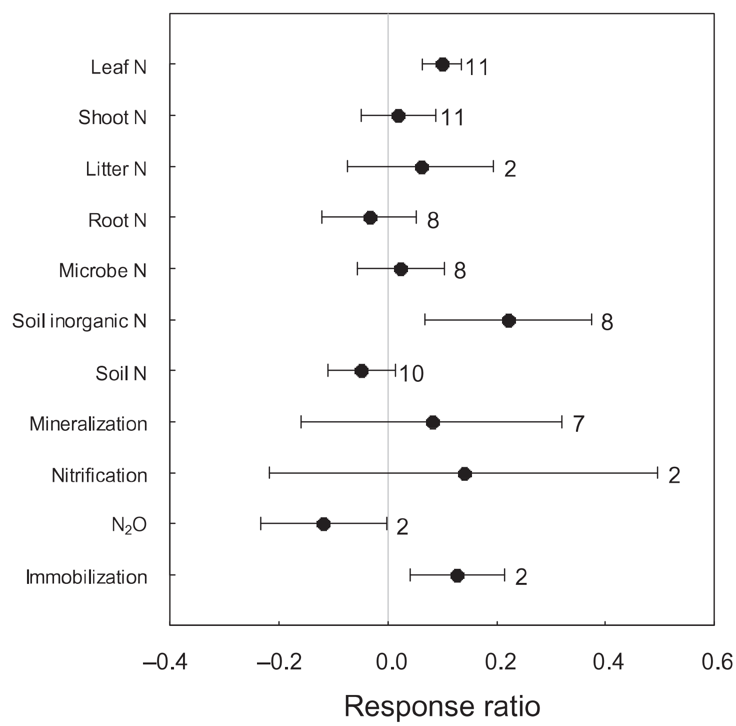

Fig. 4 A summary of the response ratios of nitrogen processes to experimental warming in grasslands. Error bars represent 95% confidence intervals. The numbers beside the error bars are sample sizes.

The neutral responses of microbial immobilization to warming might be the net result of the positive effects of elevated temperatures on soil N availability (Yin et al., 2012) and the negative effects of water and heat stresses on microbial activity (Fierer et al., 2003; Wittebolle et al., 2009). For net nitrification rate, the local adaptation of microbes may play an important role. According to previous studies, the optimum temperature for nitrifying microbes decreased along temperature gradients from warmer to colder regions (Dalias et al., 2001). Therefore warming could stimulate nitrification if the raised temperature was under the physiological optimum for the nitrifying microbes or suppress nitrification if the raised temperature exceeded the optimum temperature, regardless of thermal niche. For both immobilization and net nitrification, warming-induced changes in microbial community composition may contribute to microbial adaptation to warming (Avrahami and Conrad, 2003; Zhang et al., 2005).

The denitrification rate in grasslands increased under warmer environments—a possible result of several mechanisms. First, warmer soil could not only enhance enzyme activities but also enrich denitrifiers in the soil microbial community (Braker et al., 2010). Second, substrates for denitrification were accumulated under warming, due to increased dissolved organic carbon and inorganic nitrogen in soil (Tscherko et al., 2001; Barnard et al., 2005; Bai et al., 2013). Third, as an anaerobic process, denitrification can be stimulated in a more anaerobic environment, which could be achieved by more O_2 consumption due to increased soil respiration at elevated temperatures (Castaldi, 2000). However, warming-induced soil drought and promotion in nitrification might also depress denitrification due to the changes in soil aeration and O_2 content (Smith et al., 2003).

Nitrogen leaves ecosystems via N_2O emissions and N leaching. The effects of warming on both processes are very uncertain in grasslands (Bai et al., 2013). The emission of N_2O from soil could be derived from either nitrification or denitrification. Therefore the response of N_2O emissions to soil warming depends on the relative contributions of nitrification and denitrification, as well as factors regulating warming responses of these two processes (Maag and Vinther, 1996; Stres et al., 2008). On the one hand, higher temperatures decreased nitrification-derived N_2O but increased denitrification-derived N_2O (Maag and Vinther, 1996). On the other hand, lower soil moisture induced by warming increased nitrification-derived N_2O but decreased denitrification-derived N_2O (Bijoor et al., 2008). As a result, the ultimate response of N_2O emissions to soil warming is determined by the relative strength of the increased temperature and decreased soil moisture, something that could largely vary from site to site in grasslands. For the warming response of nitrogen leaching, changes in soil moisture and inorganic nitrogen may be the most important factors (Bai et al., 2013). However, current observations have been mostly conducted in wet environments, and have exhibited very large variations, preventing us from drawing solid conclusions.

Nitrogen uptake by plants was found to be promoted by warming, resulting in an increased leaf N content (Bai et al., 2013). This may be due to enhanced N availability and plant demands under warming. Increased N availability alleviated the limitation of N on plant growth by allowing more biomass allocation to aboveground organs and more nitrogen to be invested in the leaves (Fan et al., 2009) in order to enhance photosynthetic capacity and increase carbon assimilation (Kattge et al., 2009). However, in the long term, the enhanced growth of plants will maintain a high demand for nitrogen, while N in soils may be progressively depleted, which will eventually cause nitrogen limitation to plants (Luo et al., 2004).

Carbon and nitrogen coupling

The coupling between carbon and nitrogen cycles is usually characterized by the C:N ratio in different compartments of ecosystems. According to our analysis, no significant effects of warming were found on the C:N ratio of plant organs, microbes, or soils across grasslands (Fig. 5). Previous studies also reported few changes in the C:N ratio of plants and soils in response to warming across global biomes (Lei et al., 2007; Rosenblatt and Schmitz, 2014; Yuan et al., 2017). These might reflect the relatively stable stoichiometry in both plants and soils, and the strong coupling between carbon and nitrogen cycles. However, as the sample size was small, conclusive interpretation requires further studies to be conducted in a variety of grasslands.

Modeling grassland ecosystem dynamics under future climates through assimilating empirical data

Many ecosystem models have been developed during the past 30 years, for example, CENTURY (Parton et al., 1988), CASA (Potter et al., 1993), TEM (McGuire et al., 1995), SDGVM (Woodward et al., 1995), Ecosys (Grant, 2001), LPJ (Sitch et al., 2003), and TECO (Weng and Luo, 2008). Most of these models share similar conceptual components (Fig. 6): photosynthesis is simulated using the Farquhar model (Farquhar et al., 1980), modified by environmental factors including light, CO_2 concentration, temperature, and nutrients and upscaled to the ecosystem level

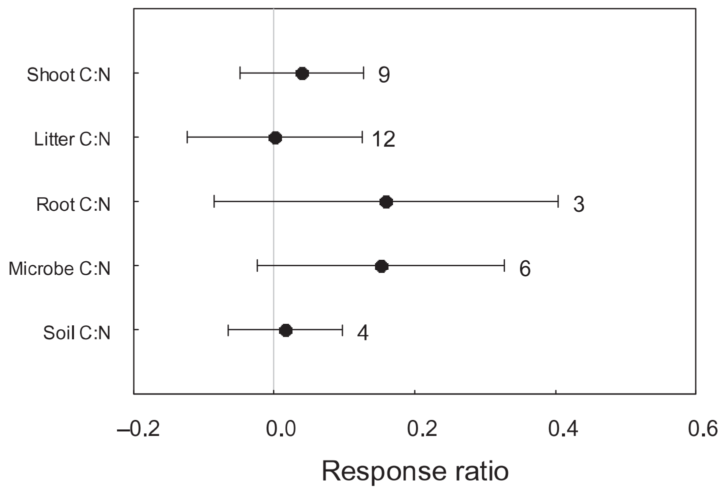

Fig. 5 A summary of the response of C:N ratio to experimental warming in grasslands. Error bars represent 95% confidence intervals. The numbers beside the error bars are sample sizes.

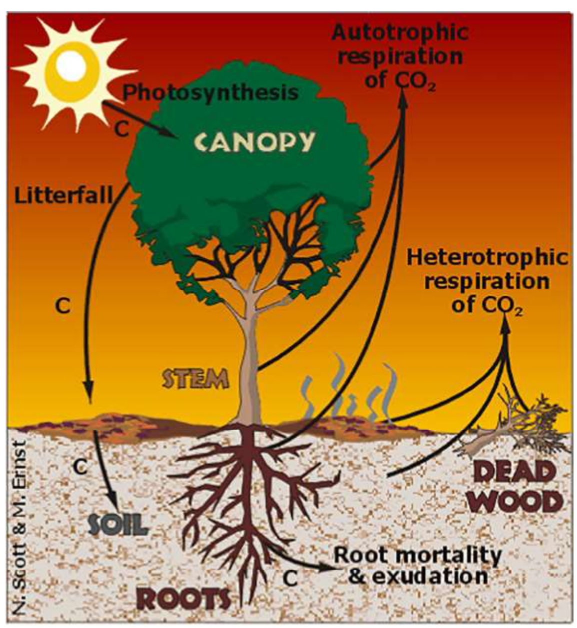

Fig. 6 Illustrative example of terrestrial ecosystem carbon cycling: plant photosynthesis, carbon allocation, plant growth, litterfall, litter, and soil decomposition.

by leaf area index; photosynthetically assimilated carbon is allocated to plant organs (leaf, stem, and root) with fixed or flexible allocation coefficients further modified by resources and/or plant phenology (Zaehle et al., 2014); death of plant organs (litterfall) is simulated by its turnover rate modified by environmental factors; litter and soil carbon are usually compartmented into conceptual pools, such as metabolic and structural litter pools and fast and slow soil carbon pools, characterized by their respective residence time; and carbon transfers from litter to soil and among soil pools are governed by pool size and specific transfer coefficients as affected by environmental factors.

Although there are similar structures shared among these ecosystem models, large differences in simulated variables exist among the models. For example, allocation coefficients of NPP showed great divergence among 10 ecosystem models (Fig. 7A) used to simulate ecosystem dynamics in a semiarid grassland (De Kauwe et al., 2017). Simulated carbon fluxes in forest ecosystems varied considerably among 19 models (Fig. 7B–D; Keenan et al., 2012). The difference mainly stems from different parameterization and submodel structures (e.g., response functions to temperature and moisture). Specifically, the major difference results from the schemes (i.e., different versions of the same concept) used for stomatal conductance, carbon allocation (De Kauwe et al., 2017), plant stoichiometry (Zaehle et al., 2014), nitrogen limitation (Niu et al., 2016), and sensitivity to temperature and water change (Medlyn et al., 2015).

One of the main objectives of developing these models is to explore ecosystem responses to climate warming. Climate warming has the potential to affect almost every aspect of an ecosystem. For example, increased temperature can affect metabolic reaction rates, growing season length, soil water content, and species composition and competition and therefore could affect both ecosystem photosynthesis and respiration. Plenty of modeling activities have explored the responses of grassland ecosystems to climate warming. Ecosystem processes including carbon, nutrient, and water cycling in grasslands have been simulated to investigate their responses to climate warming. Specifically, relevant variables include NPP, ecosystem respiration, soil respiration, N mineralization, N uptake, nitrification and denitrification, evaporation, transpiration, and runoff. Different, in some cases contradictory, findings have been reported due to model structures, parameterization, and site-specific responses.

The magnitude and sign of ecosystem responses to climate warming are site- and model-specific and depend on simulated warming magnitude.

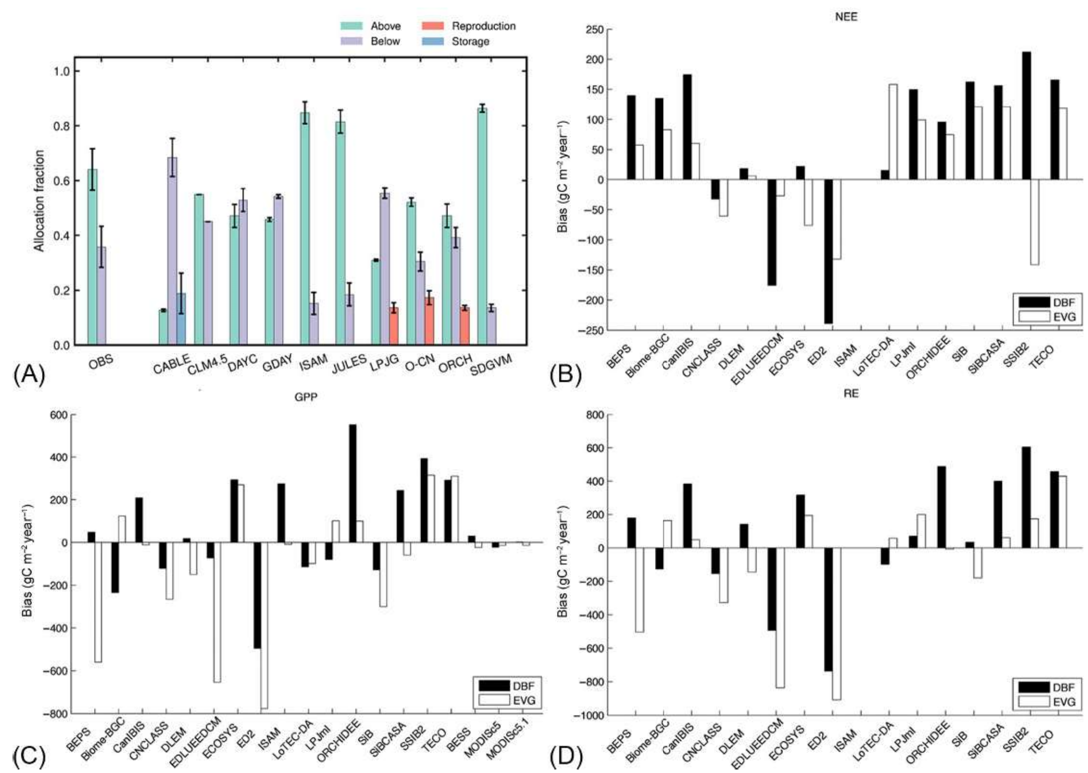

Fig. 7 Differences in simulated variables: (A) allocation fraction; (B) net ecosystem exchange (NEE); (C) gross primary productivity (GPP); and (D) ecosystem respiration (RE) among multiple ecosystem models. *(A) Modified from De Kauwe, M. G., Medlyn, B.E., Walker, A.P., Zaehle, S., Asao, S., Guenet, B., Harper, A. B., Hickler, T., Jain, A.K., Luo, Y., Lu, X., Luus, K., Parton, W.J., Shu, S., Wang, Y.-P., Werner, C., Xia, J., Pendall, E., Morgan, J.A., Ryan, E.M., Carrillo, Y., Dijkstra, F.A., Zelikova, T.J., Norby, R.J. 2017. Challenging terrestrial biosphere models with data from the long-term multifactor Prairie Heating and CO_2 enrichment experiment. Glob. Chang. Biol. 23, 3623–3645, © 2017 John Wiley & Sons Ltd; (C and D) modified from Keenan, T. F., Baker, I., Barr, A., Ciais, P., Davis, K., Dietze, M., Dragoni, D., Gough, C. M., Grant, R., Hollinger, D., Hufkens, K., Poulter, B., McCaughey, H., Raczka, B., Ryu, Y., Schaefer, K., Tian, H., Verbeeck, H., Zhao, M., Richardson, A. D. 2012. Terrestrial biosphere model performance for inter-annual variability of land-atmosphere CO_2 exchange. Glob. Chang. Biol. 18, 1971–1987, © 2012 Blackwell Publishing Ltd.*

For example, multiple ecosystem models predicted neutral responses of NPP to warming (+2°C) in an annual grassland in Jasper Ridge but negative responses at the Konza tallgrass prairie (Luo et al., 2008); the four models predicted either positive or negative responses of NPP to warming for the Jasper Ridge annual grassland. A temperature increase of 5°C consistently decreased NPP with a distinctive species composition in the grasslands of Colorado and Kansas, United States, and Kenya in an ecosystem model (Coughenour and Chen, 1997). Simulated NPP showed a nonlinear relationship with warming magnitudes, demonstrating varied responses (Zhou et al., 2008).

In contrast to the diverse responses of NPP to warming, simulated heterotrophic respiration (Rh), that is, the decomposition of SOC, generally shows a positive response across sites, models, and warming magnitudes (Luo et al., 2008; Zhou et al., 2008). Even though warming increases Rh, the response curve with different warming magnitudes is still nonlinear (Zhou et al., 2008), with Rh increasing and then decreasing across warming magnitudes (up to a temperature increase of 10°C). As a result of the simulated responses of NPP and Rh to warming (Fig. 8A), the carbon sink of a grassland ecosystem, referred to as NEE, may increase or decrease under warming (Fig. 8B). The conceptual response functions (Fig. 8A) illustrate that increased temperature can either increase or decrease photosynthesis or respiration, more likely reducing photosynthesis than respiration.

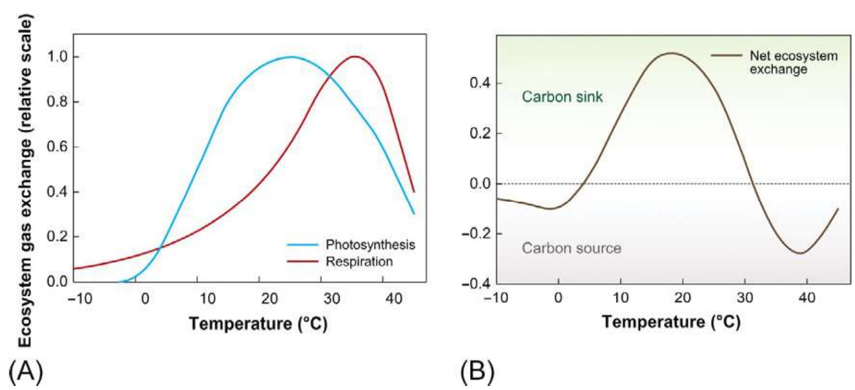

Fig. 8 Idealized response functions of ecosystem photosynthesis and respiration (A) and net ecosystem exchange (B) to temperature. *Modified from Luo, Y. 2007. Terrestrial carbon-cycle feedback to climate warming. Annu. Rev. Ecol. Evol. Syst. 38, 683–712.*

The differential responses of photosynthesis and respiration contribute to the net response of NEE to warming (Fig. 8B).

Multiple mechanisms regulate the responses of grassland carbon cycling to warming, among which are plant physiology, plant phenology, species composition, species competition, and nutrient and water dynamics (Fig. 9; Luo, 2007). Most of the mechanisms have been incorporated into these ecosystem models (Medlyn et al., 2015). Physiological response functions to warming, applied in ecosystem models, explain to some degree the responses of plant growth, respiration, and ecosystem carbon exchange (Luo, 2007). Increased N mineralization by warming favors plant growth in ecosystem models (Schimel et al., 1990), soil drying under warming could adversely affect NPP (Weng and Luo, 2008), and elevated temperatures extend the growing season length (Hunt et al., 1991). However, perspectives from species composition, species competition, and seed dispersion have not been adequately integrated into these models. Moreover, the thermal acclimation of photosynthesis and respiration (Smith and Dukes, 2013) and the priming

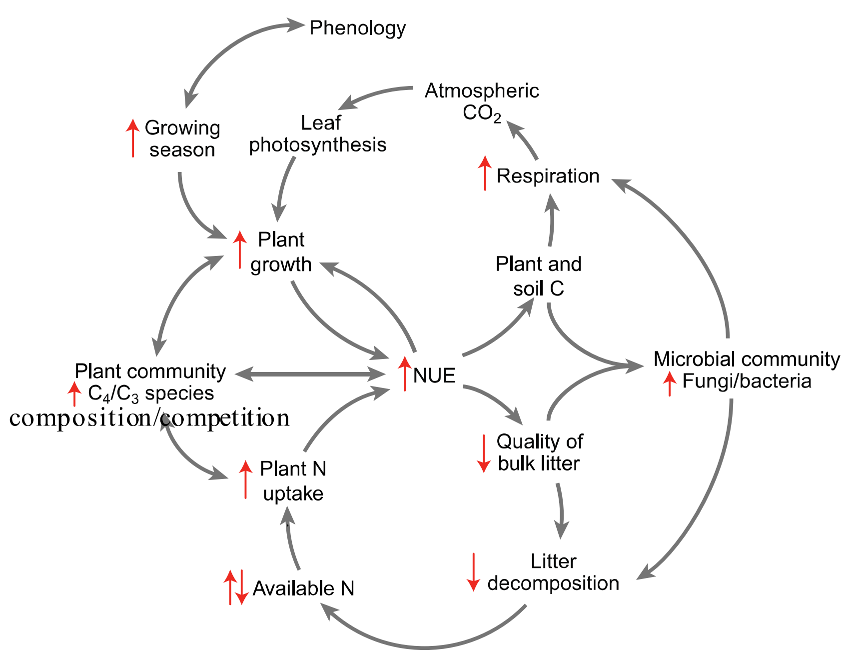

Fig. 9 Mechanisms regulating ecosystem responses to climate warming in grasslands. *From Luo, Y. 2007. Terrestrial carbon-cycle feedback to climate warming. Annu. Rev. Ecol. Evol. Syst. 38, 683–712.*

of soil carbon decomposition (Luo et al., 2016) are still at the initial stages of being incorporated into models.

To improve models to achieve more accurate projections and better representations of ecosystem processes, data assimilation approaches have recently been developed in ecology (Niu et al., 2014). Data assimilation techniques have been applied to constrain parameters, evaluate alternative response functions, and assess uncertainties in model structures (Raupach et al., 2005; Wang et al., 2009; Peng et al., 2011; Hararuk et al., 2015). Data assimilation is a statistical method that allows incorporating multisourced convoluted measurements into ecological models to constrain model parameters and to evaluate model structures (Fig. 10). Eventually, trained models would be used for accurate ecological predictions (Fig. 10). Such techniques have been successfully applied to estimate key parameters in terrestrial carbon cycling models, using data either from flux observations (Braswell et al., 2005; Sacks et al., 2007; Santaren et al., 2007; Wang et al., 2007; Tang and Zhuang, 2008) or a combination of flux and biometric measurements (Luo et al., 2003; Williams et al., 2005; Xu et al., 2006; Richardson et al., 2010; Zhang et al., 2010; Weng and Luo, 2011).

For example, Braswell et al. (2005) used eddy flux data and carbon stock data from Harvard Forest to evaluate an ecosystem carbon flux model (SIPNET) to estimate the rate of carbon sequestration. By assimilating soil respiration and biometric carbon data from Duke Forest, Xu et al. (2006) applied probabilistic inversion to quantify uncertainties in model parameters and predicted carbon pool dynamics. Wang et al. (2007) estimated parameters in land surface models using eight collections of eddy flux data and concluded that models with optimizing photosynthetic parameters showed improved model performance in terms of predicting carbon and water fluxes. Keenan et al. (2013) evaluated information content in different types of data sets and found that carbon fluxes in combination with stocks provide more information. Weng and Luo (2011) quantified relative information contributed by the model only, and by the model and data together, to short- and long-term predictions. They concluded that relative information contributions of the model and data varied with forecasting time and carbon pools. Lastly, instead of using batch data assimilation approaches, Gao et al. (2011) applied an ensemble Kalman filter to assimilate carbon flux and biometric carbon data, and found that after data assimilation the model made forecasts of long-term dynamics with greater confidence (Fig. 11).

Moreover, data assimilation has also been performed to evaluate the changes in carbon cycling model parameters under various experimental

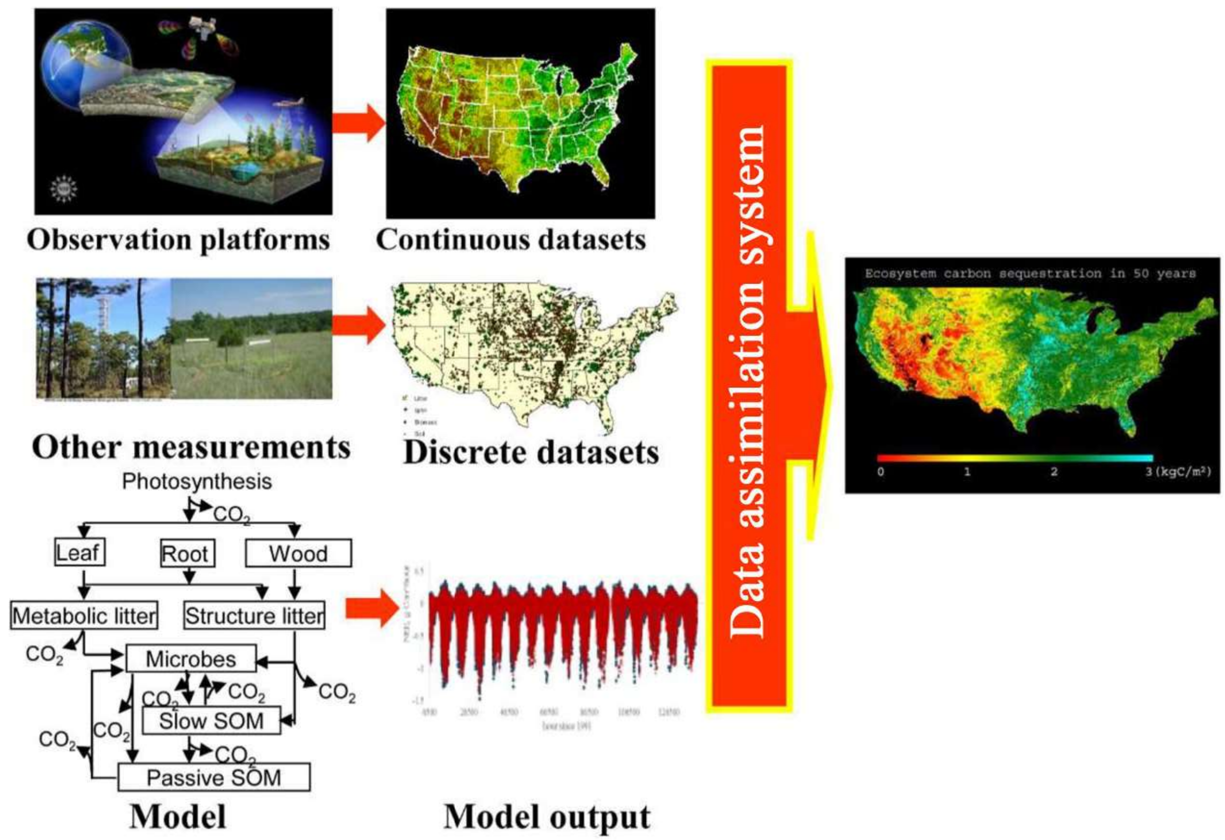

Fig. 10 Operational framework for data-driven ecological predictions. Data from multiple sources are used to train model parameters in order to accurately describe the past and current states of a predicted system and finally predict future states. *From Niu, S., Luo, Y., Dietze, M.C., Keenan, T.F., Shi, Z., Li, J., Chapin III, F.S. 2014. The role of data assimilation in predictive ecology. Ecosphere 5, 1–16.*

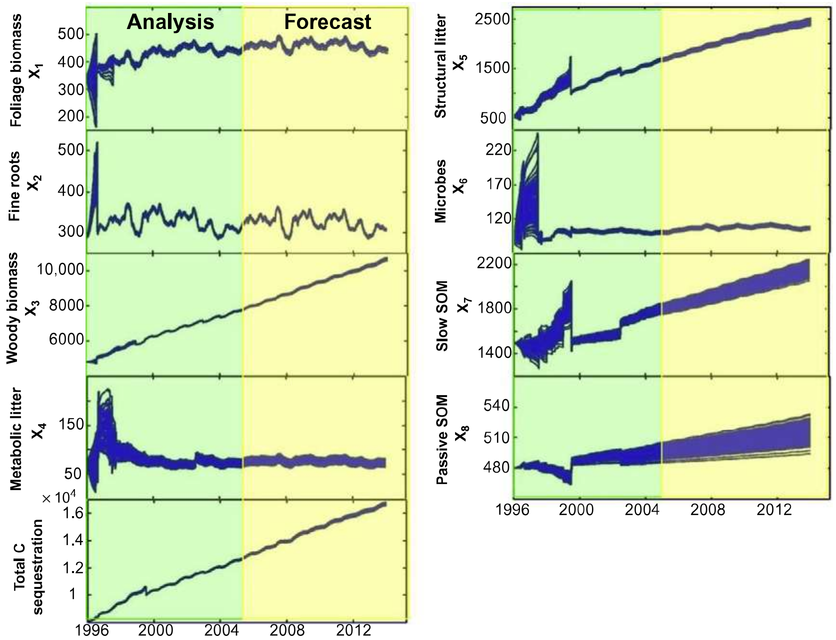

Fig. 11 Data assimilation with an ensemble Kalman filter, showing greater confidence in forecasting long-term dynamics after data assimilation. *Modified from Gao, C., Wang, H., Weng, E.S., Lakshmivarahan, S., Zhang, Y.F., Luo, Y.Q. 2011. Assimilation of multiple data sets with the ensemble Kalman filter to improve forecasts of forest carbon dynamics. Ecol. Appl. 21, 1461–1473.*

treatments. For example, Luo et al. (2003) examined changes in C residence times in various ecosystem components under elevated CO_2. Likewise, Zhou et al. (2010) investigated changes in C residence times in plant, litter, and soil pools in response to experimental warming using a Bayesian probabilistic inversion approach. Shi et al. (2015b) illustrated warming-induced changes in key model parameters using multiple carbon data sets in both control and warmed experimental plots using the Markov Chain Monte Carlo inversion method. Overall, previous research showed that data assimilation was an effective tool to estimate parameter values, assess model uncertainties, and improve model predictions.

Summary

From the synthesis of warming effects on various aspects of grasslands, grassland ecosystems across the world have been profoundly altered by experimental warming. Some processes exhibited consistent responses across sites, such as phenology, microbial biomass, NPP, soil respiration, N mineralization, and SOC, while other processes, for example, plant species composition, microbial diversity, and NEE, showed diverse, even divergent responses to warming among studies. The mechanisms behind the observed responses to warming vary with specific processes. Some changes, for example, decomposition rate, are due purely to increased temperature. Other changes, for example, denitrification, may be caused by warming-induced changes in other factors, often soil moisture and N availability, or by combinations of elevated temperature and other covarying factors. Modeling grassland dynamics in response to climate warming has been active in recent years, and the data sets obtained from observations and manipulative experiments can be assimilated into ecosystem models to improve model performance for more accurate projections of grassland dynamics under possible future climates.

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