



Nonlinear responses of temperature sensitivities of community phenophases to warming and cooling events are mirroring plant functional diversity

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ABSTRACT

Lack of understanding of how plant diversity of different flowering functional groups mediates response patterns of community phenophases to climate change limits our ability to predict future phenology. We used reciprocal transplant experiments across four elevations (i.e., 3200, 3400, 3600 and 3800 m) on the Tibetan Plateau for three years to investigate how temperature change (i.e., warming and cooling) affects the temperature responses of plant functional diversity and community phenophases and their relationships. Our results showed that a nonlinear regression model was the best fitting model for most temperature responses of SDI and community phenophases under warming and cooling. Meanwhile, decreased diversity of early-spring flowering (ESF) and mid-summer flowering (MSF) groups under warming, and increased diversity of ESF under cooling, reduced temperature sensitivities of nearly all community phenophases. These results illustrate that changes in plant diversity should be taken into account when predicting the response pattern of temperature sensitivities of community phenophases.

1. Introduction

Phenology is an important ecological trait that is sensitive to climate change, especially to temperature (Menzel et al., 2011, 2006; Peñuelas et al., 2002; Rafferty and Ives, 2011; Wang et al., 2014a,b). Globally, most studies have found that climate warming significantly advanced the timing of most phenophases, and delayed senescence (Arft et al., 1999; Fu et al., 2015; Ladwig et al., 2016; Wang et al., 2014a,b; Wolkovich et al., 2012; Zhang et al., 2013). Although linear regression models have been identified as the major model that fits phenophase changes with temperature increase (Vitasse et al., 2009; Wolkovich et al., 2012), a growing body of studies have found responses of phenophases to continued warming or cooling spells that do not follow linear relationships (Iler et al., 2013; Jochner et al., 2016; Meng et al., 2016b; Morissette et al., 2009; Pope et al., 2013; Sparks et al., 2000). For example, long-term observations and warming experiments have found that temperature sensitivities of early phenophases decline with

continued warming (Fu et al., 2015; Meng et al., 2016b). However, most reports of nonlinear phenological responses have been based on observations at the species level or observations of single phenological events (Iler et al., 2013; Jochner et al., 2016; Pope et al., 2013). Few studies have focused on responses of community phenophases, especially to cooling (Meng et al., 2016a, 2017).

Currently, nonlinear responses of plant phenophases to warming are attributed to plant adaptation to warming (Fu et al., 2015; Iler et al., 2013; Meng et al., 2016b; Piao et al., 2011; White et al., 1999; Wolkovich et al., 2014). Although temperature is an important factor influencing phenology, it does not entirely account for observed phenological changes, especially those of community phenophases (Forrest et al., 2010; Meng et al., 2017; Wolf et al., 2017). Biotic factors, such as plant evenness or richness, may also alter phenological responses of the plant community (Meng et al., 2017, 2016b; Wolf et al., 2017). Plant diversity (including evenness and richness) can be significantly altered by temperature changes (Tilman and Lehman, 2001; Alexander et al.,

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2015; Morisette et al., 2009; Suttle et al., 2007; Tylianakis et al., 2008; Wang et al., 2012). Thus, the interactive effects of temperature change and plant diversity change may have a much larger impact on plant community phenology than temperature change alone. We previously found that coverage changes of different flowering functional groups have a significant influence on community phenophases (Meng et al., 2017, 2016b). Especially, different species and functional groups can have divergent responses to temperature change, which may lead to a compensation effect that would affect community phenophases (Cleland et al., 2006, 2007; Wang et al., 2014b). Therefore, similar to species-level responses, we also hypothesized that the responses of community phenophases to climate change could be nonlinear, because species adapting to warming and cooling in different directions and magnitudes could cause a compensation effect on community phenophases.

To better understand the mechanisms involved in the effects of plant biodiversity change on temperature sensitivities of community phenophases under warming and cooling, we used reciprocal transplant experiments across four elevation gradients

(i.e., 3200, 3400, 3600 and 3800 m) and investigated: (1) whether the temperature responses of both plant community diversity and community phenophases have nonlinear responses to warming and/or cooling; and (2) the relationship between changes in plant diversity of different flowering functional groups and community phenophases under climatic change on the Tibetan plateau.

2. Materials and methods

2.1. Study sites and data collection

We used three continuous years of records of phenophases from alpine meadows at four elevation gradients (i.e., 3200, 3400, 3600 and 3800 m) at Haibei Alpine Meadow Ecosystem Research Station (HBAMERS), Qinghai province, China (37°37' N, 101°12' E) (Meng et al., 2017; Wang et al., 2014a,b). The alpine site is characterized by a short growing season, with green-up and senescence typically occurring in May and October, respectively. Twelve soil quadrats with 1 m × 1 m × 0.3–0.4 m depth (i.e., 0.3 m depth only at the 3800 m site due to the shallow soil layer) were dug each elevation (i.e., 48 quadrats for the four elevations in total) in early May 2007, and nine of them were randomly transferred to the other three elevations (i.e., three replicates at each elevation) (Meng et al., 2017; Wang et al., 2014a). To insulate from the effects of nutrient exchange and root invasion from the surrounding environment, all the soil quadrats were sealed by impervious materials.

The observational quadrat (1 m × 1 m) was segmented into 100 grid cells. Species richness and evenness were monitored at each point in mid-August of every year using the quadrat method. All species were divided into three categories based on their flowering time (i.e., early-spring (ESF, blooming before June), mid-summer (MSF, blooming between June and July) and late-autumn flowering (LAF, blooming after July) functional groups as detailed in Meng et al. (2016a, 2017). The frequency of sampling from 2008 to 2010 to examine community phenological sequences was 3–4 days, monitoring each species phenology occurring on the 100 points. The phenological sequences were divided into 7 phenophases, including onset of leaf-out (OLO, emergence of visible leaf), first flower bud (FB, emergence of unopened blossom bud), first flowering (FF, emergence of bloom), first fruiting-set (FFS, emergence of fruit), post-fruiting vegetation (OPFV, date of end fruiting), first leaf-coloring (FLC, emergence of leaf coloring) and complete leaf-coloring (CLC, complete leaf coloring). The timing of each phenophase was the date on which 15% of the observed species experienced the phenological event. CLC was the date on which 95% of observed species had completed senescence (Meng et al., 2017, 2016b).

Soil temperature and soil moisture were continuously monitored from 2008 to 2010 (soil temperature in Fig S1, Wang et al., 2014b).

Mean annual soil temperatures at 5 cm depth were 3.9, 2.5, 2.0, 0.4 °C and mean annual soil moistures at 20 cm depth were 26%, 21%, 30% and 8% across the four increasing elevations, respectively (Wang et al., 2014a,b). Temperature change is the difference between original site and transferred site for transplanted plants at each year.

2.2. Computation of temperature sensitivities of Simpson's Diversity Index (SDI), community phenophases and accumulated soil temperature (AST)

Different species and functional groups have divergent response magnitudes and directions, their mutual compensation effect could shape community phenophases. Therefore, changes in species richness and evenness (i.e., plant diversity) of functional groups could reshape community phenophases due to their divergent phylogeny. SDI was used to quantify the plant diversity of the community, which consists of species richness and evenness (1). The AST of community phenophases was the sum soil temperature remaining above 0 °C (2). Downward and upward transfer represented warming and cooling, respectively. Positive and negative values represent an increase and decrease in SDI per 1 °C change or delay and advance of phenophases in days per 1 °C change under the transferred treatments, respectively.

$$SDI = 1 - \sum_{i=1}^s \left(\frac{n}{N} \right)^2 \quad (1)$$

$$AST = \sum_{t=0}^{ph} (T_t - 0) \text{ if } T_t > 0 \quad (2)$$

$$TS = \frac{DCP}{Td} \quad (3)$$

where s is species richness in a certain flowering functional group, n is the total individual number of a particular species in a certain flowering functional group, and N is the total individual number of a certain flowering functional group. The value of SDI ranged between 0 and 1. $t = 0$ is the first date on which the 5 cm depth soil temperature remained above 0 °C for five continuous days; ph is the date of a particular community phenophase; T_t was 5 cm depth soil temperature remained above 0 °C during the date of $t = 0$ and ph ; TS is the temperature sensitivity of SDI, AST and community phenophases; DCP is the differences of SDI, AST and community phenophases, and Td is the temperature difference.

2.3. Data analysis

We used a general linear model to test the effects of treatments and their interactions on the temperature responses of SDI of different flowering functional groups and of community phenophases in SPSS version 23. We adopted Type III SS.

We used linear and nonlinear regressions to fit the responses of temperature sensitivity of SDI, of community phenophases and of AST to temperature changes. The linear model was fitted by the function $lm()$. The nonlinear model was analysed by the package `Segmented` in R. We used Akaike's Information Criterion (AIC) to compare the fitness of two different models (Migliavacca et al., 2012; Richardson et al., 2013; Turkheimer et al., 2003). The smaller the AIC, the better the fit. Meanwhile, the P value (< 0.05) was used to examine the significance of each linear regression. These functions and packages were performed in R 3.3.3 (R.C. Team, 2017). We calculated partial correlations between temperature responses of SDI and temperature sensitivities of community phenophases, setting temperature changes as the controlling variable, to explore the effects of SDI on community phenophases. Because the community phenophases were calculated based on all monitored species in 100 points. Therefore, changes in plant diversity (including species richness and evenness) could affect community phenophases. There was incomplete data at 3600 m due to partial destruction of the experimental site in 2009 and complete destruction in

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