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

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ABSTRACT

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

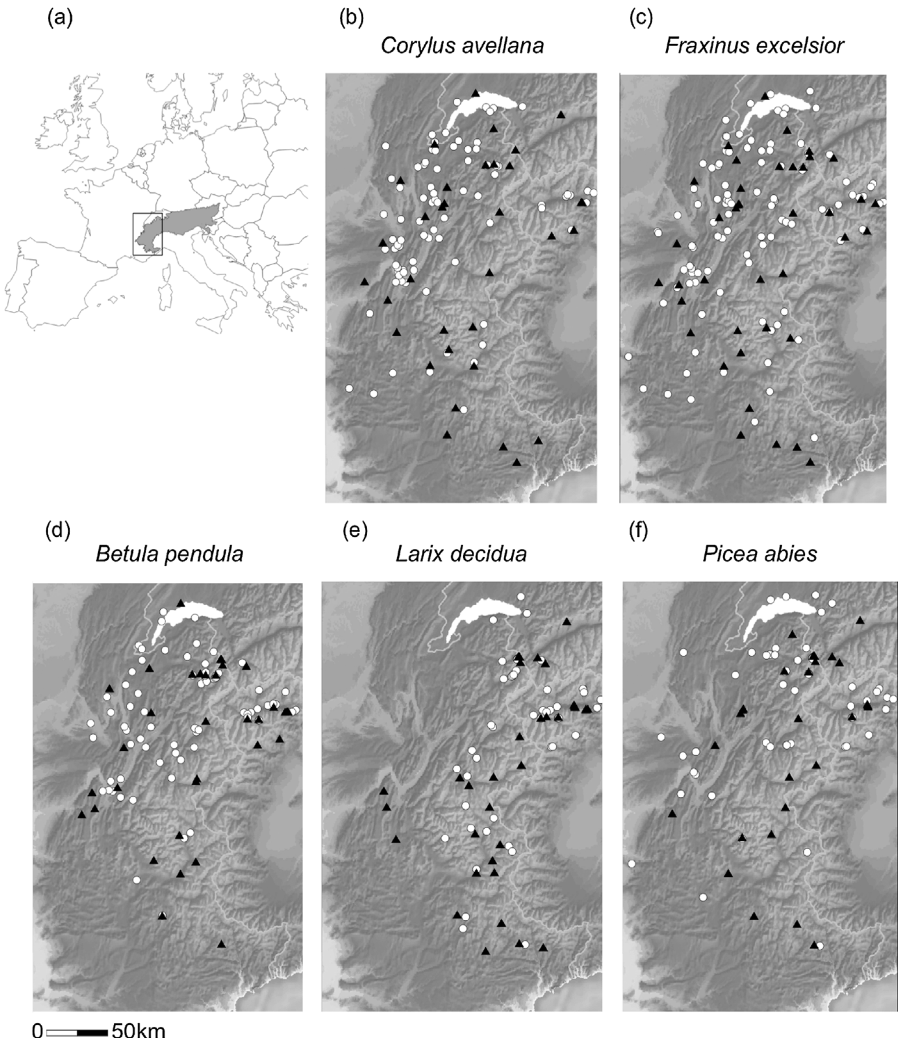

Fig. 1. Map showing the location of the study area (western part of the Alps) at the scale of Europe (a). Maps showing the location of the sites with phenological records for the five species in the Western Alps (b–f): *Corylus avellana* (hazel) (b), *Fraxinus excelsior* (ash) (c), *Betula pendula* (birch) (d), *Larix decidua* (larch) (e), *Picea abies* (spruce) (f). Filled white circle correspond to sites having phenological records only. Black triangle corresponds to sites having phenological records and equipped with temperature stations.

database. These observations cover a time period ranging from spring 2007 to spring 2014. The study species were three broad-leaved deciduous trees: hazel (*Corylus avellana* L.), ash (*Fraxinus excelsior* L.), birch (*Betula pendula* Roth); and one deciduous and one evergreen coniferous tree respectively: larch (*Larix decidua* Mill.) and spruce (*Picea abies* (L.) Karst.). All five species cover various elevation gradients with *Corylus* having the lowest and narrower and *Larix* the highest and largest (Fig.1). Thus, this set of species allowed us to assess phenological variations over large elevational gradients.

In the Phenoclim protocol, budburst is defined as the first day at which 10% of the vegetative buds of the crown on a given individual are opened (BBCH 07). Similar to budburst, flowering is defined as the first day at which 10% of the male flower buds are opened (BBCH 61). At each site, observers survey at least two individuals per species. These individuals are chosen to be adult and dominant trees taller than 7 m, sharing similar environmental conditions (*i.e.* soil, slope and aspect) and at a maximum horizontal distance of 100 m from each other. Phenological observations were recorded weekly. For each species and at each site, yearly budburst or flowering dates were calculated by averaging observations from individuals. Certain species were not found at each site In addition, the number of years of monitoring varied. (Fig.1). In total, and irrespective of species, 242 sites for budburst and 224 sites for flowering were surveyed between 2007 and 2014.

Additionally, temperature was monitored on sixty sites covering a large elevation gradient ranging from 372 to 1919 m using temperature stations (Fig. 1). These stations measured air temperature at a standard 2-m height every 15 min with a DA8B20 digital thermometer placed in a white ventilated plastic shelter (Dallas Semiconductor MAXIM, www.maxime-ic.com).

These temperature sensors have an operating range of −55 to 125 °C and an accuracy of ± 0.5 °C over the range of −10 to 85 °C. The 2-m air temperature recorded by the stations was highly correlated with standard temperature obtained from national meteorological stations (e.g., in Chamonix: correlation coefficients = 0.97, 0.95 and 0.97, respectively for minimum temperature, maximum temperature and mean temperature; data from Chamonix station obtained from Meteo France; (Pellerin et al., 2012). We thus used records from the 2-m air temperature sensors of the Phenoclim stations (1) to calculate daily mean air temperature at sites equipped with stations and (2) to interpolate these daily measurements at observation sites without meteorological stations for further correlative analyses between temperature and dates of phenological events. Daily-interpolated temperatures were generated by first calibrating linear models of daily temperature as a function of elevation. These models were then used to spatially predict temperature at observation sites without temperature stations, using pixels of a 25-m digital elevation model (DEM). Each daily projection of this fitted temperature model as a function of elevation was adjusted by interpolating residuals of the regression from the calibrations points over the whole valley according to the inverse distance weighted algorithm (IDW) (see also: Kollas et al., 2014; Cianfrani et al., 2015, for further details).

2.2. Detecting the effect of exceptionally warm winters on budburst and flowering

We calibrated mixed effects models with budburst or flowering dates as response variables and with growing degree-days and chilling as predicting variables to assess the relative importance of these two temperature-based factors on the two phenological events. Mixed effects models were performed in R (version 3.1.1; R Core team, (2015)) using the library nlme (Lindstrom & Bates 1990; Pinheiro & Bates 1996) with observation sites as random effect. Indeed, there may be some site-specific adaptations, which would blur an overall relationship between the temperature indexes and budburst. As temperature index we calculated for each species and each observation site a chilling factor that was defined as the frequency of days with a daily temperature $< 5\,^{\circ}\mathrm{C}$ from September 1st to December 31st of the calendar year preceding budburst (Dantec et al., 2014). We also calculated growing degree-days (hereafter GDD) defined as the sum of positive ($> 0\,^{\circ}\mathrm{C}$) daily mean temperature from January 1st to the median date of budburst or flowering observed over the 2007–2014 observation period for a given site. The growing degree-days variable was tested here with two different thresholds (*i.e.* 0 °C and 5 °C). This 0 °C temperature threshold was chosen here instead of the more commonly-used 5-°C threshold because daily mean temperatures between 0 and 5 °C may contribute to trigger budburst events in plants found in mountainous environments, (Körner 1999; Vitasse et al. 2016). We chose Jan 1st as the starting date of accumulation of the growing degree days (GDD) for two reasons. First of all, the ecodormancy phase can begin as early as January in some species like hazel (flowering) or poplar, which requires only 6 weeks of chilling to break endodormancy (Rinne et al., 2011). Second, the beginning of the ecodormancy phase varies a lot between species, years, and sites along the elevation and latitudinal gradients because of very contrasted climatic conditions. By setting the start of the preseason period to January 1st we could estimate more correctly the GDD at early starting pre-season sites while not affecting the estimation of the GDD at late starting pre-season sites. Temperatures inferior to the threshold temperature indeed do not contribute to the GDD.

We considered models with all combinations of predicting variables, including univariate models. We calculated Akaike's Information Criterion corrected for small sample size ($\mathrm{AIC_C}$) with the R function AIC to select the most parsimonious model (Burnham and Anderson, 2002). We assessed the independent and joint contribution of predicting variables and detected possible interactions between them with variance partitioning using the library Vegan (Oksanen et al., 2013). All models were first calibrated with all observations from sites with meteorological stations, and then compared to models calibrated on the entire dataset including sites with interpolated temperature-based variables.

2.3. Identification of climatically contrasted years

We ran a second type of analyzes by comparing the most different climatic years.

We first aimed at identifying three climatically contrasted years over the observation period: (i) a cold fall and early winter followed by a warm late winter and early spring, called hereafter a typical year; (ii) a warm fall and late winter followed by a warm late winter and early spring, called hereafter a warm year and (iii) a cold fall and early winter followed by a cold warm late winter and early spring, called hereafter a cold year. The period of fall and beginning of winter (called hereafter for the sake of simplicity winter period) corresponds to the development phase of endodormancy, while late winter and early spring (called hereafter for the sake of simplicity "preseason period") corresponds to the development phase of ecodormancy. From our current understanding of the effect of temperature during winter period on endodormancy and of preseason temperature on ecodormancy, the three climatically contrasted years should respectively lead to early, medium and late budburst and flowering dates.

To identify the three climatically contrasted years, we characterized the endodormancy and ecodormancy periods according to temperature-based factors. To rank endodormancy periods, we calculated for each species and each observation sites the chilling as defined above. Similarly, to rank ecodormancy periods, we calculated the GDD as defined above. To identify the three climatically contrasted years, we compared quantile values of chilling and GDD between years for each species.

2.4. Detecting delaying effect of warm winter on budburst and flowering dates along elevation in the Alps

We calibrated for each species linear models of budburst and flowering dates as a function of elevation based on data of the three contrasted climatic years (hereafter called yearly models). Then, we calibrated global models of budburst and flowering dates as a function of elevation based on all available years of the observation period (hereafter called global models).

To estimate the deviation in budburst date between the yearly and the global model along the elevation gradient, we compared yearly models to the global models using the sum of absolute number of days of deviation between the yearly and the global model along the elevation gradient used for the calibration of models. We additionally bootstrapped yearly models (with 999 repetitions) to assess the effect of sampling bias on regression parameters.

We also calibrated linear models of budburst and flowering dates with GDD as a predictor. We then extracted residuals (observed dates – predicted dates) of budburst and flowering date predictions for the three climatically contrasted years. Linear models of the residuals as a function of elevation were finally calibrated to assess whether slopes and intercepts of these models were similar between the three years for a given species and to verify whether residuals of the year with a warm winter were positive at low elevation, suggesting a negative effect of warmer temperature in winter on budburst and flowering.

Finally, we estimated the contribution of warming temperatures during preseason by the average shift in budburst and flowering dates per degree of warming of the preseason between the year with a cold winter and a warm preseason and the year with both a cold winter and preseason. Similarly, we estimated the contribution of warming temperatures during winter by the average shift in budburst and flowering dates per degree of warming of winter between the year with both a warm winter and preseason and the year with a cold winter and a warm preseason.

3. Results

The mixed effects models which explained budburst and flowering dates the best were generally models including growing degree-days with a 0-°C threshold (GDD0) irrespective of the dataset (*i.e.* using either observed temperatures or interpolated temperatures), together with chilling as predicting variables. Budburst and flowering of *Picea* as well as flowering of *Betula* were best explained by growing degree-days with a 5 °C threshold (GDD5) together with chilling (Table 1, Appendix A in Supplementary material). GDD explained the largest amount of variance in either budburst or flowering date for all species. Variance partitioning also indicated an important joint contribution of either GDD0 or GDD5 and chilling in models for all species and the two phenological phases (Table 1, Appendix A in Supplementary material). Thus, over all 8 years and all locations, chilling did not explain much of the variance in spring phenology once forcing temperatures were taken into account except in *Picea*, and in the flowering date of *Larix* and *Fraxinus*.

Because of the widely contrasting climatic conditions from one year to another and along the latitudinal and elevation gradients, the mixed-effects models performed over all years and locations might not be able

Table 1
Linear mixed models of budburst dates as response variables and temperature-based factors as competing predicting variables. Models are calibrated both on observation sites equipped with temperature stations and on all observation sites. Adjusted R-squared (*R2*), AIC, and *P*-value of ANOVA are provided for each model. Var-part = partitions of variance between growing degree-days > 0 °C (GGD0), growing degree-days > 5 °C (GGD5), and chilling. For models with both GDD and chilling, two P values are provided, one for each effect.

		Budburst													
		With temperature stations							All sites						
		N	AIC	R^2	*P-value (anova)*	*Var-part GDD0*	*Var-part chilling*	*Var-part - both*	N	AIC	R^2	*P-value (anova)*	*Var-part GDD0*	*Var-part chilling*	*Var-part - both*
C. avellana		126							319						
	GDD0		929	0.55	***					2377	0.62	***			
	GDD5		940	0.51	***					2404	0.59	***			
	Chilling		967	0.26	*					2502	0.38	***			
	GDD0 + Chilling		**921**	0.54	***/NS	0.30	0.01	0.11		**2373**	0.62	***/NS	0.28	0.0	0.18
	GDD5 + Chilling		932	0.52	***/NS	0.24	0.01	0.12		2392	0.60	***/**	0.23	0.0	0.18
F. excelsior		152							396						
	GDD0		1132	0.65	***					2949	0.70	***			
	GDD5		1133	0.65	***					2958	0.70	***			
	Chilling		1174	0.50	*					3106	0.53	***			
	GDD0 + Chilling		**1126**	0.64	***/NS	0.24	0.0	0.22		**2944**	0.70	***/NS	0.23	0.0	0.33
	GDD5 + Chilling		1127	0.65	***/NS	0.23	0.0	0.22		2953	0.70	***/NS	0.22	0.0	0.33
B. pendula		145							307						
	GDD0		1052	0.72	***					2224	0.76	***			
	GDD5		1049	0.73	***					2227	0.76	***			
	Chilling		1120	0.54	*					2393	0.55	***			
	GDD0 + Chilling		1047	0.72	***/NS	0.34	0.0	0.2		**2220**	0.76	***/NS	0.32	0.0	0.23
	GDD5 + Chilling		**1044**	0.73	***/NS	0.35	0.1	0.3		2222	0.76	***/NS	0.33	0.0	0.23
L. decidua		155							303						
	GDD0		1113	0.68	***					2174	0.74	***			
	GDD5		1109	0.69	***					2180	0.72	***			
	Chilling		1179	0.42	*					2367	0.43	**			
	GDD0 + Chilling		1109	0.68	***/NS	0.29	0.0	0.12		**2171**	0.74	***/NS	0.36	0.0	0.13
	GDD5 + Chilling		**1105**	0.69	***/NS	0.29	0.0	0.12		2176	0.72	***/NS	0.34	0.0	0.13
P. abies		107							248						
	GDD0		752	0.79	***					1757	0.81	***			
	GDD5		743	0.81	***					1738	0.84	***			
	Chilling		833	0.44	**					1949	0.43	***			
	GDD0 + Chilling		745	0.78	***/NS	0.50	0.01	0.15		1752	0.81	***/NS	0.38	0.0	0.28
	GDD5 + Chilling		**733**	0.81	***/*	0.54	0.02	0.14		**1725**	0.84	***/**	0.41	0.01	0.27

to detect the effect of a warmer winter on spring phenology that might have occurred only at some locations and during particular years. We thus analyzed more specifically the spring phenology of the most climatically contrasted years. For all five species, winter and preseason periods were the warmest in 2007 with low chilling and high growing degree-days (Appendix B in Supplementary material). Preseason in 2011 was as warm as in 2007 but chilling was more important during winter (Appendix B in Supplementary material). Winter and preseason were the coldest in 2013 (Appendix B in Supplementary material). We thus used the years 2007, 2011 and 2013 to assess the impact of respectively, a warm winter followed by a warm preseason (2007, referred hereafter as the warm year), a cold winter followed by a warm preseason (2011, referred hereafter as the typical year) and a cold winter followed by a cold preseason (2013, referred hereafter as the cold year) on budburst and flowering. Appendix C (Supplementary material) provides the average temperature of the three years calculated over preseason and over winter. The typical year (2011) and the cold year (2013) differed by the temperature of preseason but had similar winter temperature, while the warm year (2007) and the typical year (2011) differed by the temperature of winter but had similar preseason temperature.

In most species, the coldest year (2013) generated the latest dates, the typical year (2011) generated the earliest dates, and the warmest year (2007) generated intermediate dates of budburst and flowering as expected, with the exception of flowering of *Corylus* and budburst of *Picea* (Fig. 2, Appendix E in Supplementary material). Bootstrapped values of the phenological differences in budburst and flowering dates between the global model and the yearly models were significantly lower in 2007 when compared to 2011 (*P*-values < .05) along the elevation gradient, except for the budburst of *Picea* and the flowering of *Corylus* (Fig. 3). Our results thus suggest that warmer winters delayed budburst for similar preseason temperature conditions along the elevation gradient in most cases.

To estimate the effect of warming temperatures in preseason, we compared the typical year (2011) to the cold year (2013). Both years exhibited similarly cold winter temperatures but differed in preseason temperatures (Table 2, Fig. 4, Appendix C and Appendix D in Supplementary material). Budburst and flowering were similarly advanced (comparing 2011–2013) by a warming of preseason from 15.2 to 24.5 days, which corresponded to a rate of advancement of 5–8 days $^{\circ}C^{-1}$ depending on the species (average 6.5 day $^{\circ}C^{-1}$, Table 2).

To estimate the effect of warming temperatures in winter, we compared the warm (2007) year to the typical year (2011). Both years exhibited similarly warm preseason temperatures but differed in winter temperature conditions (Table 2, Fig. 4, Appendix C and Appendix D in Supplementary material). Budburst and flowering dates were both delayed by a warming of fall-winter (with the exception of flowering of *Corylus* and budburst of *Picea*) from 2.1 to 12 days, which corresponded to a rate of delay of 0.5–5.6 days $^{\circ}C^{-1}$ depending on the species (average + 1.6 day $^{\circ}C^{-1}$, Table 2).

On average, the effect of a warming of winter was 2.3 times less important than of that of warming of preseason (Table 2, Fig. 4). Although a warming of winter counteracted the effect of a warming of

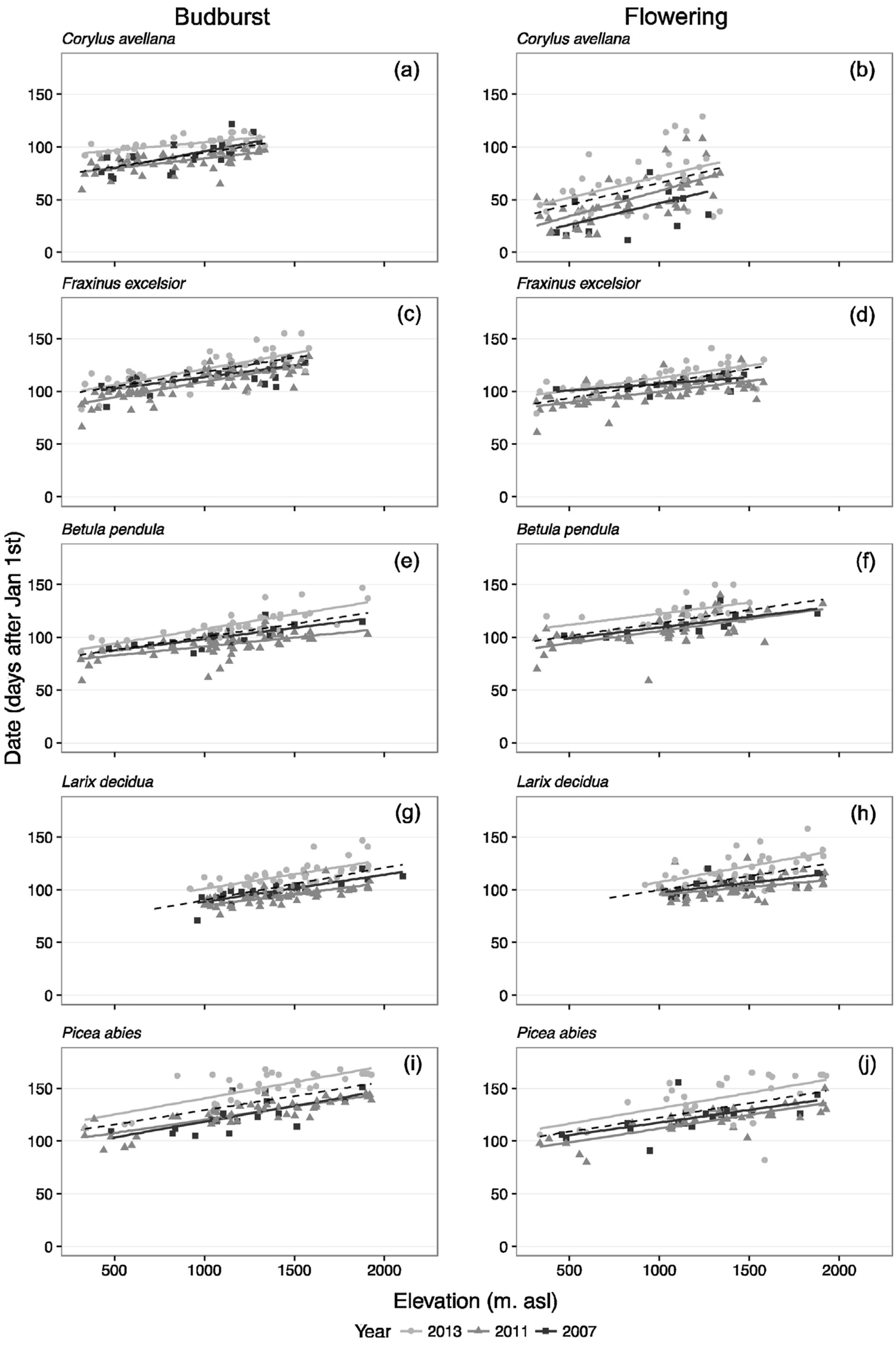

Fig. 2. Relationships between budburst (a, c, e, g, i) and flowering dates (b, d, f, h, j) of years 2007 (dark grey square), 2011 (grey triangle) and 2013 (clear grey dots) and elevation for *Corylus, Fraxinus, Betula, Larix, and Picea*. Linear models of budburst or flowering dates as a function of elevation (superimposed lines) are shown for 2007 (dark grey); 2011 (grey); 2013 (clear grey); the whole period (2007–2014) (dashed line).

preseason, it did not cancel it. Difference among species responses to winter warming was also larger than that to preseason warming, especially for flowering (SE 1.14 *vs* 1.50 days for budburst; 1.09 *vs* 2.94 for flowering, respectively).

Residuals (observed – predicted dates) of the models including solely GDD0 fitted with all observations of the warm year 2007 were always positive at low elevation whatever the species for both budburst of flowering dates, while they tended to be lower and for some cases negative at high elevation (Fig. 5). In other words, residuals were the highest at low elevation during the warm year of 2007 compared to 2013 and 2011, irrespective of species (Appendix F in Supplementary material, Fig. 5), meaning that observed budburst or flowering dates tended to occur later than predicted by GDD alone at low elevation during the warm year of 2007. Conversely, residuals were on average negative irrespective of elevation during the typical year 2011, for both budburst and flowering, and decreased with elevation in most cases, meaning that the observed dates occurred earlier than predicted by GDD and more so at high elevation.

These results suggest that a model that does not take into account the effect of winter temperature underestimates spring events occurrence dates when winter is warmer than usual and overestimate them when winter is colder than usual.

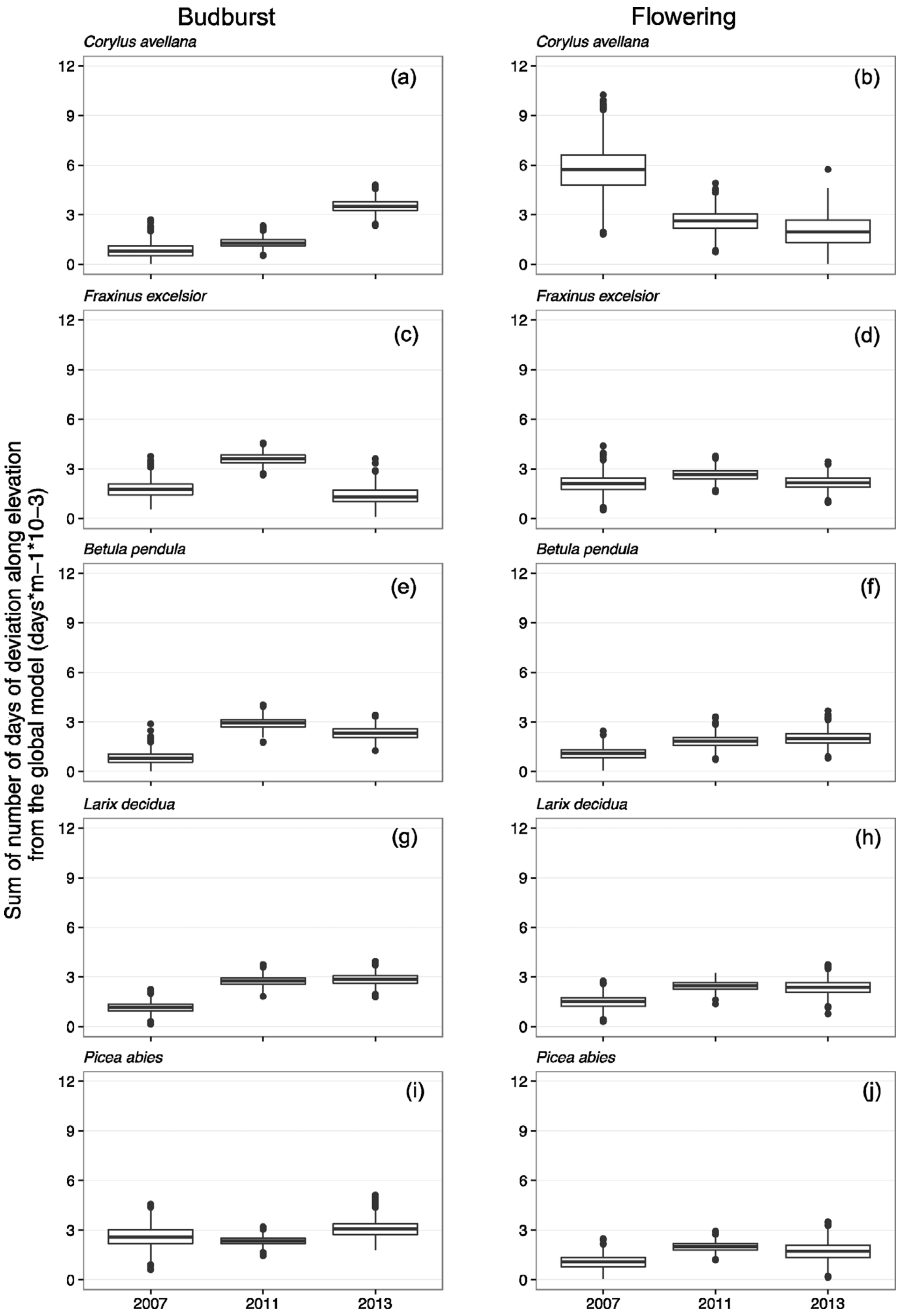

Fig. 3. Boxplots of bootstrapped values of deviation given by the cumulated number of days (days × 10^{-3}) along the elevation gradient between the global and yearly model of budburst date (a, c, e, g, i) and flowering date (b, d, f, h, j) for the three specifics years (2007, 2011 and 2013) for each species. Offsets are significantly different between years for all species and phenological events.

4. Discussion

The results of mixed effects models performed with all observations suggest that except in a few cases, winter conditions in the Alps have not affected spring phenology from 2007 to 2014. However, focusing on particularly warm winters, we showed that for similar winter temperature conditions, warmer preseason significantly advanced budburst and flowering (−5.3 to −8.4 days °C^{-1}); while for similar preseason temperature conditions, warmer winters significantly delayed budburst along the elevation gradient (+0.9 to + 5.6 days °C^{-1}), excepted for the flowering of *Corylus* and the budburst of *Picea* (Table 2). The average difference in leaf-out and flowering dates between the two extreme years 2011 and 2013 across all species was three weeks. More importantly, the shift in budburst in all deciduous species was not constant along the elevation gradient between 2007, the warm year, and the average over the 2007–2014 period with the shift at low elevation being less important than at high elevation, except for the flowering of *Corylus*. In contrast, *Picea* showed overall a constant shift in budburst and flowering dates along the elevation gradient.

4.1. Declining effect of warming on phenological shifts

Previous studies have debated the linearity of the response of budburst and flowering to temperature warming (Chuine, 2010; Luedeling et al. 2013; Chuine et al. 2016; Fu et al. 2015). Linear trends observed so far in budburst and flowering dates were caused principally by two factors: (i) a warming of preseason which accelerates cell elongation almost linearly up to an optimal temperature which has not been

Table 2
Estimation of a preseason warming and a winter warming effect on budburst dates (a) and flowering dates (b). Preseason warming effect is estimated by comparing the typical year (2011) to the cold year (2013), and winter warming effect by comparing the warm year (2007) to the typical year (2011). Δ date: difference in phenological date between the two years. Δ mean winter/preseason temperature: mean temperature difference either on the preseason period or the autumn-winter period between the two years. Note that mean temperatures are different for each species because species do not occur strictly at the same sites. In brackets: confidence intervals. Response: shift in budburst (a) and flowering (b) dates per degree, either calculated relatively to the preseason mean temperature (Jan 1st to median of spring phenological date) or the winter mean temperature (Sept 1st–Dec 31st) (days °C^{-1}).

(a)

Budburst	Preseason warming effect		
	Δ date (day)	Δ Mean spring temperature (°C)	Response (day °C^{-1})
C. avellana	−16.7 [+3.9]	2.6 [+0.6]	**−6.5**
F. excelsior	−15.2 [+5.5]	2.9 [+0.7]	**−5.3**
B. pendula	−21.4 [+4.8]	3.5 [+0.7]	**−6.1**
L. decidua	−19.3 [+3.8]	3.1 [+0.5]	**−6.3**
P. abies	−24.5 [+6.3]	2.9 [+0.8]	**−8.4**

Budburst	Winter warming effect		
	Δ date (day)	Δ Mean winter temperature (°C)	Response (day °C^{-1})
C. avellana	6.7 [+6.0]	2.8 [+0.8]	**2.4**
F. excelsior	8.1 [+5.2]	2.8 [+0.7]	**2.9**
B. pendula	9.4 [+4.5]	3.1 [+0.8]	**3.0**
L. decidua	3.9 [+4.4]	4.3 [+0.6]	**0.9**
P. abies	−2.1 [+7.7]	4.2 [+0.7]	**−0.5**

(b)

Flowering	Preseason warming effect		
	Δ date (day)	Δ Mean spring temperature (°C)	Response (day °C^{-1})
C. avellana	−17.7 [+10.6]	2.6 [+0.6]	**−6.8**
F. excelsior	−15.4 [+4.8]	2.9 [+0.7]	**−5.3**
B. pendula	−19.6 [+5.7]	3.3 [+0.7]	**−5.9**
L. decidua	−18.7 [+4.8]	2.9 [+0.5]	**−6.4**
P. abies	−20.6 [+9.4]	2.5 [+0.9]	**−8.2**

Flowering	Winter warming effect		
	Δ date (day)	Δ Mean winter temperature (°C)	Response (day °C^{-1})
C. avellana	−6.4 [+11.3]	2.7 [+0.9]	**−2.4**
F. excelsior	12.2 [+4.1]	2.2 [+0.7]	**5.6**
B. pendula	7.1 [+6.3]	2.8 [+0.8]	**2.5**
L. decidua	2.7 [+4.2]	3.9 [+0.6]	**0.7**
P. abies	2.1 [+7.3]	4.2 [+0.8]	**0.5**

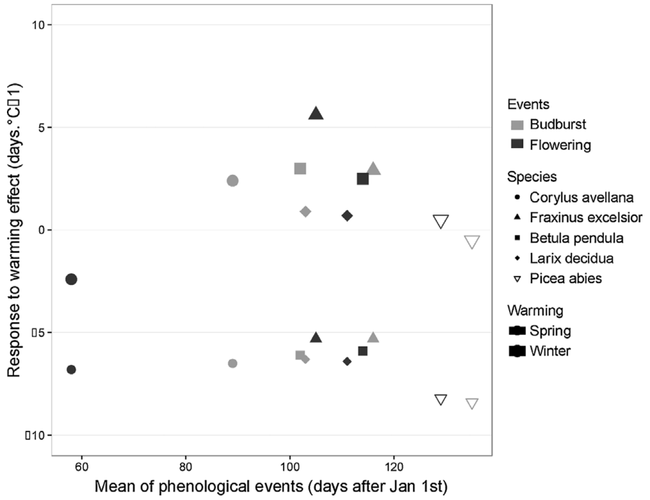

Fig. 4. Relationships between the mean of budburst dates (light grey) or the mean of flowering dates flowering dates (dark grey) during the study period and response of warming preseason (small size symbols) or warming winter (big size symbols) for *Corylus, Fraxinus, Betula, Larix, and Picea.*

reached yet in most temperate regions; (ii) a level of warming of winter which has been so far insufficient to impede endodormancy break. Our results showed that the latter condition may no longer be true during some exceptionally warm winter such as in 2006–2007, especially at lower elevations in the Alps. Additionally, these results were consistent with those of Fu et al. (2015), also suggesting a dampening of the response of budburst to warming temperature over the past 25 years for dominant European tree species at lowlands in central Europe. Here the authors invoked a reduced number of chilling days in winter.

The consequences of warmer winters might actually be positive on a short term. Indeed, delayed budburst and flowering at lower elevations may reduce the risk of exposure of leaves and flowers to late spring frost. Consistently this risk was shown to have increased at higher elevations in the Swiss Alps because spring phenology has advanced at a faster rate than the frost-free period but has remained unchanged at lower elevations because of the reduced phenological advance to spring warming (Vitasse et al., 2018). However, in the long term, warmer winters might impede endodormancy break, ultimately compromising the quality of leaf and flower development (Chuine et al., 2016).

Other factors such as photoperiod have been shown to co-control budburst as well, at least in some species such as European beech (Zohner & Renner 2015; Laube et al. 2014; Körner et al. 2016). The sensitivity of budburst to photoperiod has been seen as an additional

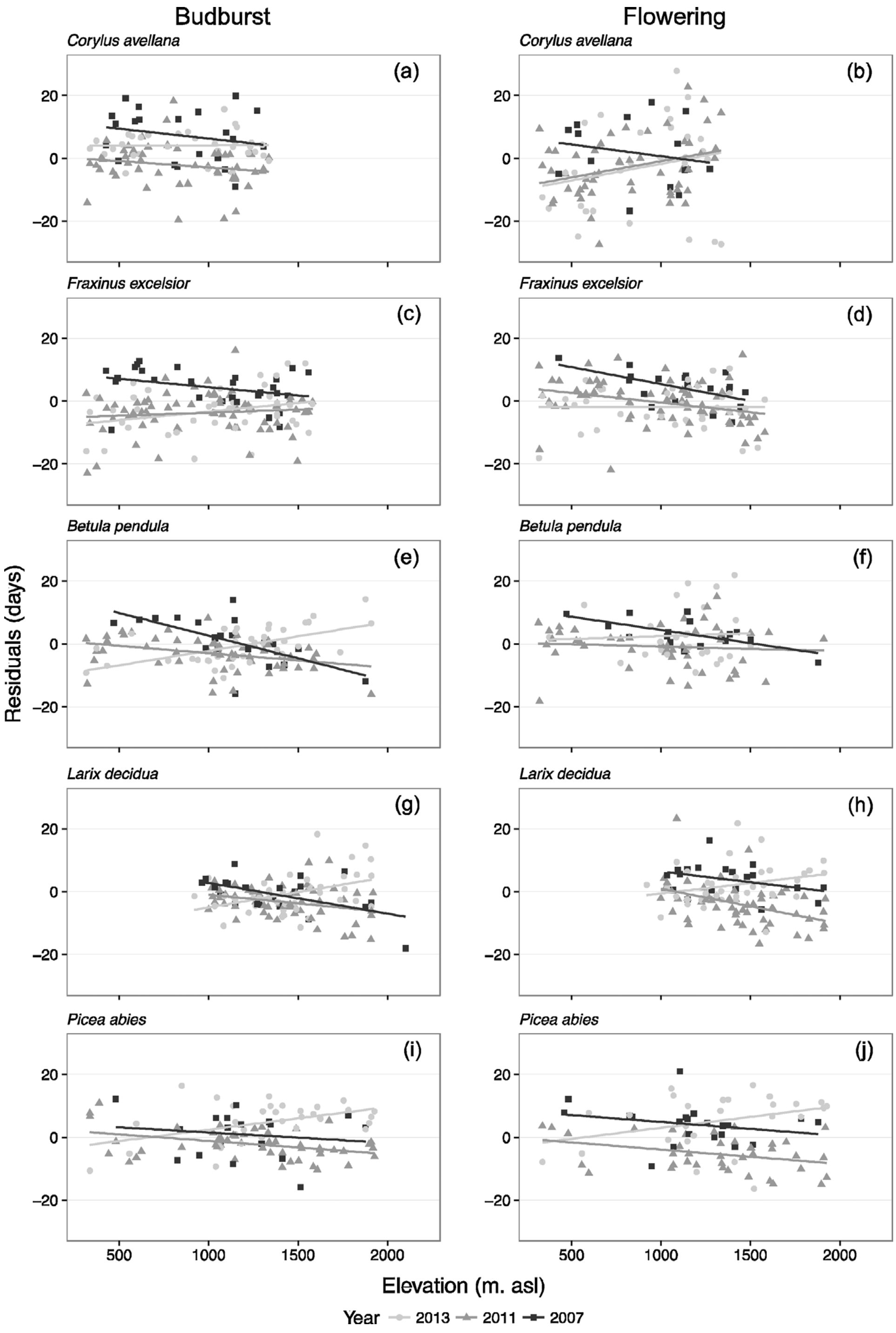

Fig. 5. Residuals of the best model fitted to budburst (a, c, e, g, i) and flowering (b, d, f, h, j) dates of all sites with growing degrees days in 2007, (light grey dots), 2011 (grey triangles) and 2013 (dark grey squares). Superimposed lines are linear regression of residuals on elevation (same color as symbols).

security against frost damages that could slow down or even revert the phenological trends after a certain level of warming because photoperiod might become limiting (Basler and Körner, 2012). However, very few species seem to be photosensitive for budburst or flowering (Zohner & Renner 2015; Laube et al. 2014; Way and Montgomery, 2015), and its effect seems to balance chilling depletion and be much weaker than that of temperature (Caffarra & Eccel 2011; Laube et al. 2014; Zohner et al., 2016).

Our results also suggest that chilling requirements are still met at high elevation during years with warm winter in the four deciduous species *Corylus, Fraxinus, Betula* and *Larix*. Recent studies suggest that at high elevation in the Alps, winters are usually too cold for optimal chilling and that a warming of winter can actually increase the number of chilling days and thus advance spring phenology (Güsewell et al., 2017). Thus, warmer winters can have opposite effects on spring phenology at high compared to low elevation, by advancing or delaying dormancy break respectively, which may partly explain the reduction of the phenological discrepancy across elevations observed in the Swiss Alps over the last decades (Vitasse et al., 2017). However, mountain summits are expected to warm faster than lower elevation sites (Mountain Research Initiative EDW Working Group, 2015). Therefore, chilling reduction might also concern higher elevations at one point.

4.2. Intra-specific and inter-specific variations in phenological shifts

Two phenological events showed contrasted responses to a warming of winter compared to the others: flowering of *Corylus* and budburst of *Picea*, which were still advanced during the warm year and not delayed, and are respectively the earliest and the latest events. Therefore, it seems that flowering of *Corylus* and budburst of *Picea* were much less affected by a lack of chilling than the other phenological events. In contrast, these two events were the most responsive to a warming of spring as found in a previous study (Basler and Körner, 2012).

It has been suggested that temperature requirements and successional strategy are tightly linked, with late successional species having higher chilling requirements than early successional species (Basler and Körner, 2012; Laube et al., 2014). The hypothesis behind this relationship highlights the trade-off between the length of the growing season and the risk of frost damage, either in early autumn or late spring (Larcher, 2003; Bennie et al., 2010; Chuine, 2010; Lenz et al., 2013). Whereas early-successional species are supposed to adopt a more 'risky' strategy, which would translate in low chilling requirement, late-successional species are supposed to show a more 'conservative' strategy, which would translate in higher chilling requirement. Our results confirm this hypothesis for *Corylus*, which is an early successional species and which flowering date was not delayed during the warmest winter, suggesting low chilling requirement, (note that budburst occurs much later in this species). This hypothesis does not seem to hold true for *Picea* which budburst was also not delayed during the warmest winter but is not considered as an early successional species. However, budburst of *Picea* has been shown to be sensitive to photoperiod, with short photoperiod delaying budburst despite a high degree of chilling (Basler and Körner, 2012). Photoperiod sensitivity is supposed to be, with high chilling requirement, another way to avoid early risky budburst (Basler and Körner, 2012). Our results therefore suggest, along with those of Basler & Körner (2012) that budburst of *Picea* require low chilling but long photoperiod together with high temperature.

5. Conclusions

Using a 8-year dataset from a citizen-science program, we have shown that although not widely visible, the impact of winter warming on budburst and flowering dates is visible at low elevation in the Alps during warmer winters. Our results thus support the hypothesis proposed by Fu et al. (2015) that the global slowing down of spring events advancement might be due to winter warming that counteracts the advancing effect of preseason warming. Up to a certain point, this opposite effect of winter warming might be beneficial in reducing the risk of exposure to late spring frost. However, it is expected to become detrimental if the chilling requirement to break endodormancy is not met anymore, which might occur no later than the end of the 21st century at low elevation. Detecting the effect of winter warming on plants phenology is still difficult because warm winter conditions are still rare in records. However, we can expect that warm winters in the upcoming years should help us to deepen our analyses and strengthen our conclusions.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agrformet.2018.01.030.

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