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Warmer winters reduce the advance of tree spring phenology induced by warmer springs in the Alps

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A R T I C L E I N F O

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A B S T R A C T

Mountain regions are particularly susceptible and influenced by the effects of climate change. In the Alps, temperature increased two times faster than in the Northern Hemisphere during the 20th century. As an immediate response in certain tree species, spring phenological phases, such as budburst and flowering, have tended to occur earlier. However, recent studies have shown a slowing down of phenological shifts during the last two decades compared to earlier periods, which might be caused by warmer winters. Indeed, cold temperatures are required to break bud dormancy that occurs in early fall; and dormancy break is a prerequisite for cell elongation to take place in spring when temperature conditions are warm enough.

Here we aimed at evaluating the effects of winter warming *vs.* spring warming on the phenological shift along mountain elevation gradients. We tested the hypothesis that a lack of chilling temperature during winter delayed dormancy release and subsequently spring phenological phases. For this, we used eight years of temperature and phenological records for five tree species (*Betula pendula, Fraxinus excelsior, Corylus avellana, Picea abies and Larix decidua*) gathered with the citizen science program Phenoclim (www.phenoclim.org) deployed over the French Alps.

Our results showed that for similar preseason (*i.e.* after dormancy break) temperatures, warmer winters significantly delayed budburst and flowering along the elevation gradient (+0.9 to +5.6 days $°C^{-1}$) except for flowering of *Corylus* and budburst of *Picea*. For similar cold winter temperatures, warmer preseasons significantly advanced budburst and flowering along the elevation gradient (−5.3 to −8.4 days $°C^{-1}$). On average, the effect of winter warming was 2.3 times lower than the effect of spring warming. We also showed that warmer winter temperature conditions have a significantly larger effect at lower elevations.

As a consequence, the observed delaying effect of winter warming might be beneficial to trees by reducing the risk of exposure to late spring frost on a short term. This could further lead to partial dormancy break at lower elevations before the end of the 21st century, which, in turn, may alter bud development and flowering and so tree fitness.

1. Introduction

Mountain regions and their unique biota are and will be particularly exposed to climate change and temperature increase (Rangwala & Miller 2012; Nogués-Bravo et al. 2007). In some regions of the Alps, temperature has already increased twice as fast than in the northern hemisphere during the 20th century (Rebetez and Reinhard, 2008). Moreover, recent evidence indicates that the current warming rate increases with increasing elevation (Mountain Research Initiative EDW Working Group, 2015). As a consequence, mountain summits might

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warm faster than lower elevation sites, suggesting that mountain ecosystems might react non-linearly to climate change along elevation gradients.

Forests cover nearly half of the land surface in Europe (Fao, 2011) and in the Alps and provide important ecosystem services in mountain regions such as protection against soil erosion and avalanches, and for wood production (Schröter et al., 2005). Because the long life-span of trees does not allow for rapid selection to environmental changes, forests are particularly vulnerable to climate change. Tree species responses to climate warming take place at different time scales: from the scale of years by acclimation through phenotypic plasticity (Chevin et al. 2013; Duputié et al., 2015), to the scale of decades and centuries through migration (Davis and Shaw, 2001) and micro-evolution (Franks et al., 2014; Lefèvre et al. 2013; Alberto et al. 2013). A consistent upward presence shift of about 70 m has been observed for tree species in the western and central part of the Alps, which is partly due to the ongoing climate change (Lenoir et al. 2008; Bodin et al., 2013). However, it remains unclear whether natural migration *via* seed dispersal will be sufficient to reach the isotherm shift due to climate warming in the future and whether biotic interactions will allow it.

Many studies have shown that spring phenological events are well correlated with temperature of the previous weeks/months (Claudio Defila & Clot 2005; Walther et al. 2002) and studies based on observational and experimental elevation transects have shown that environmental effects overwhelm genetic effects (Vitasse et al. 2010, 2013), at least in a short term. As a consequence, phenological plasticity is an important way for trees to respond quickly to increasing temperature, enabling them to track ongoing climate change (Duputié et al., 2015). More generally, phenology has been shown to control species range limits at a global scale (Chuine & Beaubien 2001; Chuine, 2010) and along elevational gradients in mountain regions (Körner et al., 2016). Phenology is thus a key feature of temperate, boreal and alpine plant species niche because it defines the season and duration of growth and reproduction, modulating largely the probability of survival of individuals, especially in case of adverse climatic events. For instance, to ensure the reproductive success, the timing of flowering must be well synchronized among individuals and with the advancement of spring in order to avoid late spring frost that could damage the reproductive organs (Post 2003; Sparks et al. 2003; Chuine, 2010). Similarly, the timing of budburst is highly important since it marks the start of the photosynthetic period, which affects the fruit and other tissues growth, as well as the build-up of carbohydrate reserves required for tissue maintenance (Hoch, 2005). Because emerging leaves in spring are extremely sensitive to frost, the timing of budburst must also be well synchronized with environmental cues to minimize the risk of frost damages (Lenz et al., 2016). For this reason, late flushing species are often less resistant to frost (Lenz et al., 2013). The interplay between freezing resistance, phenology, and the time required to mature tissue, has recently been proposed as a key determinant of the upper elevation limits of trees living below the treeline (Kollas et al. 2014; Körner et al., 2016).

Since the 1970s, spring phenology has been reported to occur earlier in response to warming (Walther et al. 2002; Menzel et al. 2006; Fu et al. 2014). In particular, Fu et al., (2014) detected shifts of around two weeks from 1982 to 2011 in Europe for several species including *Betula pendula* Roth., *Fraxinus excelsior* L., and *Corylus avellana* L. (Güsewell et al., 2017) shows that the advance is more pronounced at high elevation in the Alps. To prevent buds from developing during a warm spell in winter, most of the temperate and boreal trees have developed a key adaptation: the inability to resume growth despite favorable growing conditions in terms of temperature and water. This physiological state called endodormancy requires from a few weeks to several months of cold temperature (usually assumed around 4 °C) to be broken (Lang et al., 1987). Endodormancy is followed by a second phase called ecodormancy, which is broken when buds are exposed to warm temperature (forcing temperatures) and ends with budburst. Several studies have pointed out that climate warming may lead to insufficient chilling in winter to fully break dormancy release (Yu et al. 2010; Chuine, Morin, et al. 2010), which could delay, or even compromise leaf unfolding (Chuine et al., 2016). Such a situation is more likely to occur in populations inhabiting the warm edge of a species range and/or at lower elevations in mountain regions. In this context, a recent study has shown that the apparent response of leaf unfolding to warming decreased by about 40% between 1980 and 2013 for seven dominant European tree species at 1245 sites (Fu et al., 2015). The authors hypothesized that the dampening of the phenological response to spring warming was due to reduced winter chilling during the last 15 years and/or increasing photoperiod limitation. Other studies also support that, in additional to insufficient chilling, photoperiod might prevent spring phenological phases to occur earlier (Körner and Basler, 2010; Gaüzere et al. 2017).

Experimental studies have shown that low level of chilling during endodormancy delays budburst (e.g. (Murray et al., 1989; Laube et al., 2014; Caffarra et al., 2011)). In agreement, modeling studies suggest that the effect of the warming in winter on endodormancy break should progressively balance the advancing effect of the warming in spring on budburst date (Chuine et al. 2016). However, there is no evidence so far of such effect in phenological observations.

The incomplete understanding of the response of spring phenology to warming temperature makes predictions of tree phenology and *in fine* range distribution rather uncertain (Richardson et al. 2013; Piao et al. 2015). To address this issue, an increasing number of studies have tried to elucidate the determinism of leaf unfolding both using experiments (Zohner and Renner, 2014; Laube et al., 2014) and long-term series of phenological observations using large phenological networks or remote sensing data (Zhang et al. 2003; Reed et al. 2009). Both a better understanding and more accurate predictions of spring phenology require long-term observations over large geographic extents and elevational gradients. Citizen science programs have the potential to expand the scope of data collection useful to scientists, and especially their spatial and temporal scale (Hand 2010; Fuccillo et al., 2015; Hurlbert and Liang, 2012; Barlow et al. 2015). In the field of phenology, several programs have been running for several years now, especially in Europe, and have brought a considerable amount of data to researchers (Scheifinger and Templ, 2016). In this context, the CREA (Centre de Recherches sur les Ecosystèmes d'Altitude, Chamonix, France) initiated in 2004 the citizen science program Phenoclim (www.phenoclim.org), which aims at assessing the long-term effects of climate changes on plant phenology over the French Alps. The specificity of the Phenoclim program, compared to other existing citizen science initiatives, lies not only in its geographic coverage in mountain environments, but also in its simultaneous acquisition of accurate temperature records in addition to phenological observations. Taking advantage of this long-term and large-extent program, we aimed at using eight years of spring phenological observations for five major tree species to answer the following questions:

(1) Are warmer temperatures shifting spring phenology homogeneously along elevation?
(2) Can we already detect a delaying effect of exceptionally warm winters on budburst and flowering?
(3) How does winter warming affect the phenological shift along elevation compared to preseason warming (*i.e.* after dormancy break)?

2. Methods

2.1. Climate and phenology data

We used observations of two spring phenological phases, budburst and flowering, for five tree species extracted from the Phenoclim