ESSAY REVIEW

Where, why and how? Explaining the low-temperature range limits of temperate tree species

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Summary

1. Attempts at explaining range limits of temperate tree species still rest on correlations with climatic data that lack a physiological justification. Here, we present a synthesis of a multidisciplinary project that offers mechanistic explanations. Employing climatology, biogeography, dendrology, population and reproduction biology, stress physiology and phenology, we combine results from *in situ* elevational (Swiss Alps) and latitudinal (Alps vs. Scandinavia) comparisons, from reciprocal common garden and phytotron studies for eight European broadleaf tree species.

2. We show that unlike for low-stature plants, tree canopy temperatures can be predicted from weather station data, and that low-temperature extremes in winter do not explain range limits. At the current low-temperature range limit, all species recruit well. Transplants revealed that the local environment rather than elevation of seed origin dominates growth and phenology. Tree ring width at the range limit is not related to season length, but to growing season temperature, with no evidence of carbon shortage. Bud break and leaf emergence in adults trees are timed in such a way that the probability of freezing damage is almost zero, with a uniform safety margin across elevations and taxa. More freezing-resistant species flush earlier than less resistant species.

3. *Synthesis*: we conclude that the range limits of the examined tree species are set by the interactive influence of freezing resistance in spring, phenology settings, and the time required to mature tissue. Microevolution of spring phenology compromises between demands set by freezing resistance of young, immature tissue and season length requirements related to autumnal tissue maturation.

Key-words: biogeography, climate, elevation, evolution, freezing resistance, fundamental niche, latitude, phenology, plant–climate interactions

Introduction

Organisms inhabit certain habitat types and do not expand beyond specific geographical boundaries. There are a multitude of potential reasons for such boundaries. Where on the planet certain organisms can thrive and how they manage to do so is one of the key questions in biology. Understanding their range limits is commonly most instructive for explaining organisms' environmental demands. Distribution maps and correlations with presumed environmental drivers may provide proxies of likely controls (Austin & Van Niel 2011), but they do not yield mechanistic explanations, and may match

certain drivers by coincidence (Higgins *et al.* 2012a). For instance, no biological process has been identified that could causally be linked to mean annual temperature (MAT), but MAT is often used in species distribution models (SDM), sometimes yielding seemingly meaningful correlations (Thomas *et al.* 2004; Thuiller *et al.* 2005) that lack a mechanistic foundation.

The two dominant global climatic drivers of plant distribution are temperature and water availability. Both act in a gradual as well as a threshold manner. Gradual responses affect growth and development either directly or via the length of the growing season. In contrast, threshold responses (e.g. responses to extremes) decide over 'to be or not to be'. Threshold responses are clear-cut with regard to temperature,

because both heat and low-temperature resistance are associated with abrupt cell disorder over a very narrow range of temperatures. Once a threshold has been exceeded, the affected tissue is dead, so there is no dose effect. However, at a whole-plant level, there may still be a dose effect in the sense that the frequency of the loss of sensitive tissue may affect survival, growth and regeneration rates. Hence, for threshold analyses, recurrence rates and the fraction of tissue lost are important. This project explored the mechanisms behind low-temperature limitations. The warm, often drought-associated limits would be another task (e.g. Jump, Hunt & Penuelas 2006).

All species on earth find a low-temperature range limit, beyond which their specific thermal requirements are not met. The most prominent of these are the limits of angiosperm life at the edge of polar or high-elevation deserts, or the upper or polar limit of the life-form 'tree', the so-called alpine or arctic treeline. While these limits are reasonably well understood (Körner 2003a, 2011, 2012), the range limits of tree taxa that do not reach the alpine or arctic treeline (i.e. the majority of taxa) are largely unexplained. While it is obvious that there is some sort of thermal limitation (e.g. Humboldt & Bonpland 1807; Whittaker 1975; Hulten & Fries 1986; Woodward 1990; Loehle 2000; Mellert *et al.* 2011), the very nature of that limitation and the biological processes involved remain unresolved. In the past, correlative approaches have been used to explain the range limits of individual tree species, and only a few studies have attempted a process-based approach so far (e.g. models by Chuine 2010; Morin, Augspurger & Chuine 2007). Some even employ carbon relation-related models (e.g. Higgins, O'Hara & Römermann 2012b), although no species has ever been shown to reach a range limit because of C shortage (Körner 2003a,b, 2015). Thus, no mechanism-based theory, founded upon empirical data, has emerged to date (Dormann *et al.* 2012).

CORRELATIVE APPROACHES AND ENVIRONMENTAL NICHES OF SPECIES

There is a rich literature on the correlation of species range limits with various measures of temperature. The classical example is Iversen's (1944) fitting of mean winter isotherms with the range limit of broad-leaved temperate evergreen species (for a recent update see Walther, Berger & Sykes 2005). A nice example for other life-forms is the study by Mourelle & Ezcurra (1996) in cacti. Among the many attempts that have linked range limits of temperate deciduous taxa with climatic proxies, we refer to Sykes (1996), Ohsawa & Nitta (2002), Manthey & Box (2007) and Rabasa *et al.* (2013) as important studies. These researchers explored best-fit measures of mean temperatures over large geographical scales. Others assumed critical thresholds such as winter minima (Gloning, Estrella & Menzel 2013) or interannual variability of winter temperature (Zimmermann *et al.* 2009) and again find correlations. Correlative data have been used to also project the future geographical position of species range limits in a 'space for time' approach, using climate and species distri-

bution archives or morphological plant traits, the actual functional meaning of which remained unproven (e.g. Gegout 2005; Thuiller *et al.* 2006; Bellard *et al.* 2012; Buckley & Kingsolver 2012; Amano *et al.* 2014; Stahl, Reu & Wirth 2014). A major limitation of these approaches is the assumption that weather station derived data reflect what plants actually experience, which is clearly not the case in low-stature plants (Scherrer, Schmid & Körner 2011), thus leading to rather mislead conclusions, particularly when topography is considered (Halbritter *et al.* 2013, see discussion in Austin & Van Niel 2011). Given their aerodynamic coupling to the free atmosphere, there is more hope that this assumption is valid in trees, as will be shown here.

Knowing the actual drivers and responses is essential for departing from probabilistic and correlative descriptions and moving towards mechanism-based definitions of range limits (Purves 1989; Way & Oren 2010; Savage & Cavender-Bares 2013). By mechanism, we mean the physiological processes decisive for survival. For instance, the inclusion of extreme temperatures instead of means improves predictions of tree distribution (Zimmermann *et al.* 2009), with the exact mechanisms remaining unclear.

The actual species distribution and range limits cannot be explained by climate alone (e.g. Hampe 2004; Svenning & Skov 2004). Species never occupy the full geographical range they would, if climate were the only external driver (their fundamental niche). As a consequence, species are geographically absent from certain terrain for reasons related to (i) biotic interactions (competition, pathogens, herbivory, lack of symbionts); (ii) disturbances, ranging from windthrow, fire, flooding, erosion, lack of suitable substrate to human action; and (iii) dispersal limitations, related to habitat connectivity or seed and vector traits. Hence, the realized niche of species occurrence is largely unpredictable from a process viewpoint. This is the reason why this project aimed at explaining the low-temperature edge of the fundamental niche of deciduous tree species, and not the range limit as a whole. Yet, when employing a fundamental niche concept, we need to assume that the niche boundary can be identified and had been conserved in space and time (e.g. Huntley 1989; Randin *et al.* 2006; Pearman *et al.* 2008). Palaeorecords appear to support niche conservation for dominant European trees. Empirical SDMs trained on current distribution data were successfully projected backwards in time and predicted the past (6 ky BP) distribution ranges of dominant species when tested against pollen data. Likewise, SDMs trained on pollen data (6 ky BP) successfully predicted the current distribution range of dominant tree species (Pearman 2008).

Our basic assumption in this study is that each species may reach positions in the landscape, where disturbances, interactions with other species and historical effects are not masking low-temperature controls, that is, positions, where the species' physiological constitution sets the absolute limit for growth and successful reproduction. As rare as such locations may be, these are the most promising places to explore the state and causes of the low-temperature boundaries of the funda-

mental species niche. Individuals at such outpost positions are nature's experimental field for adaptation and fitness testing, and we are exploring the outcome of this 'experiment'.

DEFINITIONS

Distinguishing various measures of temperature is essential to disentangle physiological temperature effects. In the following, we will address temperatures as means, when hourly sampled data have been averaged over defined periods of time (days, month, season). When we address temperature minima, these are absolute minima, that is the single lowest hourly record during a day, a month or a year. With this definition of minimum, we account for the very nature of the action of freezing temperatures on plants. We will not employ 'mean minima' (e.g. for a month) because there is no biological meaning associated with this term. Yet, as with earthquake risk, it is not the mean probability, but the actual occurrence of an event that matters. Hence, when we wish to address the frequency of low-temperature stress, we are using probability expressions such as recurrence rate (in terms of numbers of years). As is common in bioclimatology, we will use °C for temperatures and the Kelvin (K) for temperature differences to avoid confusion between the two, and we will use 'elevation' for the position of plants above sea level and will restrict the use of 'altitude' to free atmosphere conditions only (McVicar & Körner 2013).

'Phenology' is (i) a dynamic plant state; (ii) a type of physiological response; and (iii) a scientific discipline that studies 1 and 2. In the current context, we view tree phenology as the visible expression of developmental (physiological) stages that run under genetic control, modulated by the environment. The underlying genetic and hormonal signals control the seasonal progression of plant growth, reproduction and stress resistance.

The term 'stress' is often used for any departure from optimality. Because plants do not normally grow under physiologically optimum conditions (e.g. in a nutrient solution), such a wide definition makes the term meaningless and it becomes a synonymous for everyday life of plants. Here, we refer to gradual restrictions of growth in the physiological range as 'limitation' (sometimes termed 'eu-stress'), while we apply 'stress' for exceptionally severe, damaging influences (pathological effects, 'dis-stress'; Kranner *et al.* 2010).

A FRAMEWORK TO STUDY THE CAUSES OF SPECIES DISTRIBUTION

Any study of species range limits must answer four basic questions (Fig. 1): Where are the limits of the fundamental niche? What are the life conditions at such limits? Why can tree species not thrive beyond these range limits? and How do climatic conditions physiologically influence tree species at these range limits? Aiming at answering these questions for low-temperature range limits, we first assessed the geographical position of the species' range limit and the climatic conditions trees experience at that limit. We searched for outpost positions at high elevation in the Swiss Alps and at high latitude in Scandinavia (the closest approximation of the fundamental niche boundary). Should a species have reached the same relative (rank) position along elevation and latitude, it can be expected to have reached its thermal cold limit along both gradients. Since such range limits are not where weather stations are, we explored the actual temperatures within the forest, by placing data loggers in various locations and positions within trees, including the top of emergent tree crowns and related these data to standard weather station signals. We were particularly interested in low-temperature extremes throughout the year.

For a range limit to establish, a species must successfully recruit at the 'edge', irrespective of whether recruitment is a critical factor beyond the adult range limit. Hence, we studied seed quality, population processes, demography and adaptation of recruits to extreme climate at the adult range limit of each species. A large reciprocal transplant experiment with high- and low-elevation genotypes (provenances) was con-
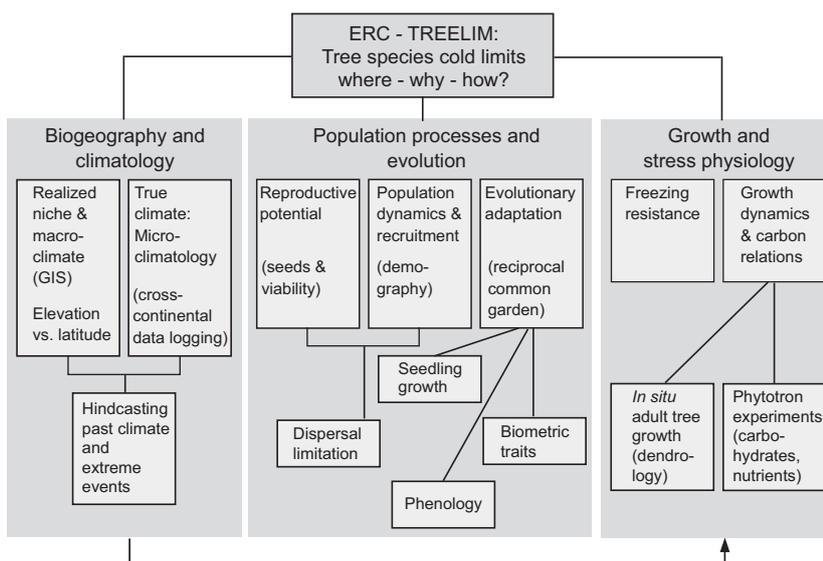

Fig. 1. The interdisciplinary approach employed here towards identifying the causes of tree species range limits. This approach is recommended for any study aiming at deciphering the causes of biogeographical range limits of taxa. ERC-TREELIM refers to the project acronym for 'A functional explanation of low-temperature tree species limits' (ERC is the European Research Council).
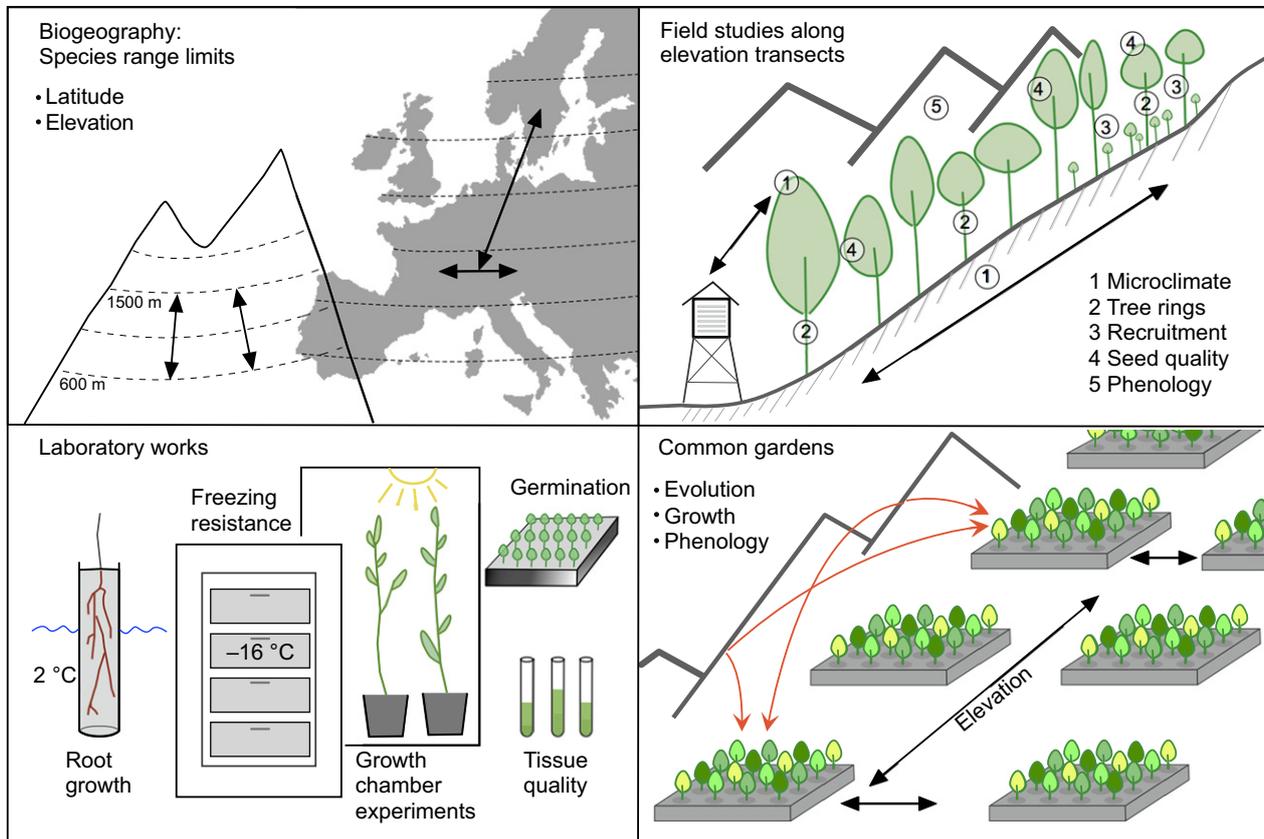
Fig. 2. The methods employed to identify the causes of low-temperature range limits of broadleaf deciduous tree species. Note the different scales, from tissue level to continental scale comparisons, and observational vs. manipulative works.

ducted to explore evolutionary adaptation in phenological, morphological and growth traits (Fig. 2).

Finally, we assessed adult tree growth (tree rings) and stress physiology in adult trees near and at the range limit, as well as sapling responses under controlled experimental conditions. Low temperatures influence tissue production (growth) and development gradually and directly, but also indirectly, by affecting tissue maturation *via* the effective length of the growing season (Körner 2006). Organs and tissues must enter winter in a mature state to survive (a threshold response), and hence, the two types of responses are interlinked. We thus explored (i) gradual low-temperature effects on tissue formation; (ii) effects of low-temperature extremes on tissue survival; and (iii) species-specific phenology controls of both growth and stress tolerance.

The critical physiological thresholds that potentially control range limits vary during the course of a year and are set by the progression of phenology. Low-temperature extremes are only decisive during a certain phenophase, which explains the central role of phenology for species range limits (Lenz *et al.* 2013; Savage & Cavender-Bares 2013; Amano *et al.* 2014). A temperature of -8 °C is meaningless in mid-winter (dormant state) for any temperate tree species, whereas it would lead to serious damage during spring flushing. Hence, there is not a single critical temperature, but there are several critical temperatures, one for each phenological stage, depending on the thermal history preceding a specific event. Escaping phe-

nologically from stressful early spring periods by a later bud burst has the trade-off of reducing the duration of the remaining growing season (e.g. Bennie *et al.* 2010), which co-determines competitiveness and the completion of the annual developmental cycle (maturation). The time to maturation is deeply rooted in phylogeny, in traits such as seed size (big seeds simply take longer to mature), bark development (fire resistance) or wood and bud maturation (anatomy, bud size, resistance to freeze/thaw cycles in winter).

Plants must adopt secure controls over their phenology, for instance for the timing of bud break, because 'weather' is not providing 'trustworthy' signals, with the occurrence of a late spring freezing event not being predictable from late winter and early spring weather conditions in a particular year. Thus, while the final steps of spring development show relatedness to concurrent temperature, the safeguards against trees tracking warm spells at the wrong time must rest on evolutionary deeper rooted signals such as the experience of sufficient winter chill and photoperiod (Körner & Basler 2010). The theory of plant phenology is still poorly developed, and assuming simplistic temperature-only controls is not a promising avenue. Much of the existing phenology theory has been developed from correlative data or from domestic or exotic taxa that have not undergone regional evolutionary selection. Further, a distinction must be made between early and late successional taxa, with the first more likely to behave opportunistically ('risky') than the latter, and data obtained

for young trees (seedlings or small saplings) are not appropriate proxies for mature tree phenology (Vitasse 2013).

This synthesis builds largely upon recently published work. Hence, we will highlight the design and the conceptual framework only (Fig. 2) and refer readers to the individual publications for methodological detail.

Field sites and methods

STUDY AREAS

The field part of this study was conducted along c. 0.8–1.3 km elevation gradients in the Swiss Alps (47° N), with replicates in the eastern and western part, and in southern Sweden (from Göteborg to Arvika, c. 57–59° N). These regions include the species-specific cold limits of all studied taxa, plus reference locations at lower elevation and latitude. We used occurrences of individuals of respective species along geographically replicated climatic gradients in areas where inventory data revealed maximum elevation or latitude for the studied tree species. A species is considered as present, when mature individuals are present. We avoided locations with obvious signs of past land use (e.g. tree stumps). Hence, the transects were located in the most pristine (often difficult to access) types of forest that we could find in the respective regions.

BIOGEOGRAPHY

A central question was to test whether the elevational and latitudinal range limits result in a similar ranking among species. If they do, this suggests that all species are in equilibrium with the climate during the establishment of the currently adult individuals. If the northern rank order differs (a species' range limit found at warmer conditions) from the one in the Alps, we need to assume dispersal lags, different biotic interactions, or we may have missed individuals at the edge of the species' distribution range. Because of the short distances along elevation transects in the Alps, dispersal limitation (historical effects) is highly unlikely, but with the large distances in latitude, they may occur in the north, as proposed by Svenning & Skov (2004). Yet, it is not metres of elevation or degrees of latitude, but the thermal regime that matters. For that reason, we anchored our comparison of highest and most northern tree species positions relative to the regional treeline isotherm as modelled by Paulsen & Körner (2014), and we expressed the position of the species range limit relative to the treeline position (the thermal distance to the climatic treeline; Randin *et al.* 2013).

MICROCLIMATE AND CLIMATOLOGY

Our microclimatology survey aimed at revealing the decisive actual life conditions at the edge of a species' range. This meant measuring temperatures *in situ* with more than 100 miniature data loggers. We regressed these local data for 2 years to weather station data from the respective regions. We recorded temperatures at the top of mature trees (by climbing them) and compared these readings to on-site 2 m air temperature in complete shade (Kollas *et al.* 2014b).

POPULATION PROCESSES AND EVOLUTION (COMMON GARDENS)

Seeds were collected from the five uppermost reproductive trees of each target species in each of the two test regions in the Alps and from lower elevation reference trees of the same set of species (Kollas *et al.* 2012). The population structure (presence of seedlings and saplings) was recorded along elevation transects that exceeded the elevation of the uppermost adults of each species (Vitasse *et al.* 2012). The transplant experiment consisted of eight gardens distributed along two elevational gradients, four in the western (437, 1058, 1522 and 1708 m asl.) and four in the eastern (606, 1002, 1251 and 1400 m asl) part of the Swiss Alps (Fig. 2). About 4700 individual seedlings, belonging to seven species, from 5-high and 5 low-elevation mother trees each, were distributed following a fully reciprocal design (standardized, low nutrient potting medium, deep containers in sand beds, 45% shaded to approximate natural recruitment conditions). The common substrate was a compromise, not to confound provenance and species with local soil conditions (Vitasse *et al.* 2013, 2014b).

TREE GROWTH AND CARBON RELATIONS

We cored hundreds of trees along the common study transects in the Alps for analysis of tree ring width and concentrations of non-structural carbohydrates (NSC; Hoch, Popp & Körner 2002). While the absolute level of these mobile C-stores are both species specific and not necessarily a proportional proxy for the tree carbon balance, we nevertheless expect that these reserves should decline towards the range limit of a species, should there be carbon shortage. Such a response is well known from orchard research (Körner 2003b), from trees that underwent defoliation (e.g. Mehouachi *et al.* 1995; Li, Hoch & Körner 2002; Schutz, Bond & Cramer 2011) or during peak growth or fruit masting (e.g. Miyazaki *et al.* 2002; Hoch, Richter & Körner 2003).

PHENOLOGY AND FREEZING RESISTANCE

The phenology of seedlings was monitored in all common gardens along the transects. In phytotron experiments, cuttings from adult trees from contrasting elevations were exposed to various combinations of temperature and photoperiod at various stages of endodormancy and ecodormancy during winter and spring (Basler & Körner 2012, 2014). Freezing resistance was studied using fresh collections of branches (at various developmental stages from bud break to full foliage expansion) in seven computer-controlled freezers that permitted running synchronous freezing protocols for all target levels of freezing temperature during the night following sampling (Lenz *et al.* 2013). To assess the risk of freezing damage in spring, we used phenological models for all provenances together with long time series of daily minimum temperature and leaf-out date from MeteoSwiss (Lenz *et al.* 2013, 2016).

CONTROLLED ENVIRONMENT EXPERIMENTS

The low-temperature responses of root growth in seedlings were studied in thermostated soil columns (Schenker *et al.* 2014). We also assessed survival rates, growth and NSC responses of two-year-old seedlings of 10 different broad-leaved tree species over two consecutive artificial seasons at simulated treeline temperature in computer-controlled phytotrons. The saplings were exposed to two short (20 weeks) growing seasons with seasonally and diurnally changing temperatures either averaging at 6 °C or 12 °C across the growing season (design similar to Hoch & Körner 2009). Hence, at 6 °C, these young trees grew in seasons much colder and shorter than these species would ever experience *in situ*. The two growing seasons were separated by a simulated 12-week, mild (2 °C mean) winter period (minimum temperature −1 °C).

Results

WHERE ARE THE LIMITS?

Using an expanded list of 18 broadleaf tree species (with distribution data obtained from data bases), we found a strong relationship between the thermal latitudinal and elevational species' cold limits (relative to treeline) with only marginal differences in rank positions along elevation and latitude (Randin *et al.* 2013). We also did not detect a strong deviation of the thermal latitudinal and elevational limits. Hence, the studied species appear to have reached their elevational or latitudinal cold limits (Randin *et al.* 2013). All further analyses (except for microclimatology and climate statistics) were carried out on elevational limits in the Alps.

WHAT ARE THE LIFE CONDITIONS AT THE SPECIES RANGE LIMIT?

During the growing season, the monthly absolute minimum air temperatures at 2 m, recorded directly in the forest with the target tree species, were 1.4 ± 0.2 K warmer (corresponding to a c. 250 m lower elevation) than concurrent weather station temperatures scaled (by regional monthly lapse rates) to the elevational position of the tree species limit (2.0 ± 0.2 K warmer during the 7 months, leafless, non-growing season; Kollas *et al.* 2014b). However, the top canopy low-temperature extremes are significantly cooler than the extremes of 2 m air temperature inside the forest. As a consequence, the remaining tree top vs. weather station difference in low-temperature extremes is reduced to merely 0.5 K warmer tree top minima, which we consider negligible at the scale of this continent-wide analysis and the precision of freezing tolerance data, and it corresponds to a difference of c. 90 m in elevation only.

Using long-term weather station data, we hindcasted rates of recurrence for low-temperature extremes, including the LT_{50} temperature for freezing damage to leaves during leaf emergence, and then plotted these against the time of flushing at high elevation (> 950 m a.s.l) in the Swiss Alps (Fig. 3). Using a broad spectrum of subzero temperatures, this analysis revealed that there are neither common seasonal mean temperatures (or growing degree days) nor common absolute minimum temperatures in winter that are consistently associated with the species' range limit at high latitude and high elevation. Absolute minima during winter are much lower at the high latitude compared to the high-elevation limit. Over the last century, these absolute minima never came close to what these species could tolerate in winter (their dormant freezing resistance). However, the minimum temperatures during bud break are very similar across latitudes for a given species and location and close to what is known to be critical during that sensitive phenological phase (-3 °C to -8 °C; Till 1956, Lenz *et al.* 2013; Vitasse *et al.* 2014a). The resulting length of the growing season at the upper range limit of a given species is very similar across all sites. From this, we conclude that spring temperature and the associated flushing phenology

are likely to exert a decisive influence on the cold range limit of these species. As will be shown later, this is consistent with freezing resistance, growth and phenology data.

DO TREES SUCCESSFULLY REPRODUCE AT THE SPECIES RANGE LIMIT?

Our hypothesis that seed set will be diminished, seed quality and viability will be reduced and germination will be less successful in high compared to low-elevation seed provenances was falsified. There is no indication that the reproductive potential at the upper range limit of any of these taxa is diminished under current climatic conditions (Kollas *et al.* 2012). Seed traits such as seed size, seed carbohydrate reserves and seed nitrogen concentration indicate no decline in seed quality as one approaches the adult species range limit. Although the scattered occurrence of mature trees at the range limit did not permit a seed rain study, there was plenty of seed to collect from such trees and from individuals at slightly lower elevation from where seed could disperse upslope. From that, we did not expect a decline of the reproductive potential in the investigated species as we approach the adult range limit.

Accordingly, we observed abundant reproductive success at the cold edge of adults and beyond. Across species, seedlings as well as taller saplings were found on average 70 m above the adult range limit and this discrepancy was more pronounced, up to 200 m, for dominant European species such as *Fagus sylvatica*, *Acer pseudoplatanus* and *Quercus petraea* (Vitasse *et al.* 2012). When we compared the mean summer temperatures at those range limits across the Swiss Alps, they were very similar (Vitasse *et al.* 2012; Kollas, Körner & Randin 2014a). It is difficult to tell whether the abundance of recruits above the adult tree limit is the normal exploratory expansion of young cohorts that may never become adults or whether this reflects upslope migration of trees in response to the 1.3 K warmer temperature in the study region during the two last decades, compared to the 1960–1989 reference period (Vitasse *et al.* 2012). Young trees may profit from forest shelter and enter a phase of strong selection once trees reach the canopy and become exposed to the full action of radiative freezing on clear nights. Also for the climatic treeline, there is no evidence for a consistent decline in amount and quality of seeds (Körner 2012). Presumably, there are good and bad years, with the former becoming more frequent as the climate keeps warming.

ADULT TREE GROWTH AND CARBON RELATIONS

As evidenced by the annual radial growth, adult trees grow vigorously without a substantial change over a wide elevational range (Lenz *et al.* 2014). Tree rings became narrower only over the last few hundred metres of elevation, but species differ in this respect. Some species (e.g. *Prunus* or *Fagus*) show a rather abrupt decline in tree ring width, similar to what has been observed near the alpine treeline (Paulsen, Weber & Körner 2000), and others (e.g. *Acer*) show a more
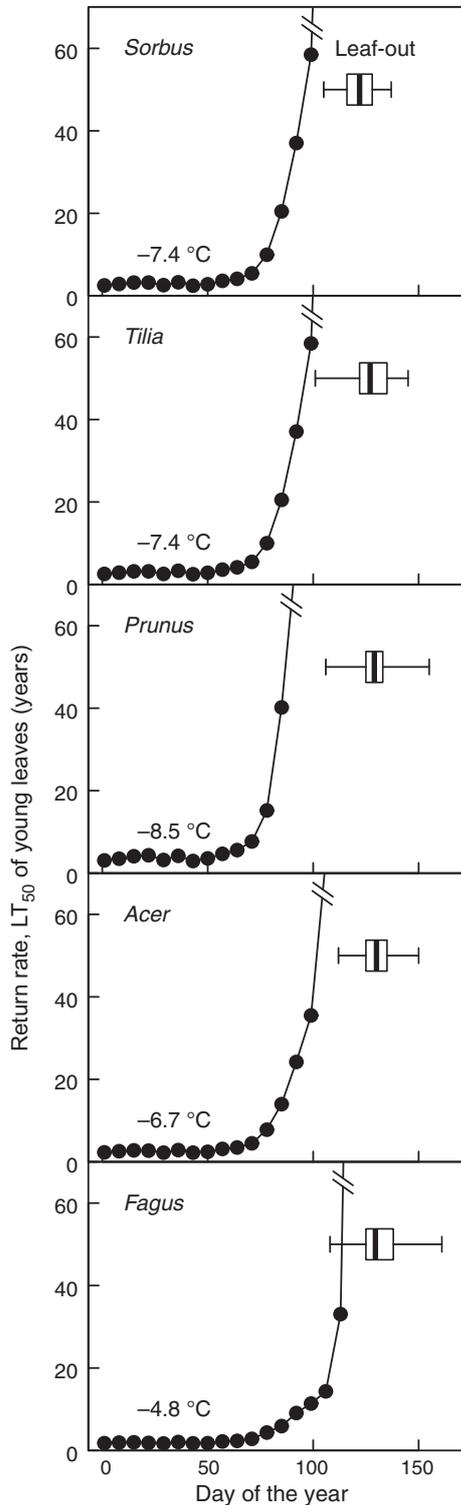
Fig. 3. Recurrence rates of critically low temperatures for freezing damage in unfolding foliage (LT$_{50}$; the temperature that is lethal for 50% of all leaves) across the year, for all species, based on long term weather from the phenology observation sites. Boxplots indicate the phenology window for budbreak over the 16–30 years of phenology data (adapted from Lenz *et al.* 2016).

gradual decline (Lenz *et al.* 2014). Adult individuals get scarce as one approaches the range limit, and it seems that tree height declines at a faster rate than does annual radial

increment (Körner 2012). Right at the range limit, the uppermost five trees per species, showed less than 50% of the mean ring width compared to trees from lower elevation (up to the point from where a decline with elevation could be depicted), except for *Fraxinus*, which still showed 80% of the low-elevation mean of ring width at its high-elevation limit (Lenz *et al.* 2014). Although we cored a total of > 400 trees, a few exceptionally fast growing individuals (presumably associated with humid, fertile, topography-driven microsites) added a lot of variation to the mean at lower elevation, and at the range limit such individuals were absent. The scarcer individuals of the same species become with elevation, the less likely such fast growing individuals can be found. Since such favourable topography is not elevation-specific, soil conditions *per se* are unlikely to influence the position of the species' range limit, but they do influence the vigour of individuals.

Radial growth of our sampled trees always correlated with growing season mean temperature, irrespective of elevation. A multiyear comparison revealed that the annual variation of the length of the growing season has an effect on radial growth only when temperatures are generally warmer (i.e. at lower elevation; Lenz *et al.* 2014). Because the time required for new cell formation increases nonlinearly with decreasing temperatures (Körner 2003a,b, 2006), a longer season at low temperatures will only produce few additional cell rows, whereas a longer season at high temperatures can produce many more cell rows, particularly when spring is warm, which sets the size of the cambial zone (Lenz, Hoch & Körner 2013; Delpierre *et al.* 2015). Unexpectedly, we also did not observe an increase in the frequency of exceptionally narrow tree rings with elevation (negative 'pointer' years; Lenz *et al.* 2014). *Fagus* is an exception, though, with more years with very narrow rings near the upper range edge. Further, the concentration of non-structural carbohydrates in wood did not change with elevation, and hence, we found no reduction in osmotically inactive reserves (Lenz *et al.* 2014). Some species, for example *Sorbus aucuparia,* revealed even a significant increase of NSC towards the upper distribution range, which is in line with previous findings in a global comparison of alpine treelines (Hoch & Körner 2012). It is thus highly unlikely that the cold range limit of these species is related to carbon shortage. We conclude that within a given species, tissue formation at the range limit is negatively affected by lower temperatures in general, but not, or much less, by the length of the growing season of a given year, since the end of tissue production and the onset of winter bud formation are controlled by photoperiod in late summer (Salisbury 1981; Thomas & Vince-Prue 1997), with autumn weather only modulating the rate of maturation and transition to full dormancy.

HOW DO TREES COPE WITH LOW-TEMPERATURE EXTREMES AT THEIR COLD RANGE LIMIT?

During dormancy in winter, the study taxa tolerate much lower temperatures at the high-elevation range limit than

would ever occur *in situ*. Interestingly, species with a range limit at lower (warmer) elevations turned out to be more at risk of freezing damage in winter than species with higher limits (Lenz *et al.* 2013). Yet, there is substantial short-term acclimation to weather conditions. For instance, the freezing resistance in *Fagus sylvatica* increases by up to 15 K (down to –40 °C) after artificially hardening tissues for 5 days at −6 °C followed by 3 days at −15 °C (Lenz, Hoch & Vitasse 2016). Thus, at their cold range limit, the examined tree species are safe from freezing damage in winter, both in Sweden and the Alps. Based on freezing resistance data for the Alps, the safety margin in winter is smaller at high latitude than at high elevation, if we assume the same freezing resistance and hardening potential in trees at high elevation and at high latitude.

In contrast, freezing resistance during the onset of the growing season permits a clear differentiation among the studied taxa and these data match the phenological rank order (time of bud break) of the species. In cold climates, emerging leaves of earlier flushing species are more freezing resistant than those in late flushing species (Fig. 4, Lenz *et al.* 2013). Most importantly, we demonstrated that the later flushing date at higher elevations minimizes the probability of freezing damage during flushing. This interaction between freezing tolerance during flushing and the date of flushing results in a uniform safety margin across the entire elevational distribution range of all taxa studied (except *Fagus*, see below), that is, trees experience the same (low) risk of freezing damage irrespective of elevation. *Fagus* operates at a higher risk, reflecting observational evidence of occasional spring damage in fresh foliage (that the tree is able to rapidly replace). More freezing-resistant tree species can flush earlier than less freezing-resistant species. Thus, species-specific freezing resistance during leaf-out explains the difference in flushing date among different species.

Just as maximum freezing tolerance and thus absolute minima in winter have no predictive value for the range limit of these taxa, freezing tolerance in fully active, mature foliage is very similar across taxa and thus, is uncritical as well (Lenz *et al.* 2013). Mature foliage never did face damaging temperature extremes at the upper range limit for as long as weather records were available (80 years). The risk of freezing damage is also negligible in autumn. Interestingly, the late season onset of hardening does not depend on elevation, and all examined trees start hardening at the same time between 600 and 1700 m a.s.l. in the Swiss Alps, pointing to a common photoperiod control, and resulting in a high freezing tolerance before temperatures do drop below zero (Sakai & Larcher 1987, Tranquillini & Plank 1989, unpubl. MSc thesis by S. Saelinger). This common response may reflect the short geographical distance and thus high gene flow across the elevation gradient, although we found genetic differentiation in phenology and growth related traits in the common garden experiment with seedlings (see below). Alternatively, selective pressure for a differentiation in phenology does not differ along the elevation gradient, given that temperature inversion during cold periods often leads to colder temperatures at the valley bottom, and thus, to greater risk of freezing damage.
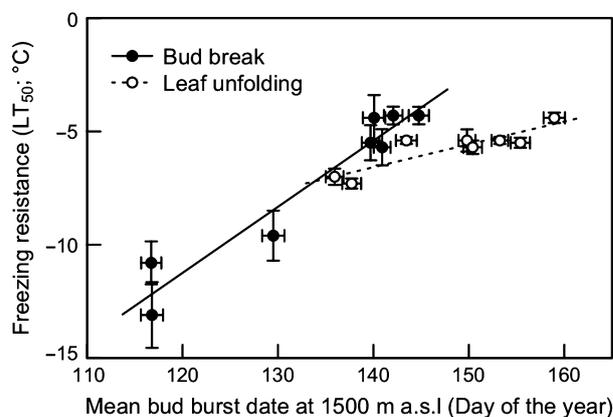

Fig. 4. Freezing resistance of foliage at bud break and shortly after, when leaves unfold, vs. the date of bud break and flushing obtained from phenological observations for the different deciduous tree species studied (LT_{50} as in Fig. 3; adapted from Lenz *et al.* 2016).

The main message of this screening for freezing tolerance is the critical role of spring and the apparent fine-tuning with phenology, as will be discussed below.

GENOTYPIC VS. PHENOTYPIC RESPONSES OF GROWTH AND PHENOLOGY

In spite of the presumably high gene flow that occurs along elevational gradients (Alberto *et al.* 2013; Pluess *et al.* 2016), the common garden experiments revealed small, but consistent genetic (ecotypic) differentiation of spring phenology among provenances of seedlings originating from different elevations, except for the treeline species *Sorbus aucuparia* (Vitasse *et al.* 2013), underlining the importance of the timing of growth and development for tree success. For *Acer pseudoplatanus*, *Fraxinus excelsior*, *Prunus avium* and *Sorbus aria*, the high-elevation provenances were found to flush significantly later than the low-elevation provenances, especially in the lowest gardens. The other species showed the same trend, except for *Fagus sylvatica*, which revealed the opposite genetic cline, that is high-elevation provenances tended to flush earlier than those from low elevations, as was observed previously (Vitasse *et al.* 2009a). Interestingly, the phenological shift among common gardens as a result of decreasing temperature at higher elevation was found to be smaller for high-elevation provenances in all species (Vitasse *et al.* 2013). In addition, provenances from high elevation tended to set their buds earlier in autumn than provenances from low elevation. All in all, the phenology of populations from high elevation was less responsive to temperature, and presumably, more strongly tied to chilling requirements and/or photoperiod, than in populations from low elevation, a trend known from forestry research a century ago (Körner 2012). In line with results for adult trees, the transplant experiments revealed that the sensitivity of phenology to temperature is highly dependent on species. For example, *Fraxinus excelsior* is the most and *Fagus sylvatica* the least sensitive of the studied species to a temperature increase, as was found earlier by Vitasse *et al.* (2009b).

Irrespective of growth location, high-elevation provenances exhibited slower growth rates than low-elevation provenances in half of the studied species (no such genetic difference in the other half of the species), namely *Fraxinus excelsior*, *Acer pseudoplatanus*, *Sorbus aria* and *Sorbus aucuparia* (Vitasse *et al.* 2014b). While leaf thickness and leaf mass per area increased with increasing elevation of the common garden, provenances did not differ. Although we could transplant only young trees, we have shown that seedlings and adults exert the same freezing resistance during flushing, provided data for the same stage of bud/leaf development are compared (Vitasse *et al.* 2014a).

EXPERIMENTAL SPRING PHENOLOGY IN ADULT TREES

Cuttings of *Acer*, *Fagus*, *Quercus* and *Picea* sequentially sampled from adult trees at different elevations during winter and early spring showed a genotypic differentiation in the sensitivity to thermal forcing and photoperiod: in *Acer* and *Fagus*, low-elevation cuttings exhibited 3–5 days earlier bud burst than high-elevation cuttings, whereas the reversed pattern was present in *Quercus*, irrespective of growth chamber temperature or photoperiod (6 °C vs. 9 °C daily mean temperature, 10 K diurnal amplitude; photoperiod initially 9.2 h vs. 10.8 h, increasing daily by the natural daily increase of photoperiod at 46.5° N; Basler & Körner 2014). *Picea* cuttings from high elevations exhibited a larger sensitivity to photoperiod than those from low elevations (up to 8 days difference in the mean time of bud burst, depending on sampling time in late winter), while no distinct pattern was found in response to different temperatures. These elevational patterns in the timing of bud burst weakened and/or disappeared with later sampling dates and thus shorter exposure to the contrasting treatment conditions (Basler & Körner 2014).

TISSUE LEVEL GROWTH RESPONSES

Cold-adapted plants show hardly any growth below 5 °C (Terry, Waldron & Taylor 1981; James, Grace & Hoad 1994; Alvarez-Uria & Körner 2007; Rossi *et al.* 2007; Körner 2008, 2012), and this also holds for the trees studied here. Below that critical temperature, cell division and cell differentiation become so slow that growth rate becomes almost immeasurable. Our records show that such critically low temperatures below 5 °C are quite rare above-ground and non-existent below-ground during the growing season at the range limit of these deciduous taxa. Yet, the elevational range limit of the species studied does correlate with the temperature at which root growth rates are reduced to zero. Species with distribution limits at higher elevations have lower temperature limits of root growth than species restricted to lower elevations (Schenker *et al.* 2014). Although ecologically hardly relevant, these zero-growth thresholds still indicate a species-specific low-temperature adaptation of metabolism and growth that is likely to allow for higher root production at higher but still cool temperatures, eventually allowing a species to grow better at colder temperature.

Saplings grown over two cold growing seasons at artificial phytotron climates set to mimic natural treeline conditions (growing season mean temperature of 6 °C) allowed all species except *Carpinus betulus* (a low-elevation species that we added to this experiment) to survive (G. Hoch & A. Lenz, unpubl.), similar to the seedlings in the uppermost transplant gardens (Vitasse *et al.* 2013). However, in several species, we observed incomplete winter bud formation (i.e. green leaf buds at the end of the season) and wood maturation (insufficient xylem lignification, visible in microtome stem-cuttings under polarized light), which would limit survivorship in a realistic winter. In a cold, 6 °C environment, species with a higher elevation limit tended to grow faster than those reaching their natural limit at lower elevations. For example, *Fagus sylvatica* and *Quercus petraea* showed hardly any net growth and only a c. 10% increment of stem diameter after two seasons at cold temperatures, while *Sorbus aucuparia* (a species reaching the alpine treeline) exhibited a 15-fold increase of the initial biomass and a twofold increase in stem diameter at the same low-temperature conditions. By the end of the second artificial growing season, all investigated species, except *Acer*, showed the same or higher stem NSC concentrations in the cold compared to the warm treatment. On average, NSC concentrations in stem wood of cold treated saplings were about 10% higher compared to the warm controls (G. Hoch & A. Lenz, unpubl.).

In summary, these experimental findings suggest that species can grow at significantly lower temperatures than those corresponding to their current range limit, but they fail to produce mature tissue under such conditions, which, in turn, constrains survivorship during winter. Immature shoots are known to fail to survive winter conditions (e.g. Baig & Tranquillini 1980, Wardle 1981, Tranquillini & Platter 1983). These late season requirements are pointing to a critical role of the species-specific beginning and overall length of the growing season.

The triangular concept for explaining low-temperature range limits of temperate tree species

In summary, our results allow, for the first time, to establish a theory of low temperature range limit controls for non-treeline, temperate zone tree species. The overarching influence of thermal extremes during spring is obvious, but these do not act in isolation. As we have shown, species sensitive to freezing during early spring flush later, and thus, are at a similar risk of being damaged by late freezing than more tolerant, earlier flushing species. This risk mitigation has a trade-off in terms of the remaining length of the growing season. Hence, the evolutionary selection for later flushing in those species cuts the growing period short. This may not matter over most of the species' range, but it matters at the species' range limit, where the climatic conditions and plant internal developmental controls constrain the duration of the season. Some species may tolerate shorter seasons than others, related to their specific seasonal life cycle. Our data do not suggest that this limitation is tied to

reduced carbon acquisition, because we found no evidence of carbon shortage at the range limit of any species.

One important conclusion for modelling species range limits is that neither any temperature means, nor extremes of winter temperature are directly involved in the biological mechanisms responsible for the formation of range limits at the scales explored here. In cases where correlations between upper range limits and winter temperatures were found, it may be due to the proxy nature for other facets of temperature. Deciduous tree range limits are most likely tied to events during the early growing season, no matter how cold the winter might be, provided the remaining season is long enough to permit tissue maturation, that is, ripening seeds, completing the sapwood, late wood and bark formation, mature winter buds (including flower primordia) and current year shoots. Should these developmental processes remain incomplete by the time trees are forced into autumnal dormancy, they are not going to survive the following winter, or they will regularly fail to reproduce, or lose newly grown shoots. Obviously, this cannot be studied in surviving, healthy adult trees, but incomplete tissue maturation has been evidenced for individuals growing above the tree limit (see the above references).

We thus arrive at a triangular interaction of inherent freezing tolerance of foliage in spring, that selects for a certain phenological control of spring flushing, which in turn truncates the length of the growing season, and thus, the time available for tissue maturation (Fig. 5). While the latter is hard to study in survivors at the species range limit, it is a cascade of interactions that has its roots in freezing tolerance during spring, that is, the tolerance of biomembranes, the action of freeze-protection proteins, dehydrins, etc. during a critical phase in spring.

The control over phenology is thus central by setting the trade-off between late flushing and a long growing season. The direct (gradual) influence of temperature during the growing season and winter temperatures has little, if any, influence on range limits. While photoperiod is a still poorly understood co-determinant of spring phenology, its influence in late season phenology is overwhelming (Salisbury 1981; Thomas & Vince-Prue 1997), and it should not be mistaken as just being reflected in a sharp leaf colour change or leaf fall, which are superficial symptoms (e.g. reflecting particular weather conditions), compared to the decisive but invisible changes such as the termination of meristem activity, the setting of leaf abscission layers and re-configurating biomembranes for higher freezing tolerance before the advent of frost. These internal state changes truncate the growing season, no matter what the late season temperatures are and whether the growth cycle could be adequately completed (Delpierre *et al.* 2015), a field (particularly the maturation issue) that deserves a lot more research.

Future studies aiming at predicting species range limits will have to account for this threefold interaction of drivers. This also calls for accounting for temperature extremes rather than means in projecting tree responses to future climates. Since traits such as seed size or wood anatomy, and associated growth dynamics, as well as freezing tolerance during leaf emergence are likely to be deeply rooted in phylogeny, microevolutionary optimization of phenology emerges as the central tuning point. The overarching role of photoperiod and thus, season length control over growth, was recently evidenced for a large number of N-American *Salix* and *Populus* species from different latitudes (Savage & Cavender-Bares 2013).

Once we arrive at a mechanistic understanding of tree phenology, and species-specific freezing tolerance in spring is known, the probability of tree failure due to low-temperature extremes can be distilled from climate data bases that report extremes (absolute minima, see Lenz *et al.* 2016). In a broad comparison of currently available phenology models, it emerged that the models that employ

Fig. 5. The triangular control of species range limits: the species-specific trade-off between (1) the risk of freezing damage in spring and (2) the risk of entering the dormant season with immature tissue, is optimized by (3) the timing of spring phenology. Stochastic freezing damages to immature tissue in spring and late autumn are framing the 'safe' window into which tree phenology is 'fitting' tree development. While freezing resistance and the minimum time required to complete the seasonal growth cycle (life-history related) are deeply rooted in phylogeny, phenology is under short-term selection. In the case of trees, short-term means a few tree generations (centuries), explaining the existence of latitudinal and elevational phenology ecotypes.
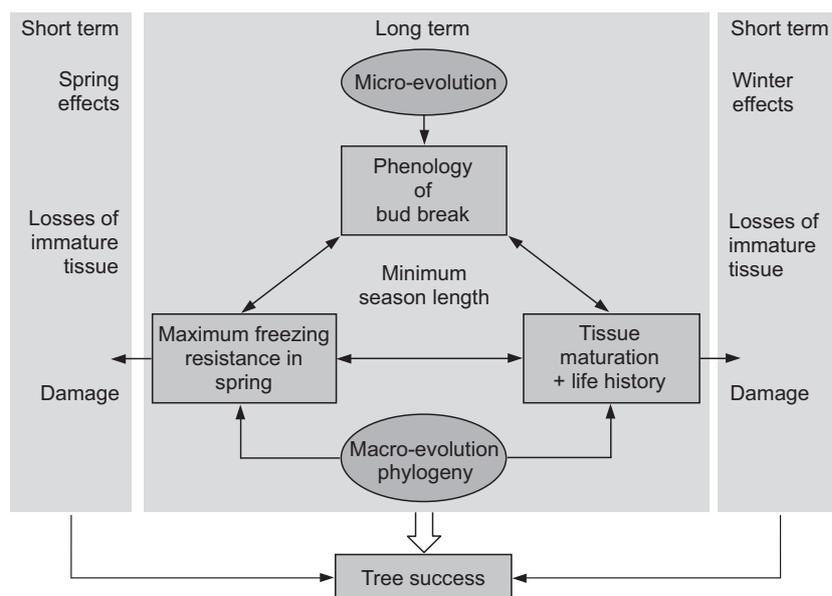
rather different degrees of sophistication with regard to the assumed 'mechanisms', yield rather similar predictions. Yet, these models commonly only work for locations from which parameterization was adopted and they systematically underestimate the inter-annual variation of spring phenology, thus indicating that the actual mechanisms of bud development are not correctly implemented (Basler 2016). Similar to the results presented here, any attempt at isolating one single factor (e.g. heat sums, temperature means) is prone to failure, because native species most likely respond to the interactive, nonlinear influences of several climatic factors such as chilling signals (telling the plant whether it is autumn or spring; Murray, Cannell & Smith 1989), photoperiod signals (the weather-independent astronomic calendar) and actual temperature ('thermal forcing'), with the last gaining influence, once the first two permit (Körner & Basler 2010).

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Authorship declaration

CK conceptualized and planned the work and wrote the manuscript. NZ helped with theory and finding the best test regions. YV, CR, GH, CKollas, AL and DB conducted the field and laboratory work and analysed the data, and all co-authors contributed to the final text.

Data accessibility

This essay review does not use original data.

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