Do the elevational limits of deciduous tree species match their thermal latitudinal limits?

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ABSTRACT

Aim We compared the upper limits of 18 deciduous tree species with respect to elevation in Switzerland and latitude in Europe. We hypothesized that species would exhibit the same relative positions along elevation and latitude, which can be expected if species have reached their thermal cold limit along both gradients.

Location Europe and Switzerland.

Methods We developed a method to identify a least biased estimate of the elevational and latitudinal cold temperature limits of species and for comparing the relative rank positions with respect to these two limits. We applied an algorithm to calculate the elevation of the potential tree line for each point in the gridded landscape of Europe and Switzerland. For each occurrence of each species, the elevation was extracted from digital elevation models. The vertical distance between the elevation of the potential regional climatic tree line and the uppermost species occurrences was calculated and used for comparisons between elevation and latitude.

Results We found a strong relationship between the thermal latitudinal and elevational distances of species' cold limits to the potential tree line, with only marginally significantly different rank positions (P = 0.057) detected along elevational and latitudinal gradients. A first group of nine species showed very similar thermal distances to the potential tree lines along elevation and latitude. Among these species, eight showed a significant decrease in their elevational limit towards high latitudes across mountainous regions of Europe. A second group of seven species occupied a climatic niche closer to the tree line at the edge of their latitudinal range, and only two species did not fill their thermal niche.

Main conclusions Our study provides support for the common concept of a species range–environment equilibrium. Notably, we did not detect a stronger deviation for the filling of thermal niches at latitudinal limits compared with elevational limits, although the former involves a species covering a much greater geographic distance.

Keywords Climate equilibrium, deciduous trees, elevation, Europe, latitude, leading edge, post-glacial history, Swiss Alps.
The post-glacial migration-lag hypothesis

Although the climate is considered to represent the prime determinant of the distribution of temperate tree species at global to subcontinental scales (Woodward, 1990), historical factors at the continental scale may also affect the ranges of tree species through time-lagged range expansion or more persistent dispersal limitation (Johnstone & Chapin, 2003). Naturalization of tree species or planted trees beyond their native range in Europe indicates the importance of dispersal and establishment constraints or competition effects on the range patterns of tree species. In this context, Svenning & Skov (2004) suggested that the ranges of European tree species may have been affected by dispersal constraints during post-glacial expansion, with the result that many species currently only fill a part of their potential climatic niche, their geographic range or both environmental and geographic spaces.

In contrast to the hypothesized gap between the potential and realized northern latitudinal limits of species, the discrepancy between the realized and potential upper elevational limits of tree species in mountainous regions of central Europe can be expected to be small or null because of the short distance between the core and the upper limit of species elevational distributions. If all species are in equilibrium with the climate, their range limits should exhibit similar rank positions along both elevational and latitudinal temperature gradients. Indeed, tree species should have reached their climatic boundary at least occasionally, with the connecting line between those ‘outposts’ representing the potential range limits set by climatic factors alone. Latitudinal thermal limits that are lower than expected based on elevational thermal limits would suggest a thermal non-equilibrium as well as well a non-equilibrium of the geographic range due to an expansion lag to the north, thus indicating that competitive exclusion, inappropriate soils, pathogens, a poor dispersal capacity, low propagule pressure or disturbance effects must have caused such lags. In contrast, similar latitudinal and elevational thermal limits suggest the existence of a thermal equilibrium that may or may not coincide with the geographic range equilibrium. Hence, for some species, thermal equilibrium might occur despite a non-equilibrium in their geographic ranges.

The climatic and, more specifically, temperature-driven, factors explaining the cold range limits of major deciduous tree species of Europe that do not reach the tree line have not been well studied to date. In contrast, the tree line as a physiognomic boundary had been found to follow surprisingly uniform mean growing season temperatures, despite enormous local variation in its position and nature. This predictability (Körner & Paulsen, 2004; Körner, 2007a) makes the natural tree-line position, along with the associated mean growing season temperature, an ideal biogeographic reference line for performing comparisons and rankings of non-tree-line species limits across latitude and elevation. Although the mechanisms of tree-line formation and the mechanisms responsible for the limits of non-tree-line forming tree species are likely to be different, the elevational and latitudinal tree-line isotherm still provides a bioclimatic boundary against which the position of other species limits can be compared in relative terms.

Although it has been known for years that the elevational and latitudinal range limits of taxa are likely to be correlated (e.g. Humboldt, 1817), a systematic and fact-based assessment of this assumption has not yet been carried out. This study thus aims to first compare the upper elevational limits of 18 deciduous European tree species in mountainous regions of Switzerland and their latitudinal limits in Europe. More specifically, we hypothesize that species exhibit the same rank position along elevational and latitudinal gradients. If the upper and the poleward distribution limit of tree species is mainly controlled by temperature-related drivers, then their regional upper elevation is expected to decrease with latitude. Therefore, the elevational changes in species ranges along latitudinal gradients should follow regular, predictable patterns, paralleling the reduction in tree-line elevation with increasing latitude, which has been described as Humboldt’s law (Humboldt, 1817). Testing this law constitutes a second way of verifying the effect of temperature on the cold limits of trees across latitude and elevation. If our hypothesis is correct, then the regional elevational limits (and its associated temperatures) of all dominant deciduous species will decrease predictably with latitude. Conversely, a latitudinal thermal limit lagging behind the more southern elevational limit would be expected for species that have not yet reached their potential highest latitudinal position because of factors such as large-scale dispersal limitation during post-glacial recolonization from refugia during the Holocene.
**METHODS**

**Comparisons between the elevational and latitudinal limits of broadleaved species**

**Study regions and species**

The study was conducted across a latitudinal gradient in Europe (40°–72° N, 24° W–34° E; Fig. 1a,b) and across an elevational gradient in Switzerland (45°40′–47°50′ N, 5°50′–10°30′ E; c. 41,284 km²; elevation range: 197–2361 m a.s.l.; Fig. 1a).

We selected 18 broad-leaved tree species with wide distribution ranges in Europe (Table 1). Our data on tree distribution in Europe originate from the Level I dataset of the International Co-operative Programme (ICP) on the Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests Level 1; Lorenz, 2010) and from the Global Biodiversity Information Facility (GBIF) database (http://www.gbif.org/). The ICP Forests Level I database contains information on individual trees of every species occurring in predefined plots of 100 m × 100 m. The plots are distributed on systematic national grids of 16 km × 16 km throughout Europe, covering a total of 6046 plots. In addition, we sequentially selected GBIF tree species occurrence data with: (1) geographic positions determined from observations or specimen records alone, and (2) a horizontal uncertainty of the geographic coordinates of < 100 m. The precision of the geographic coordinates (as defined in Chapman, 2005) was estimated with custom codes in R version 2.12.2 (R Development Core Team, 2011) by taking into account the number of decimal digits of latitude and longitude and the position on the earth using the harvesine formula. The occurrences of each species across Europe were visually inspected with a GIS and compared with georeferenced distribution maps provided by Meusel et al. (1964) to check for consistency with expert knowledge. Ultimately, we only considered Continental, Boreal and Arctic biogeographic regions of Europe (http://www.eea.europa.eu/data-and-maps/data/biogeographical-regions-europe-2008) in our analysis and therefore excluded Atlantic, Alpine, Steppic and Mediterranean biogeographic regions (Fig. 1a). We removed the Atlantic regions to exclude the upper limits of tree species controlled partly by a mild climate generated by ocean streams and not by climate alone. This was performed to improve comparisons between Fennoscandia and Switzerland, as suggested by the results reported by Grace (1997). We also excluded Alpine regions of Europe because we wanted to exclude the regions where the effect of elevation would be strongest and to capture the most northern limits. Finally, we did not consider Mediterranean and Steppic regions to avoid the influence of drought on species limits.

![Figure 1](image-url) Location of the regions considered in the analyses. (a) Biogeographic regions (Continental, Boreal and Arctic in dark grey) and observations (black dots) included across latitudes in Europe. (b) Mountainous regions of Europe (Alpine biogeographic regions; in dark grey) selected to test the elevation-for-latitude hypothesis (including observations along elevation in Switzerland). Conceptual views of the two analytical designs employed to compare the upper elevational limits of the 18 deciduous European tree species in the mountainous regions of Switzerland with their latitudinal limits in northern Europe (c; data from a) and to verify the elevation-for-latitude correspondence model (d; data from b).
Table 1 Ranking of the 18 species based on the thermal distance between the species elevational (on the extreme left of the table) and latitudinal (on the extreme right) cold limits and the potential regional climatic tree line. The thermal distance is expressed in kelvin. The scientific names follow the nomenclature of the Atlas Florae Europaeae (Lahti & Lampinen, 1999).

<table>
<thead>
<tr>
<th>Thermal distance (K)</th>
<th>Error (K)</th>
<th>Species</th>
<th>Ranking</th>
<th>Latitude (Europe)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.6</td>
<td>0.4</td>
<td>Sorbus aucuparia L.</td>
<td>1</td>
<td>Sorbus aucuparia L.</td>
</tr>
<tr>
<td>3.7</td>
<td>0.4</td>
<td>Acer pseudoplatanus L.</td>
<td>2</td>
<td>Populus tremula L.</td>
</tr>
<tr>
<td>4.3</td>
<td>0.4</td>
<td>Betula pendula Roth.</td>
<td>3</td>
<td>Ulmus glabra Huds.</td>
</tr>
<tr>
<td>4.3</td>
<td>0.4</td>
<td>Sorbus aria (L.) Crantz</td>
<td>4</td>
<td>Betula pendula Roth.</td>
</tr>
<tr>
<td>4.5</td>
<td>0.4</td>
<td>Fagus sylvatica L.</td>
<td>5</td>
<td>Acer platanoides L.</td>
</tr>
<tr>
<td>4.8</td>
<td>0.4</td>
<td>Ulmus glabra Huds.</td>
<td>6</td>
<td>Tilia cordata Mill.</td>
</tr>
<tr>
<td>4.9</td>
<td>0.4</td>
<td>Populus tremula L.</td>
<td>7</td>
<td>Quercus robur L.</td>
</tr>
<tr>
<td>5.2</td>
<td>0.4</td>
<td>Fraxinus excelsior L.</td>
<td>8</td>
<td>Fraxinus excelsior L.</td>
</tr>
<tr>
<td>5.5</td>
<td>0.4</td>
<td>Acer platanoides L.</td>
<td>9</td>
<td>Acer pseudoplatanus L.</td>
</tr>
<tr>
<td>5.8</td>
<td>0.4</td>
<td>Prunus avium L.</td>
<td>10</td>
<td>Fagus sylvatica L.</td>
</tr>
<tr>
<td>6.1</td>
<td>0.4</td>
<td>Tilia platyphyllos Scop.</td>
<td>11</td>
<td>Prunus avium L.</td>
</tr>
<tr>
<td>6.5</td>
<td>0.4</td>
<td>Quercus petraea Liebl.</td>
<td>12</td>
<td>Quercus petraea Liebl.</td>
</tr>
<tr>
<td>6.6</td>
<td>0.4</td>
<td>Tilia cordata Mill.</td>
<td>13</td>
<td>Tilia platyphyllos Scop.</td>
</tr>
<tr>
<td>6.7</td>
<td>0.4</td>
<td>Quercus pubescens Willd.</td>
<td>14</td>
<td>Sorbus aria (L.) Crantz</td>
</tr>
<tr>
<td>7.2</td>
<td>0.4</td>
<td>Quercus robur L.</td>
<td>15</td>
<td>Ostrya carpinifolia Scop.</td>
</tr>
<tr>
<td>7.7</td>
<td>0.4</td>
<td>Carpinus betula L.</td>
<td>16</td>
<td>Carpinus betula L.</td>
</tr>
<tr>
<td>7.8</td>
<td>0.4</td>
<td>Castanea sativa Mill.</td>
<td>17</td>
<td>Castanea sativa Mill.</td>
</tr>
<tr>
<td>9.2</td>
<td>0.5</td>
<td>Ostrya carpinifolia Scop.</td>
<td>18</td>
<td>Quercus pubescens Willd.</td>
</tr>
</tbody>
</table>

In Switzerland, we used data from the Swiss National Forest Inventory (NFI) from two inventory periods, in which sampling was performed during the years 1983–85 (NFI1) and 1995–97 (NFI2) in a regular 1-km grid for NFI1 or 1.4-km grid for NFI2. Additional tree occurrence data in Switzerland were derived from the forest plots database (Wohlgemuth, 1992). This procedure resulted in a total of n = 21,634 observations for the selected biogeographic regions of Europe (excluding Switzerland) and n = 22,130 observations for Switzerland.

Calculating the potential climatic tree line as a cold limit reference

Here, we present a method for obtaining a least-biased estimate of the elevational and latitudinal cold temperature limits of broad-leaved tree species and for comparing the species rankings between these two limits. We first calculated the elevation of the potential tree line for each cell in a gridded landscape (30° × 30° or c. 1 km × 1 km for Europe and 25 m × 25 m for Switzerland) using a custom code within the R environment. For Europe, we employed geographic layers of monthly mean temperatures and the digital elevation model (DEM) of the WorldClim dataset (version 1.4; http://www.worldclim.org; Hijmans et al., 2005). For Switzerland, we used monthly mean temperature layers derived from the national meteorological networks of Switzerland (MeteoSwiss; computation methods are described in Zimmermann & Kienast, 1999) and a DEM from Swisstopo (see further details below). In each cell, we derived daily values from monthly temperature values with the aspline function of the akima library in R. These daily values were then projected for elevations ranging from 0 to 5000 m a.s.l. at 10-m lapse rates derived from mowing windows of 5 km × 5 km around the focal cell. The position of the potential climatic tree line was finally defined based on the combined effect of a minimum length of the growing season of 94 days (constrained by the first and last transition of a weekly average daily mean air temperature of 0.9 °C) and a mean air temperature during that period of at least 6.4 °C (Körner et al., 2011).

Finally, for each occurrence in Europe, the elevation was extracted from a 100 m × 100 m DEM built from the 90-m SRTM DEM (version 4.1) and the 30-m ASTER global DEM (GDEM) (north of 60° N). The elevation of tree occurrences in Switzerland was extracted from the 25-m DEM of Switzerland (from the Federal Office of Topography).

For each species, the difference (i.e. the vertical distance in metres) between the elevation of the potential regional climatic tree line and the elevation of each observed occurrence was calculated for Europe and Switzerland (Fig. 1c). Only the 0% to 5% quantiles (with 0.5% increments) of these distances were tested in further analyses. Here, the 0% quantile of a species represents the single occurrence that is closest to the potential climatic tree line. Because elevation, as such, is meaningless for plants, we express this position as a thermal distance in kelvin, rather than in metres. We chose a lapse rate of 0.55 K for a vertical distance of 100 m to the potential climatic tree line.

The relationship between the corresponding thermal distances to the potential climatic tree lines in Switzerland and in
Europe was tested using Pearson correlation tests for each quantile. This correlation between the thermal distances to elevational and latitudinal tree lines was significant for all quantiles tested (0% to 5% quantiles: $P$-values < 0.05), with the correlation for the 2.5% quantile being the highest. We therefore based further analyses of the ranking of species using the 2.5% quantile. Because the uppermost limits of tree species are likely in equilibrium with the climate along elevation gradients, we chose the elevational thermal distance to the potential tree line as a reference, and we tested whether the rankings from the latitudinal distribution limits corresponded to those from the elevational limits.

The latitudinal records corresponding to the 2.5% quantile were located at the northern cold limits of all species (see Appendix S1 in Supporting Information).

### Estimation of error in the analytical framework

We estimated the potential error accumulating from different sources when calculating the distance to the potential tree line, and we obtained the error sum from three main components:

$$
\epsilon_{\text{Total}} = \epsilon_{\text{DEM}} + \epsilon_{\text{Elevation range within plots}} + \epsilon_{\text{Tree-line model}}.
$$

The first source of error ($\epsilon_{\text{DEM}}$) originates from the vertical error of the DEM from which the plot elevation was extracted in Switzerland and in Europe. The vertical error of the 25 m × 25 m DEM in Switzerland is 8 m in mountainous regions (http://www.swisstopo.admin.ch/internet/swisstopo/fr/home/products/height/dhm25.html). The 100 m × 100 m DEM of Europe is a combination of the SRTM90 (90 m × 90 m; up to 60° N) and the ASTER GDEM (30 m × 30 m; from 60 to 83° N) resampled at a 100 m × 100 m resolution. ASTER has an estimated accuracy of 20 m at a 95% confidence level for vertical data, whereas the vertical absolute height error should be less than 16 m for 90% of the data in the SRTM DEM (Rodríguez et al., 2005). Here, we took the value of 20 m, corresponding to the accuracy of the ASTER DEM.

The second error component ($\epsilon_{\text{Elevation range within plots}}$) is an estimate of the range of elevations from the DEM that can be observed within a typical plot (plus the location error) from which tree occurrence data were extracted. Here, we first generated buffers with a radius of 100 m for Europe and 25 m for Switzerland. This corresponds to the maximum error generated based on the precision of the coordinates in Europe and the sum of the error of from the GPS (or from map) and of the plot size in Switzerland (c. 10 m + 10 m, rounded to 25 m so that it corresponds to a shift of one pixel in each direction from the measured coordinates). We then extracted the minimum and maximum elevation values within the buffers around the plots for both Europe and Switzerland and summarized these values at a mean species-specific range. These ranges vary between 4 and 15 m in Switzerland and 4 and 12 m in Europe among the species included in the analysis.

The third error component ($\epsilon_{\text{Tree-line model}}$) corresponds to the vertical mismatch in elevation provided by the potential tree-line model. This was evaluated at < 50 m (with data from Paulsen & Körner, 2001). The sum of the three components was then converted to kelvin with the same lapse rate of 0.55 K/100 m as was used previously.

### Testing the elevation-for-latitude temperature model

#### Study regions and species

For this analysis, we used the same species occurrence dataset as for the previous analysis at the European scale. However, only mountainous regions of Europe were considered, and Swiss occurrences from mountainous regions were combined with the European dataset to include all parts of the Alps (Fig. 1b,d). These regions were selected by extracting the species occurrences within the Alpine biogeographic regions of Europe (European Environment Agency, 2008).

#### Statistical analyses

Latitude and elevation from the 100-m DEMs were first extracted for each occurrence. Next, the maximum elevation observed for each species was recorded from 41 to 71° N within 0.5° intervals. Finally, the elevation was regressed as a function of the latitude for each species with linear regressions. Here, we hypothesized that the maximum elevation reached by a species for a given latitude decreases towards its northernmost limit in a linear and predictable manner because the upper northernmost limit is controlled mainly by temperature (Fig. 1d).

### RESULTS

We detected a strong relationship ($R^2 = 0.65$; $P$-value < 0.001; Fig. 2) and a marginally significant difference (paired $t$-test, $P$-value = 0.057, d.f. = 17) between the thermal latitudinal and elevational distances of species cold limits. In addition, we found a strong and very significant relationship between the rank positions of species along the elevational and latitudinal gradients ($p = 0.620$; $P$-value = 0.007). The thermal distance in kelvin to the tree line was often smaller in the north, along latitude (12 species), than in the Alps, along elevation (six species). *Sorbus aucuparia* was found to be the closest species to the potential climatic tree line at both elevation and latitudinal limits (Table 1).

We distinguish three groups of species in our comparison between elevational and latitudinal rankings (Fig. 3). A first group consisting of half of the studied species (*Sorbus aucuparia, Acer pseudoplatanus, Betula pendula, Fagus sylvatica, Fraxinus excelsior, Prunus avium, Carpinus betulus, Castanea sativa* and *Tilia platyphyllos*; Table 2) showed very similar thermal distances to the potential climatic tree line at high elevation and high latitude (absolute difference between elevational and latitudinal distances < 1.2 K). The first five of these nine species, together with *T. platyphyllos*, showed a significant decrease in their maximum elevation limits with increasing latitude across the mountainous regions of Europe (Table 2;...
Figure 2. Relationships between the 2.5% quantile of the distance from the potential regional tree line (elevation difference expressed in kelvin) for the 18 species in Europe and the Swiss Alps (Pearson correlation coefficient 0.652; P-value 0.002). The dashed line represents perfect agreement between elevational and latitudinal distances. Horizontal and vertical error bars represent the cumulative error (described by equation 1) of the distance to the tree line along elevation and latitude.

Figure 3. Thermal distances (in kelvin) to the potential regional tree line along elevation and latitude (based on the 2.5% quantile of occurrences located at the northern cold limits of all species). Species are ranked according to their elevational distance. Absolute differences (Δ, in kelvin) between elevational and latitudinal distances are indicated on the left. Horizontal error bars represent the cumulative error (described by equation 1) of the distance to the tree line along elevation (black lines) and latitude (grey lines). We only show the more robust 2.5% quantile of species distribution data, hence this model does not depict the uppermost/northernmost tree positions of a species.
Historic and dispersal limitations

Numerous authors have stressed that large-scale current plant species distribution ranges may be strongly controlled by large-scale historical constraints, in addition to being controlled by the climate (McGlone, 1996; Hewitt, 1999; Ricklefs, 2004). More specifically, by combining atlas data with distribution models, Svenning & Skov (2004) showed that the majority of European tree species appear to be filling less than 50% of their potential climatically suitable range. They attributed this low range filling to large-scale dispersal limitations on post-glacial recolonization from ice age refugia. In particular, the following potential range-filling percentages were given for five of our study species: *Castanea sativa* (14.4%), *Carpinus betulus* (68.5%), *Fagus sylvatica* (73.7%), *Quercus petraea* (83.3%) and *Betula pendula* (92.8%). With the exception of *B. pendula* (which appears to fill its range), we observed comparable coverage of the thermal niches of these species at the latitudinal and elevational range limits, and therefore, we did not detect thermal non-equilibrium at the edges of their latitudinal ranges. Hence, these species may exhibit geographic ranges that are not in equilibrium, despite being at thermal niche equilibrium. However, in their study Svenning & Skov (2004) used minimal rectilinear envelopes to define the potential suitable niche of the investigated species, which artificially inflated the size of the potential suitable habitats over Europe. In addition, this type of modelling approach assumes...
that there is no interaction between the bioclimatic variables considered in the determination of species potential range limits.

In line with our results, the presence of cryptic refugia in northern, central and eastern Europe, as proposed by Birks & Willis (2008), may have provided an ideal basis for rapid spreading of these trees from microrefugia during the Holocene. For instance, the available combined palaeobotanical and molecular data for F. sylvatica suggest that its main spreading occurred from populations in central and eastern Europe, rather than from major refugia south of the Alps (Magri et al., 2006). By measuring the patterns of covariation between species assemblages (instead of the ratio between observed and modelled distributions, as used by Svenning and Skov in 2004), Araújo and Pearson (2005) obtained results that also support the hypothesis that plants are often more mobile than is conventionally thought. However, and in defence of Svenning & Skov’s (2004) approach, we only tested the general distance from regional upper limits to the potential tree line in each region. We did not test whether an identical or an even more advanced cold limit compared to that found in the north is actually achieved over larger areas or if such a limit occurred along a single population front or only in particular regions, with long dispersal events producing outlier populations (Cain et al., 2000). Still, our results demonstrate that species that have reached their elevational or latitudinal cold limits may be at thermal equilibrium, at least in some parts of their geographic distribution range in both Europe and the Swiss Alps. More recently, Svenning et al. (2010) found broad support for the effect of accessibility (i.e. distance from glacial refugia) in explaining current local species richness. They concluded that local tree assemblages in Europe often fail to realize a large proportion of their potential richness, partially reflecting geographic, historical and environmental circumstances such as fragmentation and accessibility to recolonization. Further analyses should identify the geographic regions and the drivers of such thermal disequilibrium (see examples of such analysis in Ohlemüller et al., 2012).

Based on our analysis, geographic barriers or dispersal and recruitment limitations may explain the lagging thermal positions of S. aria and Quercus pubescens. For the latter species, Svenning & Skov (2004) observed potential range filling of only 49.6%, in agreement with our results. Geographic barriers such as edaphic conditions could be one explanation for the findings regarding Q. pubescens because this species grows mostly on limestone (Rameau et al., 1989; Lepais & Gerber, 2011). Additionally, it has been reported that Q. pubescens exhibits a poor ability to survive in pine understoreys (Kunstler et al., 2004), which suggests that forest management and interspecific competition could also have modified its high-latitude limits. Ultimately, comparing the seed dispersal vectors of the 18 species, S. aria and Q. pubescens are the two species that may lack an obvious vector (humans or birds) that could have accelerated their spread over long distances, especially over fragmented habitats. Sorbus aria has non-persistent fruits that fall to the ground when ripe (Herrera, 1989) and therefore might not benefit as much as S. aucuparia from birds as agents of seed dispersal.

Regional edaphic conditions could also explain the lower thermal limit of Q. robur observed in Switzerland and the important difference of 2.7 K between its high-elevation limit in the Swiss Alps and high-latitude limit in northern Europe (see Table 1).

Other potential causes of mismatches observed between Europe and the Alps

Although we generally found good agreement between the two distribution limits, elevation and latitude do not appear to represent perfect analogues. Climatic gradients exhibit steeper rates of change along horizontal transects in mountain regions than along latitude (Billings, 1973). Important environmental factors, such as precipitation, cloudiness, the length of the growing season, the snowpack and seasonal temperature extremes, may also lead to different patterns and trends in relation to increasing elevation and latitude (Billings, 1973; Körner, 2003). Although oceanic regions were excluded from the European datasets for the latitude versus elevation comparisons, the climate in Switzerland is driven by different weather systems from those affecting the climate in the north (representing non-analogous climates). In our analysis, we applied the same adiabatic lapse rate to elevation and latitude for a given distance to the tree line expressed as a difference in elevation, which could be a source of bias (although records from weather stations show similar lapse rates). In addition, the thermal range is compressed to a smaller zone, and the distance between the edges and the optimum of a species distribution is shorter along elevation in mountain ranges (Körner, 2003). Overall, in mountainous regions, the available land area rapidly decreases with increasing elevation (Körner, 2007b). In summary, steeper climatic gradients acting jointly with the decreasing available land area towards higher elevations may actually increase competition among species and prevent the less competitive tree species from fully filling their thermal niches in mountain regions.

We based our rankings and comparisons on the assumption that the same mechanisms control the upper and poleward distribution limits of tree species and that species limits are related to a temperature variable that exhibits a similar relationship to tree-line temperature conditions. In fact, this may not be entirely true, and there are several potential reasons for why we obtained similar but marginally significantly different rank positions. For instance, if the minimum annual temperature is the key factor controlling the cold distribution limit of a given species, the relationship of this factor with the growing season temperature along a latitudinal gradient versus an elevational gradient in the Alps would be affected. As a consequence, tree species with wide distribution areas might have adapted differentially to the local growing conditions in different parts of their range (savolainen et al., 2004). Therefore, although the rank order for most species might be similar, we can also expect systematic discrepancies from this pattern that would arise where the cold limits of tree species are not determined by the same mechanisms as are responsible for the tree line as a biome
boundary. Thus, latitudinal limits that are lower than expected from the elevation limits do not necessarily suggest expansion lags to the north.

Cold thermal species limits may also be controlled by thermal extremes and be less correlated with the temperature means adopted from climate databases to calculate the potential climatic tree line. Such an effect of extremes in modifying the distribution patterns of trees has been demonstrated in a recent study (Zimmermann et al., 2009). Additionally, the deviation between means and extremes will probably be larger in continental than in oceanic climates and different in the north of Europe compared with the Swiss Alps.

Macroclimate, edaphic conditions and intraspecific competition represent plausible explanations for the lower thermal limits of species in the Swiss Alps. However, we cannot exclude the effect of long-term and human management in the Alps, despite the fact that our results are based on presence data and the highest occurrences recorded along elevation. Finally, we cannot exclude the effects of strong elevational variations across the biogeographic regions selected for our analysis (high mountains falling at the cold limits of our species), combined with under-represented areas in our occurrence dataset.

**Implications for climate-based distribution models**

Our findings have important implications for projections of the impacts of climate change on plant species using correlative approaches [e.g. species distribution models (SDMs); see Guisan & Thuiller, 2005]. Such models generally rely on the ‘equilibrium assumption’, i.e. that a species’ climatic niche can be estimated from its geographic distribution (Guisan & Zimmermann, 2000). Here, we showed that the validity of this assumption, at least for thermal equilibrium, varies across our study species and between elevation and latitude. We found the assumption to be clearly supported for nine species. However, for seven species, this assumption might only be met across latitudes, and the assumption is clearly violated for two species. Thuiller et al. (2004) showed that restricting the environmental range of data strongly influences the estimation of response curves in SDMs, especially towards upper and lower distribution limits along environmental gradients. If some species are not at thermal equilibrium at their cold limits, as suggested by our results for nine species, it may lead to more conservative scenarios in terms of changes in distribution projections.

**CONCLUSION**

Our results demonstrate that half of the studied tree species have reached the thermal limits of their northern latitudinal (polarward) temperature niches compared with their elevational niche limits following post-glacial recolonization, even when evidence suggests that they exhibit geographic ranges that are not in equilibrium. These results further provide a quantitative test of the common assumption of a species range–environment equilibrium that is generally applied as a prerequisite assumption for climate change projections using species distribution models.

While most of the remaining species come closer to filling their thermal niches in the north than in the Alps, we found two species that appear to clearly lag behind in filling their thermal niches in the north compared with the Alps (Sorbus aria, Quercus pubescens).

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**REFERENCES**


**SUPPORTING INFORMATION**
Additional supporting information may be found in the online version of this article at the publisher’s web-site.

**Appendix S1** Observation points corresponding to the 2.5% quantile of the thermal distance to the potential tree line.

**BIOSKETCH**
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Author contributions: C.F.R., Y.V., C.K. and N.E.Z. conceived the idea and designed the study concept; T.W. provided the Swiss biodiversity data; J.P. contributed the tree-line model; C.F.R., Y.V., C.K. and C.Kol. contributed to the data analysis and drafting; and C.F.R. led the writing.

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