

Spring frost and growing season length co-control the cold range limits of broad-leaved trees

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ABSTRACT

Aim The aim of this study was to test, based on biological theory, which facet of temperature is most closely associated with the elevational and latitudinal low-temperature limits of seven European broad-leaved tree species. We compared three temperature-related potential constraints across three study regions: (1) absolute minimum temperature within 100 years; (2) lowest temperatures during the period of bud-break; and (3) length and temperature of the growing season.

Location Western and Eastern Swiss Alps (1165–2160 m a.s.l.) and southern Sweden (57° N–59° N).

Methods *In situ* temperature was recorded at the high-elevation and high-latitude limits of seven broad-leaved tree species and correlated with temperatures at the nearest weather stations, in order to reconstruct the temperature regime for the past 50 years. By applying generalized extreme value distribution theory, we estimated the lowest temperatures recurring during the life span of a tree.

Results At their high-elevation limits, five out of the seven tree species experienced winter minimum temperatures considerably warmer than their known maximum freezing resistance in winter. For the bud-break period, potentially damaging temperatures occurred at both the elevational and the latitudinal limits and for all four species for which phenological data were available. Three out of five species for which a latitudinal replicate was available showed a similar length of growing season at their respective elevational and latitudinal limits. The mean temperature during the growing season was always warmer at a species' latitudinal limit than at its elevational limit, and hence this variable does not bear general explanatory power for the range limit.

Main conclusions Low-temperature extremes during bud-break are the most likely candidates for controlling the elevational and latitudinal limits of broad-leaved tree species. The absolute minimum temperature in winter and the mean temperature during the growing season are unlikely to constrain the cold limits of these species. Thus, the results call for the use of temperature data (extremes) during key stages of spring phenology when attempting to explain the low-temperature range limits and to predict the potential range shifts of deciduous tree species.

Keywords

Absolute minimum temperature, bud-break, deciduous trees, distributional modelling, freezing resistance, growing season, leading edge, LT50, Sweden, Swiss Alps.

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INTRODUCTION

In order to predict potential range shifts of species in response to a warmer climate, it is essential to know which particular facet of temperature constrains the current cold limits of species and to revise the assumption that mean annual temperature is related to species limits. In a recent review, Austin & Van Niel (2011) noted the inconsistent relationship between species distribution and the commonly used parameters that are supposed to control range limits in species distribution modelling. To date, numerous studies on plant species distribution have relied on long-term averaged climate variables to define range limits, although it has been shown that using extremes can improve predictions for tree species (Zimmermann *et al.*, 2009). There is thus an urgent need to identify the effective facet of temperature that constrains the range limits of plant species.

Both the upper elevational and the northern latitudinal limit of broad-leaved tree species that do not reach the tree line are probably controlled by temperature-related drivers (Sakai & Larcher, 1987; Woodward, 1987; Dahl, 1998). Local influences, such as anthropogenic disturbance, geomorphology and competition, may influence the distribution at a regional scale (Gehrig-Fasel *et al.*, 2007), but such effects are stochastic and should disappear at a larger scale. The exact influence of temperature on the range limits of such tree species is not known. While the response of tree growth to changes in temperature is well understood (Tranquillini, 1979; Way & Oren, 2010; for a review see Körner, 2012), it remains uncertain which expression of temperature at which phenological stage is critical for the species-specific cold limits.

All tree species of temperate and boreal regions modify their organ-specific resistance to freezing temperatures according to the seasonal course of temperature and, thus, reduce the risk of damage. Exceptionally low temperatures in certain terrains will exclude a species from these terrains. We expect the range limit to reflect a boundary beyond which rare extreme events exclude certain tree taxa.

Mid-winter hardiness may shape the northern distributional limits (Sakai & Weiser, 1973; Woodward, 1987) when absolute minima of temperature injure buds or dormant meristems in adults, or eradicate young cohorts at the expanding edge of marginal populations.

A more likely scenario is damage while plants acclimate or de-acclimate to/from cold temperatures (Sakai & Weiser, 1973; Sakai & Wardle, 1978); that is, during the transition periods from a dormant to an active stage (at bud-break) and from an active to a dormant stage (at leaf-fall). Temperatures as mild as -3 ± 1 °C have been shown to kill leaves and flowers of most European broad-leaved tree species shortly after bud-break, when leaves flush and are not yet fully developed (Till, 1956).

A restricted growing season may exert another constraint for trees at their cold limits. Short seasons may cause failure of seed maturation (Pigott & Huntley, 1981; Chuine, 2010;

for further references see Kollas *et al.*, 2012), failure of seedling establishment (Jump *et al.*, 2007), or late wood formation, and in general may prevent tissue maturation.

All these potential low-temperature thresholds call for specific measures of temperature, such as absolute minima during certain critical developmental stages. Annual or monthly mean temperatures have little or even no predictive value, except where such temperatures are correlated with more specific threshold temperatures by coincidence.

In this study, we set out to identify critical temperature attributes associated with the low-temperature range limit of seven European broad-leaved tree species. More specifically, we focused on three facets of temperature that have been shown to be biologically effective: (1) absolute minimum temperature; (2) lowest temperatures during the time period of bud-break; and (3) the length and mean temperature of the growing season. We did not consider other aggregated parameters such as mean annual temperature, as they are missing explanatory power on physiological grounds. Because an earlier assessment showed evidence for lower minimum temperatures at canopy height than at 2 m above ground at the upper cold limits of broad-leaved trees (Kollas *et al.*, 2013), we focus on tree-top temperatures in this study. This is where reproductive organs are found. We linked *in situ* temperatures to weather stations in order to reconstruct temperature parameters over the last 50 years and to predict absolute minimum temperatures by applying generalized extreme value distribution theory. We then compared the three potential limiting facets of temperature across species elevational and latitudinal limits and we compared the predicted absolute minimum temperatures with literature-derived frost-resistance data.

MATERIALS AND METHODS

Study area, study species and *in situ* measurements

We first selected seven widely distributed deciduous tree species: *Acer pseudoplatanus* L., *Fagus sylvatica* L., *Fraxinus excelsior* L., *Prunus avium* (L.) L., *Quercus petraea* (Matt.) Liebl., *Tilia platyphyllos* Scop. and *Sorbus aucuparia* L. We then extracted occurrences of these species from the Swiss National Forest Inventory (NFI, two inventory periods: 1983–1985 (regular 1-km grid) and 1995–1997 (1.4-km grid)). Additional tree occurrences in Switzerland were derived from a forest plots database from Wohlgemuth (1992). This database allowed us to identify the highest elevation reached for each study species. All seven taxa reached their highest elevation either in one or both of the following two regions in Switzerland: the Western Alps (West) near Martigny (46°6' N, 7°4' E), and the Eastern Alps (East) near Chur (46°51' N, 9°32' E; Fig. 1). Based on the Swedish NFI data (Nilsson & Cory, 2011) and our own explorations in the field, we identified the latitudinal limits of a subset of five species in Sweden (North) between Göteborg (57°42' N, 11°57' E) and Arvika (59°39' N, 12°36' E). For each species,

we selected healthy, reproductive trees within the regional uppermost (Alps) or northernmost (Sweden) margin of distribution, within closed forest stands. By doing so, we avoided selecting (1) a single highest individual reflecting peculiar microclimatic conditions, and (2) individuals belonging to non-reproductive sink populations. The approach thus aims to identify the broad-scale constraining climatic factor, avoiding local peculiarities such as, for example, competition, predation and diseases.

When two or more species shared the same distributional limits (within 10 m of elevational distance or 1 km in latitude), we selected only one common site for our temperature measurements related to these species. This resulted in five measurement sites in each of the three regions (West, East and North; Table 1, Fig. 1).

At each site monitored, we placed one temperature logger (TidbiT v2 Temp UTBI-001, Onset Computer Corporation, Bourne, MA, USA) at 2 m above the ground, on the north-facing side of a tall tree in such a way that it remained completely shaded by the host tree's canopy and stem during the growing season and by only the stem during the coldest part of the year. Other loggers were placed in the tree top (the likely place of the first action of freezing conditions), in the understorey and below ground (the latter two are not considered here). The tree top and 2-m above-ground air temperatures were closely correlated. Temperature was recorded hourly from August 2009 to October 2011 in the Alps and from mid-September 2010 to mid-September 2011 in Scandinavia. In total, we employed 15 data-logging sites. Because tree tops are closely coupled to atmospheric conditions, the data we collected are not tree-specific but are specific to site and height above ground, with trees in essence serving as weather masts.

Temperature data analysis

For each site, we first distilled daily mean (in order to calculate the mean temperature during the growing season), daily absolute minimum and daily absolute maximum temperatures from the hourly measurements. Daily mean temperature was selected only for calculating growing degree-days (see below). For each temperature parameter we then calibrated three linear models by relating the first year (August 2009–July 2010) of *in situ* measured temperatures (T_{Log}) to the corresponding temperatures of the closest weather station (T_{Met}). Like the sites monitored, the selected weather stations in Switzerland were all above the elevational position of the temperature inversion occurring during the winter period in the Rhone (West) and Rhine (East) valleys (Fig. 1).

To test the quality of the resulting linear regression, we calculated the coefficient of determination for each site and each temperature parameter ($0.89 < R^2 < 0.99$).

In order to also demonstrate the strong linear relationship we reconstructed temperatures corresponding to the second year of measurements (August 2010–July 2011) for those sites where two years of *in situ* measurements were available (see Appendix S1 in the Supporting Information). Thus, we applied the linear models to the corresponding weather station temperatures of the second year. The temperatures reconstructed from weather stations were then correlated with the *in situ* measurements of the second year, and the root mean square error (RMSE) and Spearman's rho (ρ) were calculated. This represents an independent twofold cross-validation. The predictive power of the linear models was high when tested on the second year (2011) of *in situ* data. Spearman's coefficient of correlation (ρ) ranged

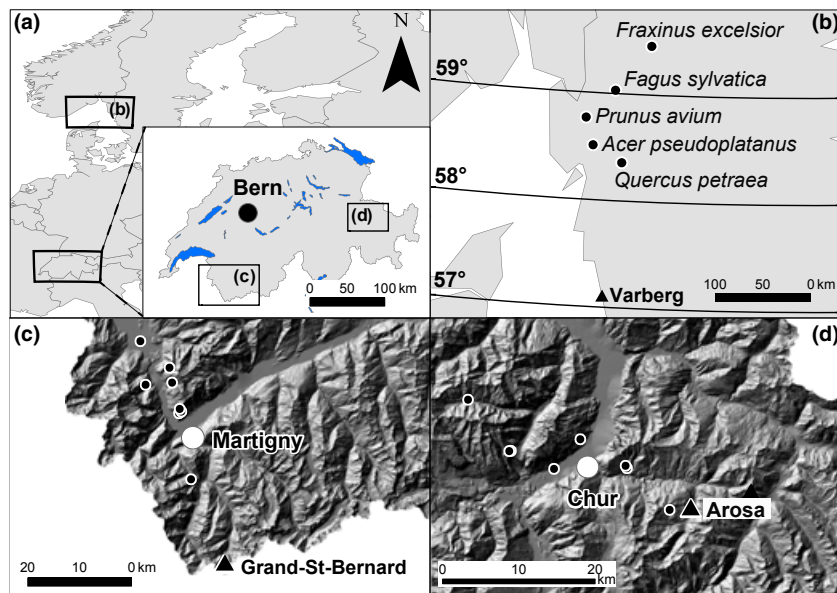


Figure 1 Map of (a) Europe showing the three main regions of study. Locations of the selected study sites (white circles round black dots) and weather stations (black triangles) for five species of European broad-leaved trees in (b) southern Sweden, (c) the Western Alps and (d) the Eastern Alps.

Table 1 Location and elevation of the study sites at the elevational and latitudinal range limits of seven deciduous tree species, and coordinates of the nearest weather stations used for temperature reconstructions in the three test regions: the Western Alps (West), Eastern Alps (East) and Sweden (North).

Region	Elevation (m)	Latitude	Longitude	Study site (affiliated species*)
<i>Sites</i>				
West	1374	46°08' N	7°04' E	Ti pl, Qu pe
	1460	46°11' N	6°59' E	Fa sy
	1523	46°08' N	7°04' E	Fr ex, Pr av
	1804	46°08' N	7°04' E	Ac ps
	2160	46°01' N	7°06' E	So au
East	1165	46°50' N	9°35' E	Ti pl
	1320	46°50' N	9°35' E	Fr ex, Qu pe
	1540	46°51' N	9°23' E	Fa sy
	1547	46°55' N	9°19' E	Ac ps
	2020	46°47' N	9°40' E	So au
North	159	58°21' N	12°29' E	Qu pe
	85	58°30' N	11°57' E	Ac ps
	90	58°46' N	11°48' E	Pr av
	83	59°01' N	12°18' E	Fa sy
	52	59°27' N	12°56' E	Fr ex
<i>Weather station</i>				
West	2966	46°20' N	7°12' E	Les Diablerets
	2472	45°52' N	7°10' E	Col du Gr. St. Bernard
East	1840	46°46' N	9°40' E	Arosa
	2690	46°50' N	9°48' E	Weissfluhjoch
North	69	59°40' N	12°38' E	Arvika
	177	59°13' N	12°04' E	Blomskog
	177	58°36' N	12°11' E	Kroppefjäll-Granan

*Ti pl, *Tilia platyphyllos*; Qu pe, *Quercus petraea*; Fa sy, *Fagus sylvatica*; Fr ex, *Fraxinus excelsior*; Pr av, *Prunus avium*; Ac ps, *Acer pseudoplatanus*; So au, *Sorbus aucuparia*.

between 0.96 and 1.00, and RMSE ranged between 0.7 and 2.4 K (see Appendix S1).

We then reconstructed 50 years (1961–2010, a limit set by the availability of data from weather stations) of daily mean, daily absolute minimum and daily absolute maximum temperatures (required for the calculation of daily means, see below) at the temperature logging sites by applying the linear model at each site (intercept and lapse rate). All temperatures were then corrected to account for the difference between 2-m air temperature and crown temperature (Appendix S2; Kollas *et al.*, 2013).

Reconstructed temperatures were later used for calculating growing degree-days (GDD), growing season length and obtaining extreme value distributions (see below).

We lost two loggers due to vandalism at the cold limits of *Fraxinus excelsior* and *P. avium* in the Western Swiss Alps (Table 1). Because two other loggers were installed on the same slope located below and above the elevation position of the missing devices (0.5 km from the missing devices), we used these two loggers to gap-fill temperature records for the lost loggers using daily regressions.

Recurrence of absolute minimum temperatures

Owing to the long life cycle of trees, low and potentially critical temperatures may recur and affect a given tree at long time intervals. We calculated lowest temperatures within

100 years, because this is the time period of the reproductive cycle for the species studied here.

Generalized extreme value distributions (GEVs) have been extensively used to estimate rare events (Coles, 2001). In this approach, within a given period (e.g. 100 years) every minimum or maximum value of a given parameter is extracted for every year, month or week. An appropriate GEV (Fréchet, Weibull or Gumbel distribution) is then fitted to the observed frequency distribution of the study parameter. The shape of the tail of the predicted distribution describes the likely occurrences of very rare events and allows extrapolations outside the observed temporal range of calibration.

As bud-burst occurs at the scale of weeks, we selected weekly absolute minimum temperatures for the analysis. The distribution of weekly absolute minimum temperatures meets the assumptions of extreme value theory (Coles, 2001) and thus belongs to the class of GEVs:

$$G(Z) = \exp \left\{ - \left[1 + \xi \left(\frac{Z - \mu}{\sigma} \right) \right]^{-1/\xi} \right\}, \quad (1)$$

where μ , σ and ξ represent the location, scale and shape parameter of the model, respectively. Prior to this analysis we transformed all minimum temperatures to their absolute values because GEVs are restricted to positive numbers (Guttorp & Xu, 2011). We back-transformed the results into their negative values after the analysis. Hence, for each site we obtained the absolute minimum temperature per week from

the reconstructed 50-year datasets. These data were found to be non-stationary, owing to climate change. The approximate increase of annual absolute minima of 0.3 K per decade (during the years 1961–2010) is consistent with findings of the 0.32 K decadal temperature increase in monthly absolute minimum temperatures in December, January and February at Neuchâtel (Rebetez & Reinhard, 2008). Thus, separately for each week of the year, we fitted two models to the minimum temperatures as follows. One model included a linear trend in the location parameter (to account for the warming trend) and the other did not have one (using the R package *extRemes*; Gilleland *et al.*, 2009). We found no significant improvement in the model that included the long-term warming trend compared with the model without that trend (likelihood ratio test). Hence, we kept the models without the trend, and by inverting equation 1 we calculated separately for each week of the year the lowest temperature that occurred within 100 years. Along with these low-temperature extremes, the corresponding return periods (time intervals of recurrence of low temperatures) were estimated. For instance, at the beginning of October at the species limit of *Fagus sylvatica*, -1°C is expected to recur every second year; -5°C , however, will recur only every 13 years (Fig. 2). A low-temperature limit of -40°C was chosen because the weather stations (used for temperature reconstruction) were always situated higher than our test sites and none of them have ever recorded temperatures below -40°C during the last 50 years. Return periods longer than 100 years were not considered because, for the species studied, the reproductive cycle is completed in that time. We applied the parametric bootstrap procedure to assess the uncertainty of low-temperature return periods. Namely, the 5th and 95th percentiles of the resulting 100 bootstrapped samples were used as lower and upper confidence boundaries (the range of recurrence) for the return period considered.

Reconstructed temperature conditions during the growing season

The thermal growing season was calculated for each site and each year. Here, we used the growing season defined as the period constrained by a daily mean air temperature above 5°C for more than five consecutive days (spring) and a daily mean temperature below 5°C for more than five consecutive days (autumn; FAO, 1978–1981). Furthermore, monthly mean temperature and monthly mean minimum temperature (mean of the absolute minima of all days per month) across the 50-year reconstruction were calculated for each site.

GDD within the thermal growing season were calculated for each site and each year using

$$\text{GDD} = (T_{\max} + T_{\min})/2 - T_{\text{base}} \quad (2)$$

(Womach, 2005), where T_{\max} is the daily absolute maximum temperature, T_{\min} is the daily absolute minimum temperature, and T_{base} is set to 5°C . Daily minimum temperatures lower than T_{base} were set to T_{base} .

In order to determine a proper estimate of the period during which broad-leaved trees are exposed to critically low temperatures, we extracted leaf unfolding dates for the four species (*S. aucuparia*, *A. pseudoplatanus*, *Fagus sylvatica* and *P. avium*) available within the MeteoSwiss phenological database (<https://gate.meteoswiss.ch/idaweb/>) and within the Pan European phenology database (PEP725, 2012). On average, six observation sites per species (within an elevational belt of ± 150 m of our sites) and 22 years of observation were available. The first and last dates of leaf unfolding were selected and rounded to the corresponding week of the year.

RESULTS

Absolute minimum temperature

The lowest temperatures predicted to occur within ≤ 100 years were -25°C (Western Alps) and -28°C (Eastern Alps) at the uppermost elevational limit of broad-leaved tree taxa (the upper limits of *S. aucuparia*; Table 2). At the lower end of the elevational ranking of the species (for *Q. petraea*), the lowest predicted temperatures were -19°C (Western Alps) and -23°C (Eastern Alps). There was a notable degree of variation in predicted temperature between the three test regions: the coldest temperature experienced was found in Sweden for all species. Lowest temperatures at the same species limit in the Eastern Alps were 4–14 K warmer than in Sweden, and in the Western Alps they were 9–17 K warmer than in Sweden (Table 2, Fig. 2). In other words, the absolute minima were far from being consistent across sites.

Absolute minimum temperature in spring

For each species at its respective upper elevational limit, weekly lowest temperatures (the coldest hour during each week) were very similar between the Western and Eastern Swiss Alps regions in defined, critical spring periods (Table 3, Fig. 2). Moreover, at the northern latitudinal species limits in Sweden the lowest temperatures per week match well with temperatures in the Alps during spring from c. week 17 (23–29 April) onwards, for example lowest temperatures of -6 , -7 and -6°C for *P. avium* in the Western Alps, Eastern Alps and Sweden, respectively.

Across the three test regions, temperatures below the freezing point (0°C) can occur until the end of May for species having the lowest elevational limits (*Q. petraea*, *T. platyphyllos*, *P. avium* and *Fraxinus excelsior*; Table 3). For the same species, leaf-killing temperatures of $-3 \pm 1^{\circ}\text{C}$ (Till, 1956; Liepe, 1993) were predicted to occur until the second week of May. In all three test regions, *Fagus sylvatica* may experience 0°C until the beginning of June and $-3 \pm 1^{\circ}\text{C}$ until the third week of May. At the species limit of *S. aucuparia* and *A. pseudoplatanus*, freezing temperatures (0°C) can occur almost all year long, whereas temperatures of

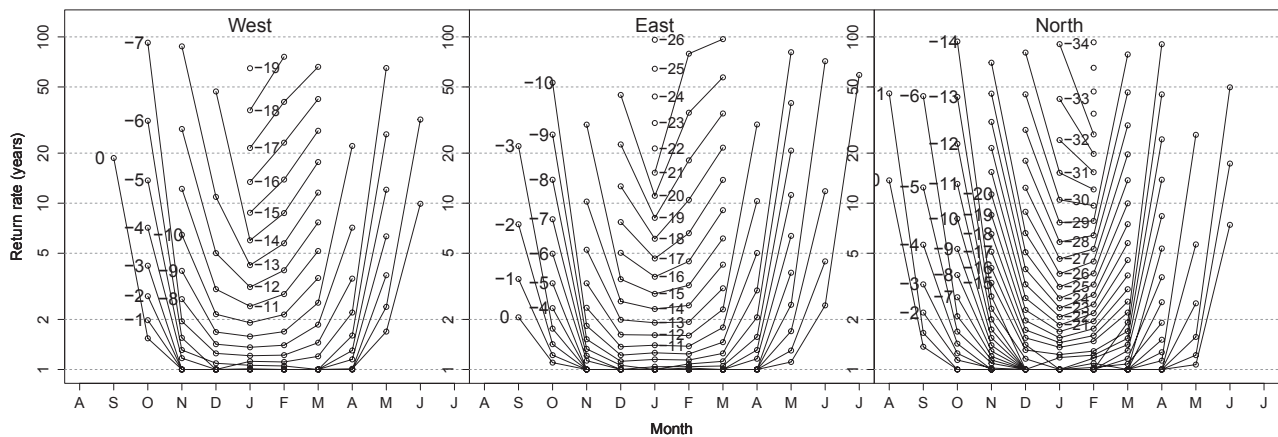


Figure 2 Predicted low-temperature extremes occurring at the limits of *Fagus sylvatica* in the Western Swiss Alps (West), Eastern Swiss Alps (East) and Sweden (North), along with corresponding return periods (time interval of recurrence) of these temperatures.

Table 2 Various measures of the temperature regime at the elevational and latitudinal range limits of seven broad-leaved tree species in the Western Alps (West), Eastern Alps (East) and Sweden (North). Length of growing season (LGS), with minimum length in 50 years in parentheses; growing degree-days (GDD); mean temperature during the growing season (MST); mean temperature during the two warmest months (TWM), all (mean \pm SD) derived from a 50-year dataset (scaled to actual site conditions using our own microclimate data); predicted absolute minimum temperature (AMT) within 100 years; range of recurrence rates (RR); and freezing resistance (LT50).

Species	Region	Reconstructed				Predicted		Measured
		LGS (days)	GDD (> 5 °C)	MST (°C)	TWM (°C)	AMT (°C)	Range of RR (years)	LT50* (°C)
<i>Sorbus aucuparia</i>	West	124 \pm 26 (59)	553 \pm 115	8.9 \pm 0.8	10.0 \pm 1.0	-25	74–104	-43†
	East	135 \pm 28 (61)	622 \pm 160	8.8 \pm 0.9	10.2 \pm 1.2	-28	71–99	
<i>Acer pseudoplatanus</i>	West	170 \pm 31 (106)	1026 \pm 139	10.4 \pm 0.8	12.6 \pm 1.0	-22	62–91	-21 and -40†
	East	150 \pm 34 (76)	742 \pm 172	9.3 \pm 1.0	10.9 \pm 1.2	-27	57–78	
<i>Fagus sylvatica</i>	North	204 \pm 21 (165)	1589 \pm 133	12.5 \pm 0.7	16.2 \pm 1.2	-31	48–75	
	West	206 \pm 34 (147)	1283 \pm 121	10.8 \pm 1.1	14.0 \pm 1.0	-20	50–79	-22
<i>Fraxinus excelsior</i>	East	159 \pm 33 (88)	803 \pm 173	9.9 \pm 0.9	11.7 \pm 1.2	-26	62–90	
	North	196 \pm 22 (143)	1529 \pm 134	12.6 \pm 0.8	16.3 \pm 1.3	-37	57–81	
<i>Prunus avium</i>	West	201 \pm 32 (146)	1250 \pm 117	10.9 \pm 0.9	13.8 \pm 1.0	-20	44–69	-27
	East	214 \pm 30 (142)	1403 \pm 192	11.2 \pm 0.9	14.3 \pm 1.2	-23	73–100	
<i>Tilia platyphyllos</i>	North	192 \pm 22 (140)	1614 \pm 133	13.0 \pm 1.1	16.6 \pm 1.3	-37	42–67	
	West	201 \pm 32 (146)	1250 \pm 117	10.9 \pm 0.9	13.8 \pm 1.0	-20	44–69	-29†
<i>Quercus petraea</i>	East	214 \pm 30 (142)	1403 \pm 192	11.2 \pm 0.9	14.3 \pm 1.2	-23	73–100	
	North	195 \pm 22 (143)	1370 \pm 120	12.0 \pm 0.8	15.3 \pm 1.2	-32	70–98	
<i>Quercus petraea</i>	West	231 \pm 35 (176)	1552 \pm 121	11.1 \pm 1.7	15.3 \pm 1.0	-19	40–67	-34
	East	214 \pm 30 (142)	1420 \pm 195	11.1 \pm 0.9	14.2 \pm 1.1	-23	79–106	
<i>Quercus petraea</i>	West	231 \pm 35 (176)	1552 \pm 121	11.1 \pm 1.7	15.3 \pm 1.0	-19	40–67	-24
	East	214 \pm 30 (142)	1403 \pm 192	11.2 \pm 0.9	14.3 \pm 1.2	-23	73–100	
<i>Quercus petraea</i>	North	207 \pm 27 (165)	1544 \pm 130	12.3 \pm 0.7	16.0 \pm 1.2	-28	54–77	

*Frost resistance of buds in winter, from Till (1956).

†From A. Lenz et al. (2013).

-3 ± 1 °C were predicted to occur until the first week of June across the three test regions.

Temperature conditions during the growing season

In the Alps, the reconstructed mean length of the growing season for 1961–2010 was the longest at the range limit of *Q. petraea* (West: 231 ± 35 , East: 214 ± 30 and North: 207 ± 27 days, mean \pm SD; Table 2) and the shortest for

the limits of *S. aucuparia* (124 ± 26 and 135 ± 28 days, with the single shortest growing season of 59 days within 50 years). For each species, growing season length was very similar across the study regions West, East and North. Excluding *A. pseudoplatanus*, the mean difference within a given species ranged from 11 to 31 days among the three regions. Among species, the sequence of decreasing growing season length (as well as of decreasing GDD) corresponded well with the elevational ranking of species cold limits in the

Table 3 The absolute minimum temperatures per week during spring predicted for the past 100 years at broad-leaved tree species limits in three regions: Western Swiss Alps (West), Eastern Swiss Alps (East) and Sweden (North).

Species	Region	Week of the year													
		12	13	14	15	16	17	18	19	20	21	22	23	24	25
		April			May				June						
<i>Sorbus aucuparia</i>	West	-14	-13	-14	-13	-11	-10	-10	-8	-6	-6	-6	-4	-2	-2
	East	-13	-14	-14	-13	-10	-11	-10	-7	-6	-5	-5	-4	-3	0
<i>Acer pseudoplatanus</i>	West	-12	-11	-11	-10	-8	-8	-8	-5	-4	-3	-4	-1	0	0
	East	-13	-14	-14	-12	-10	-11	-9	-7	-6	-5	-5	-4	-3	0
<i>Fagus sylvatica</i>	North	-19	-11	-11	-9	-8	-4	-3	-3	-2	0	-	-	-	-
	West	-10	-9	-9	-8	-6	-6	-6	-4	-2	-1	-2	0	-	-
	East	-11	-13	-12	-11	-9	-10	-8	-6	-4	-4	-4	-2	-1	-
<i>Fraxinus excelsior</i>	North	-24	-16	-15	-13	-12	-8	-5	-5	-3	-3	-2	0	-	-
	West	-10	-9	-9	-9	-7	-6	-6	-4	-2	-2	-2	0	-	-
	East	-8	-10	-9	-8	-6	-7	-5	-3	-2	-1	-1	0	-	-
<i>Prunus avium</i>	North	-25	-16	-15	-13	-12	-9	-5	-5	-4	-3	-2	0	0	-
	West	-10	-9	-9	-9	-7	-6	-6	-4	-2	-2	-2	0	-	-
	East	-8	-10	-9	-8	-6	-7	-5	-3	-2	-1	-1	0	-	-
<i>Tilia platyphyllos</i>	North	-20	-13	-12	-10	-9	-6	-3	-3	-2	-2	0	-	-	-
	West	-9	-8	-9	-8	-6	-5	-5	-3	-1	-1	-1	-	-	-
<i>Quercus petraea</i>	East	-9	-10	-10	-8	-6	-7	-5	-3	-2	-1	-1	0	-	-
	West	-9	-8	-9	-8	-6	-5	-5	-3	-1	-1	-1	-	-	-
	East	-8	-10	-9	-8	-6	-7	-5	-3	-2	-1	-1	0	-	-
	North	-16	-10	-9	-7	-7	-3	-2	-2	-1	0	-	-	-	-

Numbers in bold indicate periods of bud-break and flushing for those species and regions for which phenological data were available from the Swiss Meteorological Service (MeteoSchweiz; <https://gate.meteoswiss.ch/idaweb/>) and from the Pan European phenology database (PEP725, 2012). All temperatures were predicted to occur within a range of 41–100 years.

Alps provided by Randin *et al.*, 2013): *Q. petraea* > *T. platyphyllos* > *P. avium* > *Fraxinus excelsior* > *Fagus sylvatica* > *A. pseudoplatanus* > *S. aucuparia*. At the cold, high-latitude limits of *Fraxinus excelsior*, *Fagus sylvatica* and *A. pseudoplatanus* in Sweden, the reconstructed GDD during the growing season were always higher (i.e. warmer) compared with corresponding elevational limits in the Western and Eastern Swiss Alps. The reconstructed mean temperature during the growing season (as well as the mean temperature during the two warmest months) was the highest for *Q. petraea* (West: 10.9 °C, East: 10.8 °C and North: 12.1 °C; Table 2) and the coldest for *S. aucuparia* (West and East: 8.9 °C). Notably, among all five species for which a replicate in southern Sweden was available, the mean temperature during the growing season was warmest in Sweden.

All reconstructed monthly mean temperatures were warmest for *Q. petraea* and coldest for *S. aucuparia* (Appendix S3). Finally, monthly mean temperatures in winter (defined here as from December to February) at the species limits were always colder in southern Sweden, and mean temperatures for summer months (defined here as from June to September) were always warmer in Sweden than at the corresponding tree species limits in the Swiss Alps. However, continentality in southern Sweden and in the Alps was approximately the same (continentality index calculated from Ivanov, 1959).

Finally, paired Wilcoxon signed-rank tests showed no significant differences for the mean values of the reconstructed

season length, GDD and the minimum temperature in April and May (coldest hour of the month) when the two regions of the Swiss Alps were compared with each other ($n = 7$ species; all P -values > 0.05), and when the two regions of the Swiss Alps were compared with southern Sweden ($n = 5$ species; all P -values > 0.05). However, significant and marginally significant differences in absolute minimum temperature were found between the two regions of the Swiss Alps ($n = 5$ species; $P = 0.0222$) and between the two regions of the Swiss Alps and southern Sweden ($n = 5$ species; $P = 0.0625$ for both tests). In addition, marginally significant differences were found for the mean temperature of the growing season and the two warmest months when the two regions of the Swiss Alps were compared with Sweden (warmer in Sweden, $n = 5$ species; $P = 0.0625$ for both tests).

DISCUSSION

At the upper elevational and latitudinal limits of five broad-leaved tree species (i.e. of *A. pseudoplatanus*, *Fagus sylvatica*, *P. avium*, *Fraxinus excelsior* and *Q. petraea*), the mean temperatures during the growing season as well as the absolute minimum temperatures (within the past 100 years) revealed strong differences across test regions. Thus, both expressions of temperatures are unlikely to provide an explanation of biogeographical limits. In contrast, similar recurring minimum temperatures during the regional, site-specific period of bud-break were found at both elevational and latitudinal

limits (temperatures below a critical threshold of -3 ± 1 °C). This suggests that freezing events during the sensitive phenological stages in spring exert a significant influence on species limits. Throughout our study we have assumed that the cold limits of tree species at high elevation and at high latitude are constrained by the same temperature-related factor. This assumption is supported by a recent finding by Randin *et al.* (2013) for 18 tree species exhibiting the same relative position when their cold limits along elevational gradients were compared with their limits along latitudinal gradients. Ecotypic differentiation of temperature requirements within the distribution range of tree species has been reported frequently (reviewed in Howe *et al.*, 2003; Savolainen *et al.*, 2007; Körner, 2012); thus, we discuss the potential differentiations among the studied taxa with respect to each of our three measures of critical temperature, as follows.

Absolute minimum temperatures

The lowest minimum temperature (i.e. the absolute minimum) during the period of maximum hardening in winter has often been considered a critical factor for shaping the global distribution of large groups of taxa or plant functional types (Sakai & Larcher, 1987; Woodward, 1987; e.g. for *Rhododendron* species: Vetaas, 2002). However, within our group of temperate deciduous tree taxa, all seven species examined tolerate low temperatures between -22 and -43 °C in winter (Table 2), temperatures that five out of seven species never even closely experienced according to our analysis. Surprisingly, for three out of five species in the Swiss Alps, the lowest annual temperature predicted to occur within a 100-year period was 4–18 K warmer than the known thresholds for freezing damage of fully hardened buds in winter (Table 2; Till, 1956; Tranquillini & Plank, 1989).

Interestingly, in southern Sweden, all studied species experienced temperatures considerably colder than the tolerance thresholds determined in the Alps (Tirol, Tranquillini & Plank, 1989) and in the German lowlands (Göttingen; Till, 1956). Presumably, the northern populations acquired greater freezing tolerance in the dormant state, as was shown for *Picea* species from central Alaska and Ontario and for *Pinus sylvestris* in Scandinavia (reviewed in Parker, 1963; Sakai & Okada, 1971; Savolainen *et al.*, 2011). Because we lack freezing-resistance data from the latitudinal limits of temperate tree species, it remains unclear whether such ecotypic differentiation with regard to absolute minimum temperatures has taken place. We need to assume that it has. However, the species-specific absolute minimum temperatures experienced at the Swedish range limit were still 3 to 8 K warmer than the same species-specific site minima calculated from climatic envelopes for western Eurasia (Manthey & Box, 2007). Hence, although there might be ecotypic differentiation, absolute minimum temperatures at the species limit in Sweden are not sufficiently cold to constrain these species physiologically.

Temperature conditions during the growing season

Global comparisons have shown that the high-elevation limit of the life form 'tree' (the tree line) is related to a common mean temperature of the growing season (Körner, 1998, 2012). A similar correlation has been proposed for temperate deciduous taxa by Chuine (2010), regarding constraints for reproduction. For the Alps, we can exclude reproductive limitations at the range limit (Kollas *et al.*, 2012; Vitasse *et al.*, 2012). In all five species for which a replicate in southern Sweden was available (i.e. *A. pseudoplatanus*, *Fagus sylvatica*, *Q. petraea*, *P. avium* and *Fraxinus excelsior*), the mean temperatures during the growing season and the mean temperatures during the two warmest months were much warmer at their latitudinal limit in Sweden than at their elevational limit in the Alps. Similarly, three out of five species show higher GDD at their latitudinal limit than at their elevational limit. These results suggest that either these species are not limited by temperature during the Swedish growing season or that such expressions of temperature lack predictive value for a comparison of elevational and latitudinal range limits. Because species at their elevational limit are provided with less thermal energy than at their latitudinal limit, we have no proof of ecotypic differentiation towards the mean amount of warmth during the growing season.

In contrast, the species site-specific length of the growing season offered more consistent values for all species at both the elevational and latitudinal limits. For four out of five species (*P. avium*, *Q. petraea*, *Fagus sylvatica* and *Fraxinus excelsior*), the length of the growing season did not show significant variation between the elevational and the latitudinal limit. For the remaining species (*A. pseudoplatanus* has a longer growing season at the latitudinal limit compared with at limits in the Alps), the current position may not be in equilibrium with climate. As shown by Svenning & Skov (2004), Normand *et al.* (2011) and Randin *et al.* (2013) the species has not yet reached its northern cold limit.

Absolute minimum temperatures in spring

During the period of de-hardening and bud-break in spring there is a risk of late freezing events and tissue damage (Sakai & Larcher, 1987). During this period, the active tissue of broad-leaved tree species is damaged at -3 ± 1 °C (Till, 1956; for *S. aucuparia*, -7 °C; Taschler, 2004). In the present study, deleterious freezing temperatures during the period of bud-break (and for several weeks after) were predicted to occur consistently at the upper elevational and latitudinal limits of the four study species for which phenological data were available (i.e. *S. aucuparia*, *A. pseudoplatanus*, *Fagus sylvatica* and *P. avium*).

Effects such as freezing damage in buds, delayed de-hardening and flushing (Liepe, 1993), a reduction of radial growth by up to 90% (Dittmar *et al.*, 2006), reproductive failure and reduced final canopy density (Augsburger, 2009), but also resprouting from secondary buds (Liepe, 1993),

make late frosts highly relevant for the species range limit question. On the positive side, such extreme events may affect herbivore pressure (Inouye, 2000). In the long term, the cost to produce replacement foliage is high, and thus tree fitness may be reduced.

In trees, ecotypic differentiation towards the best timing of growth and dormancy, thus minimizing the risk of cold injury, has often been reported (Langlet, 1971; Lange, 1983). The similar length of the growing season across the cold limit of species suggests that latitude-specific ecotypes have evolved; however, the flushing dates were different across these cold limit locations. The very close operation of phenology and freezing tolerance at the actual, critical temperature regime at all sites in all species suggests that late spring freezing is a decisive factor for the species range limits. Because there is a similarity of growing season length across range limit sites, low spring temperatures and seasonality may be correlated or act interactively. The timing of bud-break (phenology control) is most critical because species hardly differ in freezing tolerance during that developmental phase at the local climatic conditions. Although we attribute a critical role to late spring freezing, the associated selective adjustment of phenology acts to constrain the length of the growing season, and with it the time available to complete seasonal development and tissue maturation (Lenz *et al.*, 2013).

CONCLUSIONS

We conclude that the risk of tissue damage by late spring freezing events at a 41–100 year return rate and, associated with it, spring phenology, are the most likely candidates for controlling the low-temperature range limits of the studied deciduous tree taxa. We cannot exclude a critical decisive trade-off between the resultant season length constraints and the escape from freezing damage in spring. Our data do not suggest a critical role for absolute minimum temperature in winter, nor one of mean temperature during the growing season.

Implications for correlative distribution models

Our findings have important implications for projections of climate change impacts on tree species distribution when using correlative approaches. Our results call for the use of absolute minimum temperatures during key phenological stages when modelling the cold limits of tree species. We thus suggest incorporating seasonal (e.g. monthly) absolute minimum temperatures in correlative modelling studies instead of using long-term means that are only proxies of unknown relevance for the physiologically critical facets of temperature that control tree performance. Because topography (including elevation) has a major influence on life conditions, we also suggest that spatial resolution should be as high as possible when building new temperature-based niche envelopes for predictive purpose (e.g. at a resolution < 100 m). Taken together, these recommendations should allow for a better approximation of the fundamental niche boundaries of tree species at their cold

limits. Given the significance of spring phenology, process-based rather than correlative phenological models need to be employed in order to better determine the interactions between development (phenology), tissue sensitivity to freezing, and the actual temperature regime at species-specific range limits (as for instance provided by Lenz *et al.*, 2013).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Validation of linear models.

Appendix S2 Crown temperature deviations.

Appendix S3 Monthly temperatures at species limits.

BIOSKETCHES

Chris Kollas studied geography and computer science at Humboldt-Universität zu Berlin, Germany. This paper is part of his PhD studies in plant ecology at University of Basel, Switzerland.

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