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ORIGINAL PAPER

Frost controls spring phenology of juvenile Smith fir along elevational gradients on the southeastern Tibetan Plateau

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Abstract

Impacts of climatic means on spring phenology are well documented, whereas the role of climatic variance, such as occurrence of spring frosts, has long been neglected. A large elevational gradient of forests on the southeastern Tibetan Plateau provides an ideal platform to explore correlates of spring phenology and environmental factors. We tested the hypothesis that spring frost was a major factor regulating the timing of bud-leaf phenology by combining 5 years of in situ phenological observations of *Abies georgei* var. *smithii* with concurrent air temperature data along two altitudinal gradients. Mean lapse rate for the onset of bud swelling and leaf unfolding was 3.1 ± 0.5 days/100 m and 3.0 ± 0.6 days/100 m, respectively. Random forest analysis and conditional inference trees revealed that the frequency of freezing events was a critical factor in determining the timing of bud swelling, independent of topographic differences, varying accumulation of chilling days, and degree-days. In contrast, the onset of leaf unfolding was primarily controlled by the bud swelling onset. Thus, the timing of bud swelling and leaf unfolding appear to be controlled directly and indirectly, respectively, by spring frost. Using space-for-time substitution, the frequency of spring freezing events decreased by 7.1 days with 1 °C of warming. This study provides evidence for impacts of late spring frosts on spring phenology, which have been underappreciated in research on phenological sensitivity to climate but should be included in phenology models. Fewer spring freezing events with warming have important implications for the upward migration of alpine forests and treelines.

Keywords Spring phenology · Bud swelling · Leaf unfolding · Conifer · Spring frost · *Abies georgei* var. *smithii* · Altitudinal gradient

Introduction

Phenology largely determines plant survival, growth, and distribution and plays an important role in ecosystem functioning and in the provision of ecosystem services (Chuine and Beaubien 2001; Inouye 2008; Forrest and Miller-Rushing 2010). However, the drivers of phenology remain partially identified and quantified (Richardson et al. 2013; Piao et al. 2015; Shen et al. 2016). Researchers attempting to generate time series long enough to make inferences about climate-

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driven changes in phenology often accumulate just one datum per year (Miller-Rushing et al. 2010). Most tree phenology data also are limited to first flowering and leaf unfolding and rarely consider variation in other aspects of tree phenology (e.g., bud swelling) that may respond to climate differently from flowering or leaf unfolding (Miller-Rushing and Primack 2008; Antonucci et al. 2015).

For many species in temperate and cold ecosystems, temperature is the key factor controlling the onset of spring phenology (Davis et al. 2015; Fu et al. 2015; Ge et al. 2015; Shen et al. 2016; Li et al. 2017), although other climatic factors (e.g., precipitation, radiation, and photoperiod) also can play a role (Davis et al. 2015; Zohner et al. 2016; Ren et al. 2018). Climatic variability also is important for understanding the climatic limits of tree species (Zimmermann et al. 2009; Jochner et al. 2013; Körner et al. 2016), but few studies have explicitly linked spring phenophases to climatic variability, such as spring frost (Ernakovich et al. 2014; Körner et al. 2016). In spring, plants experience a de-hardening period, during which a certain amount of heat is required to initialize leaf unfolding (Vitasse et al. 2014; Delpierre et al. 2016). During this period, plants are particularly vulnerable to frosts (Lenz et al. 2013; Vitasse et al. 2014; Vitra et al. 2017). One recent study showed that spring frost affected the timing of bud break which, in turn, determined the elevational and latitudinal limits of deciduous broad-leaf tree species in the Alps (Körner et al. 2016). However, less is known about the impacts of frost on spring phenology for conifers, which are the dominant species of many subalpine communities.

The southeastern Tibetan Plateau hosts mature, natural forests across a broad elevational gradient (Liang et al. 2011a) and provides an ideal platform for obtaining longer-term time series data useful for exploring key drivers of tree phenology. Satellite-based observations and process-based tree-ring growth models have confirmed that advancement of deciduous or semi-deciduous vegetation green-up dates on the Tibetan Plateau over the past three decades is tied closely to spring warming (Piao et al. 2011; Zhang et al. 2013; Yang et al. 2017). However, the impact of spring frosts on tree phenology is less known, although spring frosts before growing season onset occur frequently on the Tibetan Plateau (Shen et al. 2014).

We used a 5-year dataset of precise, bud-scale measurements of spring phenophase timings to explore climatic drivers of spring phenology for Smith fir (*Abies georgei* var. *smithii*) along two altitudinal gradients. Specifically, we (1) revealed the temporal patterns of spring phenophases along two altitudinal gradients and (2) assessed the effects of freezing events and growing degree-days on spring phenophases. We observed that spring frost occurred frequently before the onset of bud swelling on the southeastern Tibetan Plateau, and we hypothesized that spring frost would be closely associated with the timing of bud swelling. We also observed that the time intervals between the onset of bud swelling and leaf unfolding remained relatively stable, and so we hypothesized that the timing of leaf unfolding was closely linked to the timing of bud swelling.

Material and methods

Study region and climate The study region is situated in the Sygera Mountains (29° 10′–30° 15′ N, 93° 12′–95° 35′ E) on the southeastern Tibetan Plateau. The south Asian monsoon approaches the Sygera Mountains through the valley of Yarlung Zangbo River, resulting in plentiful summer rainfall (Liang et al. 2010). Records from the Nyingchi weather station (29° 34′ N, 94° 28′ E, 3000 m a.s.l.) showed that the mean annual precipitation from 1960 to 2013 was 672 mm, 72% of which occurred from June to September (Liang et al. 2010). July (mean temperature of 15.9 °C) and January (0.6 °C) were the warmest and coldest months, respectively.

Based on an automatic weather station (4390 m a.s.l.) located near the treeline on the eastern-facing slopes and installed in November 2006, the annual average precipitation at our study sites from 2007 to 2013 was 957 mm, 62% of which fell during the monsoon season (June to September). The warmest and coldest months were July (7.9 ± 0.5 °C) and February (− 8.0 ± 1.7 °C), respectively. Snowfall usually occurred from November to mid-May, resulting in a snow cover of about 50–100 cm (see also Liang et al. 2016).

Study species and study sites Smith fir (*A. georgei* var. *smithii*) is an evergreen coniferous tree species distributed on the north- or southeast-facing slopes on the southeastern Tibetan Plateau (Liang et al. 2011a). It grows along an altitudinal gradient ranging from 3550 to 4400 m a.s.l., with growth primarily constrained by low temperatures (Liang et al. 2010; Li et al. 2013, 2017). We studied Smith fir at eight sites along two altitudinal transects: four sites on a southeast-facing slope (labeled as SE3800, SE4000, SE4200, and SE4360, with the number indicating meters above sea level) and four sites on a north-facing slope (N3800, N4000, N4200, N4380) (Appendix S1) (see the Supplemental Data with this article). At each site, 10 trees were selected for measurements, except for site SE4200 where only 6 trees were measured. We used a measuring tape to determine the height of each sampled tree in April 2012, when leaf-buds were dormant. On the southeast-facing slope, trees ranged from 0.47 to 1.57 m in height and were estimated to be 13–40 years old (Appendix S2). The trees on the north-facing slope were 0.39–1.83 m in height and 10–44 years old (Appendix S2).

Phenology measurements We made phenological observations on trees weekly between May and September during five consecutive years (2012–2016). From the observations of terminal buds, we recorded the dates of bud swelling and leaf unfolding. The onsets of bud swelling and leaf unfolding were each determined as the dates when trees showed swollen buds or unfolded needles in shoot apices. The swelling phase corresponded with a swollen appearance of the bud and a change in color from dark red to light red. For all monitored trees, high-resolution photographs were taken at each phenological measurement visit with a steel ruler (accuracy of 1 mm) placed behind the shoot apex. In the "Results," we report "dates" as days elapsed since May 1 each year.

Temperature data Air temperature (± 0.2 °C) in each stand was measured hourly with a temperature logger (TidbiT v2 Temp UTBI-001, Onset Computer Corporation, Bourne, MA, USA) that was placed 2 m above the ground under the canopy of a tall mature tree. Loggers were not placed under studied trees, which had small main stems. An epoxy radiation shield designed by the logger manufacturer covered each sensor to minimize the effects of direct sunlight on the measurements.

The frequency of spring freezing events was calculated as the number of days with daily minimum temperature < 0 °C recorded from the beginning of March (Shen et al. 2014) through the last freezing date (the last spring day with daily minimum temperature < 0 °C (Schwartz et al. 2006). Safety margins were defined as the number of days between the last freezing date and the onset of bud swelling (Lenz et al. 2013). Freezing frequency between June and leaf unfolding onset was also calculated to test if rare freezing events in June may have driven the timing of leaf unfolding. Chilling requirement is considered to be an important factor that determines the onset of spring phenophases (Coville 1920). We first estimated the number of chilling days as the sum of daily temperature between 0 and 5 °C from March to bud swelling onset (Fu et al. 2015). Accumulated daily mean temperature above a certain threshold, i.e., growing degree-days, also is thought to be an important factor driving the onset of leaf phenology (Fu et al. 2014b). As compared to warmer areas, vegetation in colder environments such as the Tibetan Plateau requires lower threshold temperatures to green up (Piao et al. 2011). Previous studies in the same region revealed a mean lapse rate of daily air temperature of − 0.66 °C/100 m (Liang et al. 2011b), which suggested a similar trend for the temperature thresholds (e.g., 0, 2, and 5 °C) on spring phenophase onset. Thus, a minimum temperature of 0 °C was used as the basis from which to accumulate degree-days, starting with the date when the mean daily air temperature was > 0 °C for at least five consecutive days from March and continuing until the onset of bud swelling and leaf unfolding.

Data analysis We used regression tree modeling to investigate the influence of the many explanatory factors hypothesized to be important in controlling the timing of bud swelling and leaf unfolding (Table 1). For the onset of bud swelling ($n = 364$), we investigated the effects of both warmth-related variables (accumulated growing degree-days, minimum and maximum temperatures, mean temperature in spring) and a frost-related variable (frequency of spring freezing events). We evaluated the impacts of three variables (elevation, aspect, and year) on the safety margins. For leaf unfolding ($n = 364$), we sought to understand how different temperature variables (freezing frequency between June and leaf unfolding onset, accumulated growing degree-days, minimum and maximum temperatures) and bud swelling onset controlled the onset of this phenophase. In all models, aspect was included to control for the effects of non-thermal factor related to sampling design (Table 1). As elevation is a proxy for, and was significantly correlated with, several temperature variables in this study, it was not included in the modeling.

We used a two-stage modeling approach. First, we used random forest analysis (Breiman 2001) to estimate and rank the importance of each explanatory factor in describing variability in the response variables. Random forest analysis handles both regression and classification, while providing additional features such as measure of variable importance and partial correlation analysis (Breiman 2001). Second, we used conditional inference trees to gain further insights into the nature of relationships between each response variable and the most important explanatory factors. These two non-parametric, machine-learning methods of analysis allow for the construction of complex, non-linear models with inter-correlated predictor variables (Cutler et al. 2007). The random forest approach averages the outcomes of 9999 bootstrapped regression trees ("forests") to identify those measured explanatory variables that are the best predictor variables. We used the random forest "variable importance" measure to identify the most influential factors in explaining variation in the response variable and then used partial dependence plots to show the marginal effect of each of these factors (i.e., while holding all of the other explanatory factors at their average values) on the response variable (Cutler et al. 2007). The relative importance of the top-ranked predictor variables was investigated further using conditional inference trees (Hothorn et al. 2006) derived from a recursive partitioning method that generates a set of decision rules describing how variation in the response data is best attributed to each predictor. The conditional inference tree method requires a statistically significant difference ($P < 0.05$), as determined by Monte Carlo simulation, to create a partition in the data; this algorithm minimizes bias and prevents over-fitting and the need for tree pruning (Hothorn et al. 2006). Random forest and conditional inference tree analyses were implemented in R version 3.1.0 using the "randomForest" (Liaw and Wiener 2002) and "party" (Hothorn et al. 2006) packages, respectively.

Table 1 Description of predictor variables used in the regression tree modeling of spring phenology (date of onset of bud swelling and leaf unfolding)

Variable name	Description	In modeling	
		BS	LF
Degree_days	Cumulative temperatures (above 0 °C) from March up to phenophase onset	Yes	Yes
Min_tem	Minimum daily temperature recorded at the time of phenophase onset	Yes	Yes
Max_tem	Maximum daily temperature recorded at the time of phenophase onset	Yes	Yes
FFE	Number of days/year with daily minimum temperature < 0 °C from March to May	Yes	No
Spring_MT	Mean temperature from April to May	Yes	No
Aspect	The aspect of a given sample plot	Yes	Yes
Chilling_days	Cumulative temperatures (0–5 °C) from March to phenophase onset	Yes	No
Freeze_LF	Number of days/year with daily minimum temperature < 0 °C from June to leaf unfolding onset	No	Yes

All climate-related variables were computed for each site and measurement year based on temperature logger data. BS and LF represented bud swelling and leaf unfolding, respectively

Results

Among-site variation in phenology Bud swelling began in early May and ended in late May, and occurred on later dates at higher elevations (Fig. 1). On average, the mean lapse rate for the onset of bud swelling was 3.1 ± 0.5 days/100 m in elevation gain; the difference in the timing of bud swelling between the lowest and highest sites was 18 ± 3 days. Leaf unfolding began in late June and ended in mid-July, with a mean lapse rate of 3.0 ± 0.6 days/100 m, leading to a difference of 17 ± 3 days between the lowest and highest sites. Although the lapse rate and duration of each phenophase did not differ among trees on the north- and southeast-facing sites, the mean dates of bud swelling and leaf unfolding were 2 ± 1 days later for trees growing on the north-facing sites relative to the trees growing on the southeast-facing sites.

Spring frost in relation to warming Frequency of spring freezing events increased from 50.9 ± 7.9 to 77.2 ± 5.6 days from the lowest to highest sites. According to a lapse rate of mean air temperature of − 0.66 °C /100 m, the difference in mean air temperature between the lowest and highest sites was 3.7 °C. Based on the method of space-for-time substitution, frequency of spring freezing events decreased by 7.1 days with 1 °C of climate warming.

Explanatory modeling of phenophase timings Overall, the random forest models explained 84.8% of the variation in the onset of bud swelling and 93.1% of the variation in the onset of leaf unfolding. The frequency of spring freezing events was the most important predictor of bud swelling date (Fig. 2a). Spring mean temperature, chilling days, growing degree-days, maximum temperature, minimum temperature, and aspect had gradually lower influence (Fig. 2a). Mean safety margins were ≥ 7 ± 5 days, and increased significantly with increasing elevation ($r = 0.24$, $P < 0.0001$, $n = 364$) and among years ($r = 0.27$, $P < 0.0001$, $n = 364$) but not with aspect ($r = 0.04$, $P = 0.36$, $n = 364$). For leaf unfolding, the onset of bud swelling was the most important predictor; the sum of growing degree-days, and minimum and maximum temperature ranked considerably lower but were basically equivalent, in importance, followed by freezing frequency in June and aspect (Fig. 2b). Partial dependence plots indicated that the three response variables often were related non-linearly to the predictor variables (Fig. 3), which in turn interacted in complex ways (Fig. 4b). Bud swelling was positively and essentially linearly related to the frequency of spring freezing events, negatively related to the chilling days, sum of growing degree-days, minimum temperature (Fig. 3a), and non-linearly related to the other variables (Fig. 3a). Conditional inference tree modeling suggested that whether bud swelling occurred at later or earlier dates was largely controlled by the frequency of spring freezing events, with locations experiencing more than 62 freezing days in spring having the latest bud swelling dates (Fig. 4a).

The timing of leaf unfolding onset was positively and linearly related to the onset of bud swelling. It had a negative, *s*-shaped relationship with growing degree-days with a switch from later to earlier timing of leaf unfolding past a critical value for the sum of growing degree-days that fell within the range of 530–540 accumulated degree Celsius (Fig. 4b). A similar critical minimum temperature threshold of 7–7.5 °C was also evident (Fig. 3b). The relationship between leaf unfolding date and maximum temperature was more complex (Fig. 3b) and likely resulted from interactions among the sum of growing degree-days and maximum and minimum temperature (Fig. 4b). Rare freezing events in June also had complex impacts on leaf unfolding date (Fig. 3b).

Discussion

Many climatic variables can influence the onset and duration of plant phenophases, but research to date has

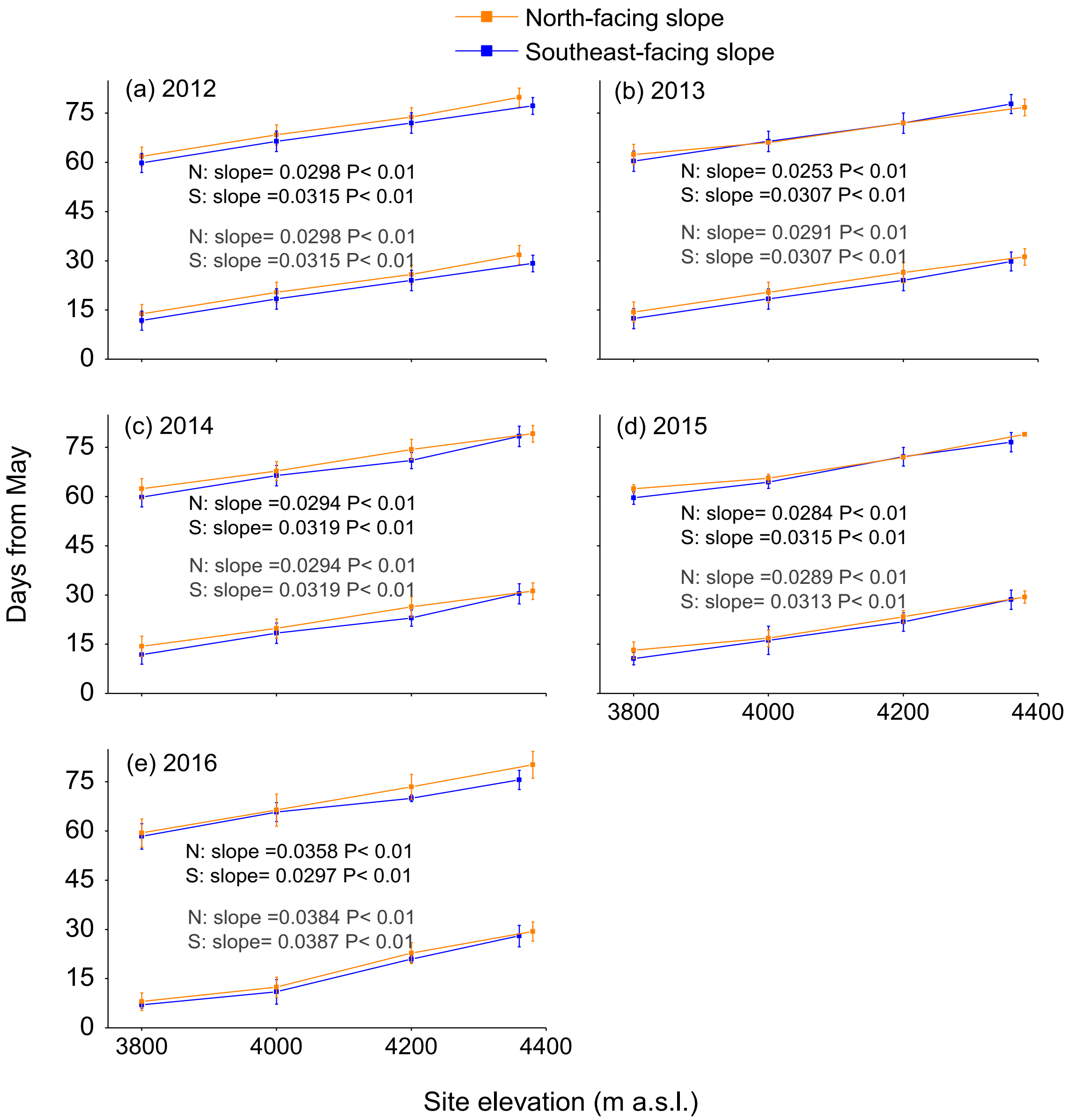

Fig. 1 Variations (means ± SD) in the onset of bud swelling (located in lower parts) and leaf unfolding (upper parts) with altitude and aspect during five study years. Slopes and *p* values of linear regressions for onset of bud swelling and leaf unfolding were represented by grey and black, respectively

tended to focus on temperature means rather than variance or extremes (Inouye 2008; Wang et al. 2014) and on later phenophases such as flowering and leaf emergence. Our findings, based on a large phenological dataset from the Tibetan Plateau, illustrate that the timing of temperature variance such as late spring frost affects the timings of bud development in spring. The onset of bud swelling is of particular importance, because it is a prerequisite to the other important and well-studied phenophases. We took advantage of 5 years of data across a steep elevational gradient to provide additional information on climatic control of bud swelling and leaf unfolding for Smith fir.

Main driver of bud swelling onset The date of onset of bud delayed with increasing elevation in all 5 years of this study. This result can be attributed directly to the effects of temperature, as tree growth of Smith fir at high elevations is known to be limited by temperature (Liang et al. 2010; Wang et al. 2012). However, at high elevations, trees are frequently exposed to large diurnal temperature fluctuations in spring (Ernakovich et al. 2014), and meristematic tissues are especially vulnerable to damage from spring frost (Gu et al. 2008). Once development starts in spring, frost resistance is irreversibly lost and trees are only partially able to re-acclimate to low temperatures (Lenz et al. 2013; Vitra et al. 2017). In particular,

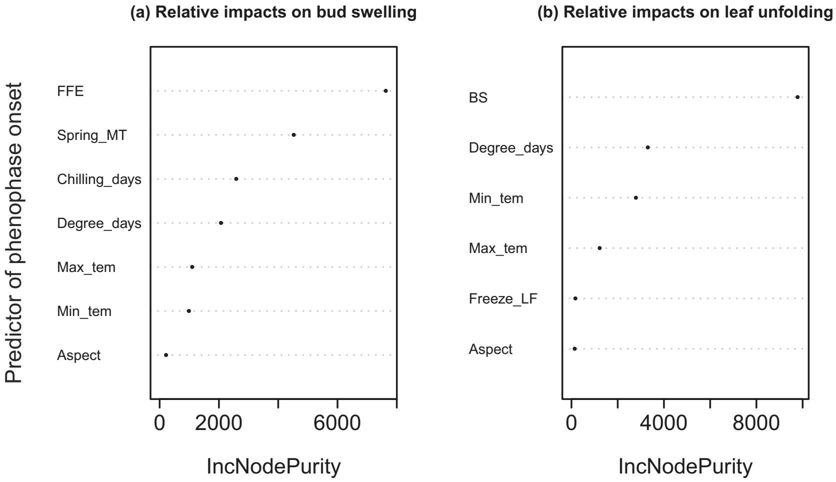

Fig. 2 Ranked, relative importance of variables included in random forest models explaining variation in the onset dates of **a** bud swelling and **b** leaf unfolding. The meaning of each abbreviation used (FFE …) is shown in Table 1. IncNodePurity represents the total decrease in node impurities from splitting on the variable, averaged over all trees. For classification, the node impurity is measured by the Gini index. For regression, it is measured by residual sum of squares

the frost resistance of trees decreases quickly as temperature increases during the de-hardening period (Lenz et al. 2013; Vitra et al. 2017). In some cases, abnormally warm weather followed by sudden cold waves (particularly freezing events) in early- to mid-spring can have disastrous impacts on plants (Gu et al. 2008). Thus, adaptations for avoidance of spring frost damage are critical for the survival and subsequent development of many tree species in temperate and cold regions (Kollas et al. 2014; Lenz et al. 2016).

In our study, the frequency of freezing events was the critical factor in regulating the timing of bud swelling. Safety margins for spring frost increased significantly with elevation, suggesting strong directional selection for avoiding the long-term probability of frost damage. The negative effects of spring frost on the survival of Smith fir seedlings (tree age ≤ 5 years) also have been reported on the southeastern Tibetan Plateau (Shen et al. 2014). It is likely that Smith fir escapes from the spring frost injury at the upper treelines by delaying bud swelling until very late spring (Wang et al. 2014). Further, both chilling days and growing degree-days had significant impacts on the onset of bud swelling. Presumably, frost is a major evolutionary constraint that has led to adjustments of the physiological requirements to chilling and forcing in a way that it matches the long-term minimum recurrence rate of frost damage risk (Körner et al. 2016). There is ample evidence that the safeguards against plants tracking warming spells at the wrong time must depend on evolutionary deeper rooted signals such as sufficient chilling, thermal forcing, or even photoperiod (Körner and Basler 2010; Lenz et al. 2016). Our results, in combination with those from the aforementioned studies, together support our hypothesis that frost avoidance occurs in early phenophases of Smith fir.

Our results also are in line with the phenological studies of deciduous broad-leaf trees in the eastern and western Alps (Lenz et al. 2013; Kollas et al. 2014) and on Japan's Mount Fuji (Gansert 2002), but different from what has been observed in warmer temperate forests where accumulation of growing degree-days is related more closely to phenological events (Peñuelas and Filella 2001; Parmesan and Yohe 2003; Wang et al. 2011; Dai et al. 2014). Although the accumulation of chilling temperatures has been shown to regulate the responses of spring phenology to climatic warming in Europe (Fu et al. 2015), a chilling requirement played only a secondary role in the timing of bud swelling in our study region. In addition, increased spring temperature variance and reduced chilling resulted in the general decline in the strength of phenological sensitivity to warming across Europe (Wang et al. 2014).

Control of the onset of leaf unfolding The onset of leaf unfolding from the lowest to highest sites occurred from late June to mid-July and was driven more by the onset of bud swelling than directly by climatic factors. This result suggests that earlier bud swelling translated into earlier leaf unfolding. Leafing is a linear chain of events producing effects on the contiguous phases where the timings of occurrence of each phase influence those of the successive one (Rossi and Bousquet, 2014). The processes of growth reactivation in trees form an integrated network of phenophases (Rossi et al. 2012; Fu et al. 2014a; Signarbieux et al. 2017). Unexpectedly, the sum of growing degree-days played only a secondary role in controlling the onset of leaf unfolding. These results differ from those of other studies conducted in temperate, boreal, and some low-elevation forests where accumulation of degree-days has been found to be the major determinant of the onset of leaf unfolding (Peñuelas and Filella 2001; Parmesan and Yohe 2003; Wang et al. 2011; Dai et al. 2014). On the Tibetan Plateau, however, the carryover effect presented in this study suggested that the timing of leaf unfolding was only influenced by spring frost indirectly, through the propagation of the effects from bud swelling towards the other phases of bud development. In addition, freezing events (< -1.36 °C) appeared in early June of 2016 at elevations of 4200 and 4400 m, whereas such rare freezing events were absent in other 90% cases. However, rare,

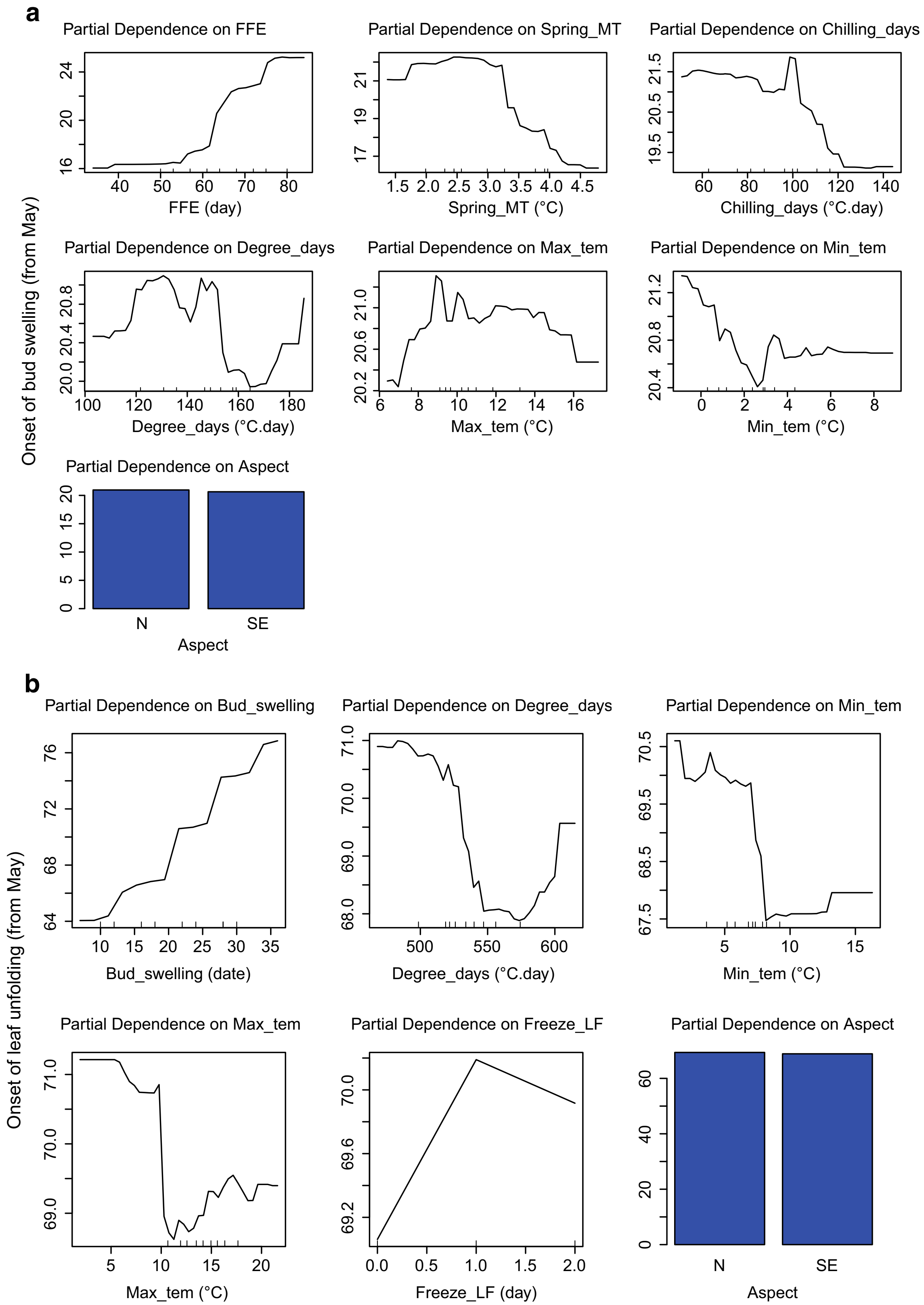

Fig. 3 Partial dependence plots, based on results from the random forest analysis, showing the mean marginal influence of predictor variables on the onset date of **a** bud swelling and **b** leaf unfolding. Each plot represents the effect of one predictor variable on the response, while holding the other predictor variables constant at their mean values

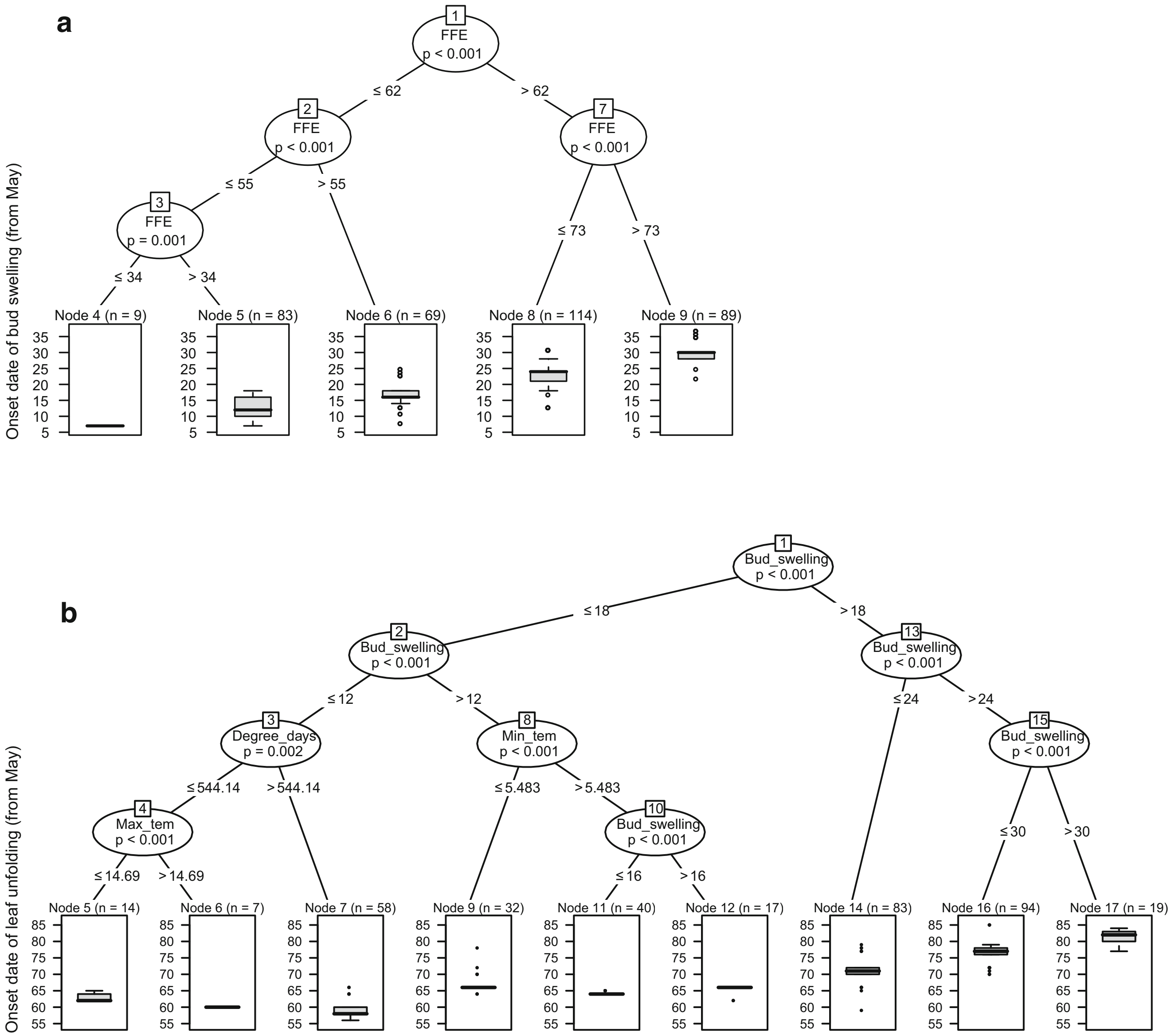

Fig. 4 Conditional inference trees explaining variation in the onset date of **a** bud swelling and **b** leaf unfolding (expressed as days since May 1) based on the sets of explanatory variables (see Table 1). The trees show pathways of how the response data were partitioned based on the explanatory variables, and the threshold values of these variables at which significant partitions were made in the response data. The observations associated with each terminal node are the results of these partitionings. For example, terminal node 3 in tree (**a**) comprise 62 observations with some of the earliest bud swelling onset dates, best-explained by conditions where there were less than 62 freezing events (FFE) per year. All other branches of the trees can be interpreted in a similar manner. *P* values at each node are from a Monte Carlo randomization test; for a split to occur, *P* must be less than 0.01

stochastic freezing events before onset of leaf unfolding could occur frequently over a much longer period (Kollas et al. 2014; Lenz et al. 2016). Thus, we cannot exclude the possibility that leaf-out always occurs right after the risk of frost exposure is completely gone.

Spring phenophases and frosts Based on 5 years of observational data in the field, we provide evidence that the onset of spring phenology of coniferous trees on the southeastern Tibetan Plateau is primarily related to spring frost frequency. Most phenological studies of trees focused on leaf unfolding phase that is just the final step of a long and complex process of bud reactivation (Antonucci et al. 2015). The process of leaf unfolding starts with bud swelling, and the successive phases are connected with the previous ones (Rossi and Bousquet 2014). The long-term probability of frost could adjust the sensitivity of buds to different environment cues (e.g., chilling, forcing) to ensure that their sensitive tissues rarely encounter frost. Further exploration is needed to clarify how different environmental cues interact to cue physiological processes that minimize long-term recurrence rates of frost damage risk.

Implications for treeline dynamics

Our data also indicated that the frequency of spring freezing events tended to decrease with climate warming on the southeastern Tibetan Plateau. An increase of mean temperature and lower risk of spring frosts are favorable for phenological development of trees (Dai et al. 2013, 2014), and may contribute to an increased tree growth, recruitment, and establishment. Indeed, NDVI-based studies found that spring phenology across the Tibetan Plateau had advanced continuously over the past three decades (Piao et al. 2011; Zhang et al. 2013; Shen et al. 2015, 2016). In parallel, ground observation data across different regions of China, including the Tibetan Plateau, revealed earlier spring and summer phenophases for 632 tree and 85 shrub species during the past 50 years (Ge et al. 2015). There also is evidence that tree growth and recruitment at treelines on the southeastern Tibetan Plateau have increased significantly during the past century (Liu et al. 2016; Wang et al. 2016). Additional climatic warming would be expected to induce a significant upward advance of alpine forests and treelines if non-climatic factors such as competition do not limit it (Liang et al. 2016; Fadrique et al. 2018; Liu et al. 2018).

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Authors' contributions E.L. designed the research; all authors analyzed data and wrote the paper.

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