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Contrasting resistance and resilience to extreme drought and late spring frost in five major European tree species

Yann Vitasse[1,2] | Alessandra Bottero[1,2] | Maxime Cailleret[1,2,3] | Christof Bigler[2,4] | Patrick Fonti[1,2] | Arthur Gessler[1,2,5] | Mathieu Lévesque[2,4] | Brigitte Rohner[1,2] | Pascale Weber[1] | Andreas Rigling[1,2,5] | Thomas Wohlgemuth[1,2]

[1]WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf, Switzerland

[2]SwissForestLab, Birmensdorf, Switzerland

[3]UMR RECOVER, Aix Marseille Univ, IRSTEA, Aix-en-Provence, France

[4]Forest Ecology, Department of Environmental Systems Science, ETH Zurich, Zurich, Switzerland

[5]Institute of Terrestrial Ecology, ETH Zürich, Zürich, Switzerland

Correspondence
Yann Vitasse, WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf, Switzerland.
Email: yann.vitasse@wsl.ch

Funding information
SwissForestLab

Abstract

Extreme climate events (ECEs) such as severe droughts, heat waves, and late spring frosts are rare but exert a paramount role in shaping tree species distributions. The frequency of such ECEs is expected to increase with climate warming, threatening the sustainability of temperate forests. Here, we analyzed 2,844 tree-ring width series of five dominant European tree species from 104 Swiss sites ranging from 400 to 2,200 m a.s.l. for the period 1930–2016. We found that (a) the broadleaved oak and beech are sensitive to late frosts that strongly reduce current year growth; however, tree growth is highly resilient and fully recovers within 2 years; (b) radial growth of the conifers larch and spruce is strongly and enduringly reduced by spring droughts—these species are the least resistant and resilient to droughts; (c) oak, silver fir, and to a lower extent beech, show higher resistance and resilience to spring droughts and seem therefore better adapted to the future climate. Our results allow a robust comparison of the tree growth responses to drought and spring frost across large climatic gradients and provide striking evidence that the growth of some of the most abundant and economically important European tree species will be increasingly limited by climate warming. These results could serve for supporting species selection to maintain the sustainability of forest ecosystem services under the expected increase in ECEs.

KEYWORDS
climate warming, climatic water balance, dendrochronology, extreme climatic events, frost risk, growing degree-days, tree phenology, tree-ring width

1 | INTRODUCTION

Extreme climate events (ECEs) such as severe droughts, heat waves, and their combination called "hot droughts" (Allen, Breshears, & McDowell, 2015), or late spring frosts are rare per definition but may largely impact forest ecosystems. They have been identified worldwide as major environmental factors acting directly or indirectly on growth, mortality, and regeneration of a wide array of tree species (Allen et al., 2015; Breshears et al., 2005; Hufkens et al., 2012), ultimately driving their spatial distribution (Smith, 2011). This is especially true for low-elevation temperate forests whose functions and dynamics are largely shaped by extreme droughts (Pederson et al., 2014). For instance, the European spring/summer hot drought in 2003 has caused abrupt and severe decreases in tree productivity

and health in western and central Europe, and transiently turned forests into carbon sources (Ciais et al., 2005). In addition, temperate tree species are highly sensitive to late spring frosts during budbreak and leaf emergence (Bigler & Bugmann, 2018; Vitra, Lenz, & Vitasse, 2017), and the tree's leaf out timing in relation to spring frosts may be a key driver of their upper elevational distribution (Körner et al., 2016). Even though trees have evolved to leaf out at the time when the statistical recurrence of frost is almost nil (Lenz, Hoch, Körner, & Vitasse, 2016), damaging spring frosts can still occur, in particular when an unusual long warm period in early spring induces premature vegetation development ("false spring," Chamberlain, Cook, Garcia de Cortazar-Atauri, & Wolkovich, 2019), as it occurred over broad areas in western and central Europe in 2017 (Vitasse & Rebetez, 2018) or in the eastern part of the United States in 2007 (Gu et al., 2008; Hufkens et al., 2012).

Extreme droughts are expected to increase in frequency, magnitude, and spatial extent (Ballester, Rodó, & Giorgi, 2010; McDowell et al., 2018; Stott, 2016). To what extent the frequency of damaging spring frosts may change remains more uncertain and site specific, because both spring phenology and the last spring frosts are currently advancing (Vitasse, Schneider, Rixen, Christen, & Rebetez, 2018). While temperate trees at lower elevations may further suffer from drought in the future decades (Pederson et al., 2014), trees at higher elevations may paradoxically be increasingly exposed to spring frosts (Vitasse, Schneider, et al., 2018) due to above-average phenological shifts (Vitasse, Signarbieux, & Fu, 2018). Thus, in order to adapt forest management for the provision of top priority ecosystem services in the near future (Lindner et al., 2010), we urgently need to assess the respective short- and long-term responses of major tree species (i.e., their resilience) to both extreme drought and spring frost, the latter being much less studied.

In such a context, the analysis of tree-ring widths is a useful approach to retrospectively assess the growth resistance, recovery, and resilience to ECEs as it reflects a tree's annual aboveground biomass increment and its capacity to withstand extreme drought and spring frost events (Lloret, Keeling, & Sala, 2011). Here, the term resilience refers to the concept of "engineering resilience" (Holling, 1996) as the ability of an organism/ecosystem to return to predisturbance conditions, distinguishing two components: the *resistance* (capacity to withstand the disturbance) and the *recovery* (recovery relative to the response induced by the disturbance episode; Ingrisch & Bahn, 2018). These two metrics can be used as early warning signals of an impending critical transition (Dakos, Carpenter, Nes, & Scheffer, 2015). For instance, a decrease in the ability of a tree to recover after a severe drought may be indicative of declining growth and vigor and thus a higher mortality risk (Rogers et al., 2018).

The interannual variability of tree-ring width is among other factors directly and indirectly regulated by climatic conditions via the limitation of the internal carbon sink (the cambial activity) or carbon source (assimilation via photosynthesis or remobilization and availability of the carbohydrates from storage; Körner, 2015). For instance, spring frosts can heavily damage the new leaves, resulting in a dramatic decrease of the photosynthetic activity especially for deciduous species, typically followed by a significant decline of reserves and allocation to radial growth (Augspurger, 2011). Similarly, during an exceptionally long and/or extremely severe dry period in the growing season, trees may be (a) forced to close their stomata to save water, which may simultaneously induce carbon depletion, or (b) subjected to hydraulic constraints inducing xylem cavitation (Choat et al., 2012; McDowell et al., 2008). As a consequence, drought can terminate the xylogenesis prematurely (Fernández-de-Uña et al., 2017) and can also affect radial growth in subsequent years (Anderegg et al., 2015). However, depending on intensity and exact timing of the ECE, impacts on tree growth might be very different and species dependent (D'Orangeville et al., 2018). Severe droughts in spring and/or early summer are expected to have the strongest impact on the current year's growth and tree functioning as they occur at early season peaks in radial growth, when soil water and nutrient availability are normally available in excess and do not limit growth (D'Orangeville et al., 2018).

Tree rings provide a precious archive documenting the direct and lagged effects of both droughts and damaging spring frosts that have occurred during the tree life. As they can be measured on numerous individuals, species, and sites at reasonable cost, they allow to retrospectively analyze the variation in resilience to ECEs among tree species with different life history and physiology, related, for example, to leaf and cambial phenology, stomatal response to drought or hydraulic safety margin. Although some studies have highlighted the differences in drought responses between angiosperms and gymnosperms (Anderegg et al., 2015; Gazol et al., 2018), we still lack of multispecies analyses along broad environmental gradients for extreme drought (but see Gazol, Camarero, Anderegg, & Vicente-Serrano, 2017) and especially for late spring frost events. In addition, we still need to detect species-specific tipping points of drought or frost intensity beyond which tree growth clearly decreases.

Here, we evaluated the potential of major European tree species to tolerate severe spring drought and late spring frost by gathering a large dataset of tree-ring width measurements encompassing a total of 2,844 trees (represented by one core each) from five different species and 104 different sites across various climatic conditions in Switzerland, from warm and dry lowlands to cool and wet subalpine regions. Specifically, we aimed at (a) quantifying the respective impacts of extreme spring frosts and droughts on the resistance, recovery, and resilience of radial growth of three major conifer species and two common broadleaved species, and (b) determining and comparing the tipping points of water deficit and frost risk beyond which radial growth abruptly declines among the five study species.

2 | MATERIALS AND METHODS

2.1 | Study species and tree-ring series

Five of the most economically important European tree species were considered in this study, including three coniferous species (silver fir, *Abies alba* Mill.; Norway spruce, *Picea abies* (L.) Karst; and

European larch, *Larix decidua* Mill.) and two broadleaved species (European beech, *Fagus sylvatica* L.; and deciduous oaks, *Quercus* spp. including pedunculate oak, *Quercus robur* L. and sessile oak *Quercus petraea* (Matt.) Liebl., while it cannot be ruled out that downy oak, *Quercus pubescens* Willd., was present in individual sites). Note that tree-ring data of sessile and pedunculate oak were pooled in our analysis as often done in dendroecological studies because of the difficulty to differentiate the two species in terms of wood anatomy and because of the high proportion of natural hybrids between the two species (Lepais & Gerber, 2011). For clarity's sake, the species are hereafter referred to as fir, spruce, larch, beech, and oak.

We gathered existing tree-ring width measurements of these five species from Switzerland that include the period 1930–2011. As data sources, we included numerous datasets published in ISI indexed journals, from the "gray" literature, or made available from the International Tree-Ring Data Bank ITRDB (see details in Table S1). A quality control of each dataset was conducted to test whether each core had been correctly crossdated using the software COFECHA (Holmes, 1983). Cores that were not correctly crossdated or that presented strong statistical anomalies in their correlations with the other individuals within the same stand were removed from subsequent analyses. Trees with less than 60 tree rings were discarded because they were difficult to check for the quality of the crossdating, which also allowed to avoid including too young individuals that may respond differently than mature trees to well-known ECEs such as the drought of 1976. The total number of trees discarded for such reasons was, however, very limited (1.8% of the total sample size). We considered tree populations which are represented by a minimum of five trees per species and site (details about the number of populations and trees per species are provided in Table S2). A total of 2,844 cores (one core per tree) have been analyzed from 104 different forest stands in Switzerland spanning an elevational range from 420 to 2,200 m a.s.l. (Figure 1a; Table S2). The elevational range of the study sites strongly varies depending on species, being the highest for larch and spruce (>1,500 m), the lowest for oak (<600 m), and intermediate for fir and beech (~900 m; Table S2). Annual mean temperature of the different sites ranges from 1.0 to 11.2°C and annual precipitation ranges from 893 to 2,492 mm (averages refer to the period 1981–2010, Figure 1b; Table S1).

2.2 | Climate data

Daily minimum and maximum temperature and daily precipitation were derived at 100 m resolution from 1930 to 2016 by interpolating daily values of MeteoSwiss (the Swiss Federal Office of Meteorology and Climatology) weather stations using the Daymet software of Thornton, Running, and White (1997). Daily minimum and maximum temperature and daily precipitation were then extracted for each of the 104 study sites using their geographic coordinates. Daily mean temperature values were computed by averaging daily minimum and maximum temperature data.

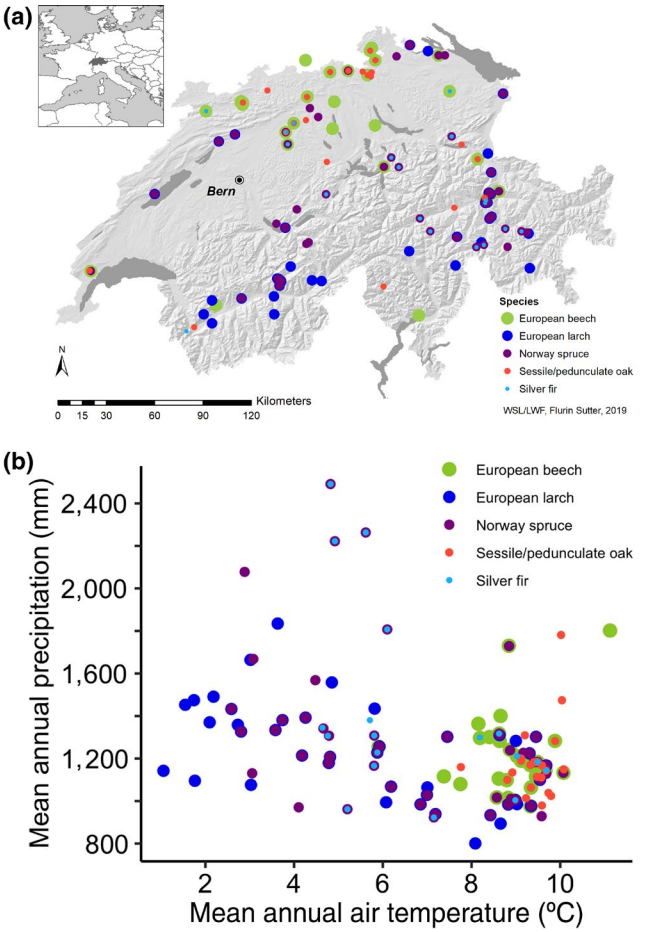

FIGURE 1 Location and climatic characteristics of the study sites. (a) Location of the 104 study sites in Switzerland. (b) Mean annual precipitation and temperature of the study sites. Note that the symbols used for the different species differ in size only for a better visualization

2.3 | Identifying potentially damaging spring frost

Spring frost can be damaging to trees, especially when it occurs during or after leaf emergence when trees are the most sensitive to freezing temperatures (Vitasse, Lenz, & Koerner, 2014). Thus, spring phenology must be accounted for when looking at potentially damaging frosts over the past. Growing degree-days, that is, daily accumulation of mean temperature above a certain threshold in late winter and spring, is a widely used proxy to predict the time of spring phenology phases for natural and cultivated plant species (e.g., Sacks & Kucharik, 2011). In Switzerland, degree-days accumulated from January 1 to mid-April show high correlation with the Swiss spring index (R^2 > 0.8), which represents the onset of vegetation development in spring using ~80 weather stations with sufficiently long data series of phenological observations (Vitasse & Rebetez, 2018). To identify the years with potentially damaging spring frosts, we therefore used accumulated degree-days, as a proxy for plant phenology advancement, calculated for every year and station as the sum of daily

mean air temperature above 5°C since January 1 to the date of the last frost day (≤−2°C: temperature threshold below which damages can be observed on numerous fruit and forest trees, see Vitasse, Schneider, et al., 2018). The higher the degree-days accumulated before the frost event, the higher is the risk for plants to be injured by frost, following the method developed by Vitasse and Rebetez (2018). Although young leaves of temperate trees have been shown to resist temperatures below −2°C in the laboratory (Lenz, Hoch, Vitasse, & Korner, 2013), radiative cooling during clear and windless nights may lead to temperatures in plant tissues several degrees lower than those measured at 2 m height under the sheltered conditions of a Stevenson screen (Ducrey, 1998). We therefore assume a threshold of −2°C to be low enough to potentially damage leaves of the study species. Besides, this value or very similar thresholds (e.g., −2.2°C) are commonly used in other studies (reviewed in Chamberlain et al., 2019).

2.4 | Identifying severe droughts

The standardized precipitation evapotranspiration index (SPEI; Vicente-Serrano, Beguería, & López-Moreno, 2010) was calculated for each site for the period 1930–2016 after aggregating the daily temperature and the precipitation data per month. SPEI can be aggregated over monthly intervals to measure short- to long-term droughts (Vicente-Serrano et al., 2010). When assessing the impact of drought on growth of temperate trees, a critical point is when the drought occurred within the seasonal cycle of the plant (Anderegg, Anderegg, & Berry, 2013). The timing of drought may indeed explain why some species respond more to one drought event than to another (e.g., early summer vs. late summer growth). For example, severe summer drought might be compensated by wet spring or previous winter conditions (Vitali, Büntgen, & Bauhus, 2018). However, spring droughts are probably the most detrimental to the growth of temperate trees as they need substantial water to supply emerging and growing leaves (Lévesque, Rigling, Bugmann, Weber, & Brang, 2014; Martin-Benito et al., 2018). After testing different time intervals, we selected the period from March to June for the calculation of the SPEI as (a) it maximizes the Pearson correlation between SPEI and the site- and species-specific chronologies of tree-ring indices across species (Figure S1), (b) it integrates the period and the pre-period of the beginning of the growing season for trees in this area when typically high production rates of xylem cells are observed (Dietrich, Zweifel, & Kahmen, 2018), and (c) the largest fraction of water taken up by trees during the growing season comes from early spring (Brinkmann et al., 2018). However, because SPEI allows to identify dry years for a given site but not to compare the drought intensity among sites since it is a standardized index, we further calculated the climatic water balance of every site between March and June. First, we calculated for every site and month the potential evapotranspiration (ETo) based on monthly mean temperatures and latitude using the Thornthwaite equation (Thornthwaite, 1948) implemented in the R package "SPEI" (Beguería & Vicente-Serrano, 2013). Second, we subtracted ETo from monthly precipitation values, which provides the climatic water balance of each site at monthly scale. As for the SPEI, we finally aggregated the climatic water balance over the period from March to June.

2.5 | Data analyses and statistics related to tree-ring series

For every individual tree and every year, we calculated the resistance, recovery, and resilience indices based on Lloret et al. (2011), as follows:

$$\text{Resistance (Rt)} = \frac{\text{Ring width}_t}{\text{Ring width}_{t-2}}$$

$$\text{Recovery (Rc)} = \frac{\text{Ring width}_{t+2}}{\text{Ring width}_t}$$

$$\text{Resilience (Rs)} = \frac{\text{Ring width}_{t+2}}{\text{Ring width}_{t-2}}$$

where Ring width_t is the radial width of the annual ring during the corresponding year *t*, Ring width_{t-2} is the average ring width for the 2 years preceding the year *t* and Ring width_{t+2} is the average ring width for the 2 years following the year *t*. All these indices were calculated at the individual tree level for each year during the period 1930–2011 (and later when available) and then averaged per site and species. We selected 2 years to ensure that the lag effect of a given extreme climatic event does not overlap with another extreme event (Anderegg et al., 2015), which was the case at least for the two main identified late spring frosts (1957 and 1981, Figure 2a) and spring droughts (1976 and 2003, Figure 2b).

To assess the growth–SPEI relationships, we built a mean-value chronology of the tree-ring width indices at every site. Tree-ring width series of each individual tree were detrended with a 50% frequency response at a wavelength of two-thirds of each series length (Cook & Kairiukstis, 1990). Then, the resulting indices were averaged using Tukey's biweight robust mean to get the site chronologies (R package "dplR"; Bunn, 2008).

2.6 | Statistics

To predict the resistance, recovery, and resilience indices in relation to growing degree-days reached at the last spring frost and to the water deficit from March to June, we used generalized additive mixed models (GAMMs) using the function "gamm4" in the R package "gamm4." The models included a smoothing spline with 4 *df* for either growing degree-days at the last spring frost or the climatic water deficit, with tree species as a factor modulating the spline and the site as a grouping variable for the random intercept. The fitted GAMMs with the associated means and confidence intervals allowed us to compare the species-specific resistance, recovery,

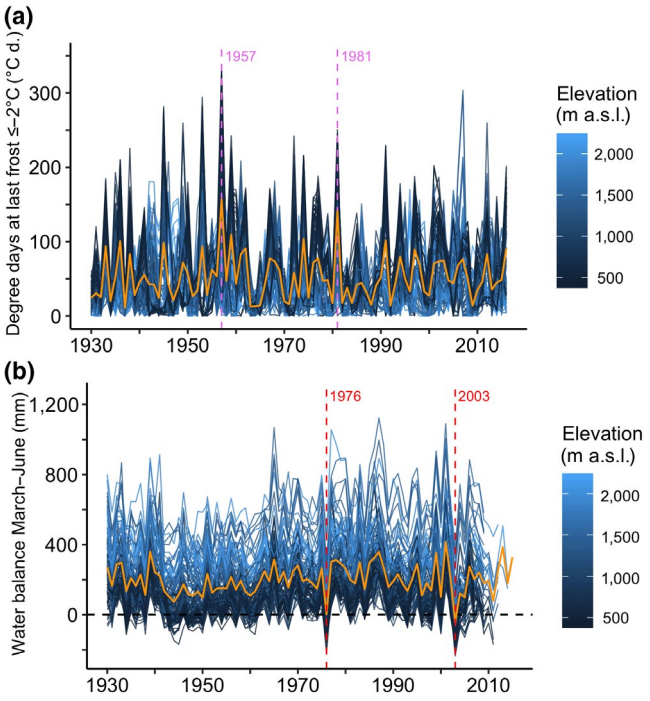

FIGURE 2 Identification of the most damaging spring frost and extreme drought years. (a) Degree-days reached at the last spring frost ≤−2°C for all 104 sites. Following the method developed in Vitasse and Rebetez (2018), the higher the growing degree-days accumulated before the frost event, the higher is the risk for plants to be injured by frost. Across all sites, 1957 and 1981 were on average the two most severe springs in terms of frost risk during the period 1930–2016 and are represented with vertical violet dashed lines. The damaging spring frost events of 1957 and 1981 occurred on May 8, and on April 19, respectively. (b) Climatic water balance (precipitation − potential evapotranspiration) from March to June in all 104 sites. Across all sites, 1976 and 2003 were on average the two driest springs during the period 1930–2016 and are represented with vertical red dashed lines. In both panels, the orange line represents the average across all sites

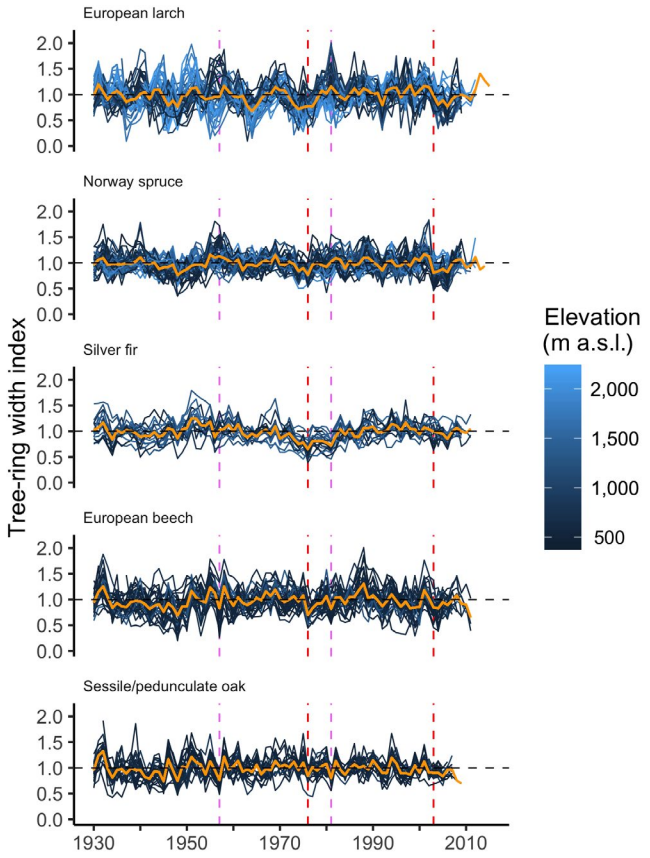

FIGURE 3 Tree-ring width chronology of each study population. Chronologies per site were obtained using spline models to detrend each individual tree-ring series. Red dashed lines correspond to the drought years 1976 and 2003, whereas the violet dashed lines correspond to the spring frosts 1957 and 1981. Orange lines represent the species-specific averages across all sites

and resilience to frost and spring drought for the same magnitude of stress. *F* values and significance levels of the smooth terms of these models are provided in Table S5.

All data analyses and statistics were performed using RStudio version 0.99.489 (R Core Team, 2015).

3 | RESULTS

3.1 | Impact of damaging spring frosts on growth

Across the 104 study sites, the 2 years 1957 and 1981 were those having, on average, the highest meteorologically defined risk of spring damaging frost during the period 1930–2016 (Figure 2a). A high frost risk was also detected locally in other years such as in 2007 for sites at elevations between 1,300 and 1,700 m a.s.l. or in 1945, 1953, 1959, and 1974 for lower elevation sites (Figure 2a). On average over the study period, 52 degree-days were reached at the time of the last spring frost below −2°C (as a proxy for the risk of frost damage, see methods), while it exceeded 140 degree-days in 1957 and 1981 with values beyond 200 degree-days in 43% and 37% of all sites, respectively, mostly at lower elevations (Figure 2a). These 2 years were not particularly dry (i.e., slightly negative and positive SPEI values across sites in 1957 and 1981, respectively; Figure S2), so that there is no confounding effect with drought.

During these 2 years, radial growth was strongly reduced for the two broadleaved species only, namely beech and oak (Figure 3). Resistance index plotted for all sites and all years in relation to the accumulated degree-days reached at the last frost ≤−2°C showed a significant decline beyond ~200–220 degree-days for beech and oak only, which mainly occurred in 1957 and 1981 at low-elevation sites (Figure 4a; Figure S3). Beyond this threshold, the resistance index was on average below 0.85 (i.e., >15% of growth reduction) for both beech and oak with values lower than 0.73 in 1957 across sites (i.e., >27% of growth reduction, Figure S4). Resistance values lower than 0.5 (i.e., more than 50% of growth reduction) were even found at a few sites (minimum of 0.27 for beech at one site in 1957, Figures S4 and S5).

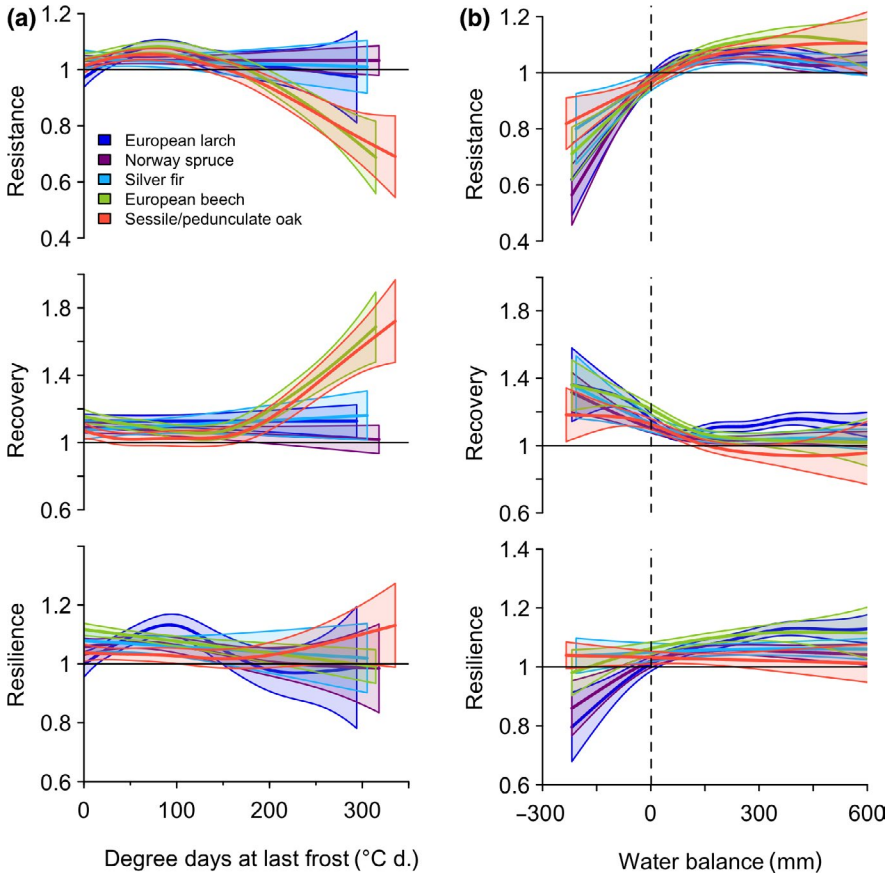

FIGURE 4 Prediction and 95% confidence intervals of the GAMM models for the resistance (top panels), recovery (middle panels), and resilience indices (bottom panels) considering all years depending on (a) degree-days accumulated before the last frost event ≤−2°C as a proxy for the risk of frost and (b) water balance from March to June. The resistance, recovery, and resilience indices were calculated using a pre- and post-period of 2 years (see Materials and Methods)

GAMMs predicted mean resistance values ≤0.75 for both beech and oak beyond 300 degree-days at the time of the last frost <−2°C (Figure 4a; Figure S3; Table S3).

Both species, however, fully recovered in the 2 years following these damaging spring frosts, leading to resilience values close to 1 for beech or even slightly higher for oak (Figure 4a; Figure S3; Table S3). In contrast, no growth decline was detected in response to these two late spring frost events for the three conifers, including the deciduous species larch (Figure 4a; Figure S3; Table S3).

3.2 | Impact of extreme spring droughts and summer temperature on growth

Our meteorological analysis revealed 1976 and 2003 as the driest springs observed from 1930 to 2016, with negative climatic water balance between March and June found for 58% (1976) and 70% (2003) of all the study sites (Figure 2b; Figure S6). Tree-ring width chronologies obtained for each site and species clearly showed that these two driest springs had a significant impact on current year growth for most species, especially at lower elevations (though less pronounced for oak in 2003, Figure 3). All species showed a significant reduction in growth resistance when the climatic water balance from March to June was negative (Figure 4b; Figure S7). However, the magnitude of this growth reduction in response to drought as well as the recovery and resilience within the following 2 years greatly differed among the species. For a water balance of −200 mm, predicted values of the resistance index from the GAMMs were lowest for spruce (0.60 ± 0.05) and larch (0.65 ± 0.06), intermediate for beech (0.73 ± 0.04), and highest for fir (0.81 ± 0.06) and oak (0.84 ± 0.04; Figure 4b; Table S4).

Remarkably, in spite of a recovery index well above 1, spruce and larch did not reach their predrought growth rates 2 years after extreme droughts (resilience index <0.87), whereas beech, oak, and fir showed resilience values close to 1 (Figure 4b; Table S4). Thus, fir and oak were more resistant and resilient than spruce and larch to extreme droughts. Beech presented intermediate values of resistance but a high resilience (Figure 4b; Table S4). To test the robustness of this pattern, we additionally assessed pre- and post-periods of 3 and 4 years before and after the drought and found very similar results (Figure S8; Table S4). More importantly, these results demonstrate that the lag effect of extreme droughts persisted for at least 4 years for spruce and larch, which contrasted with the growth of oak, beech, and fir that fully recovered within 2 years (Figure S8; Table S4).

Spruce and larch also showed a strong dependence of tree growth to mean summer temperature in relation to elevation. Below ~1,300 m, most populations of these two species exhibited negative relationships between summer temperature and tree-ring indices, while the opposite was found for higher elevations (Figure 5). For beech and oak, both positive and negative relationships were found at lower elevations. Remarkably, a positive or null effect of warmer summer temperature was detected for all populations of fir, irrespective of elevation (Figure 5).

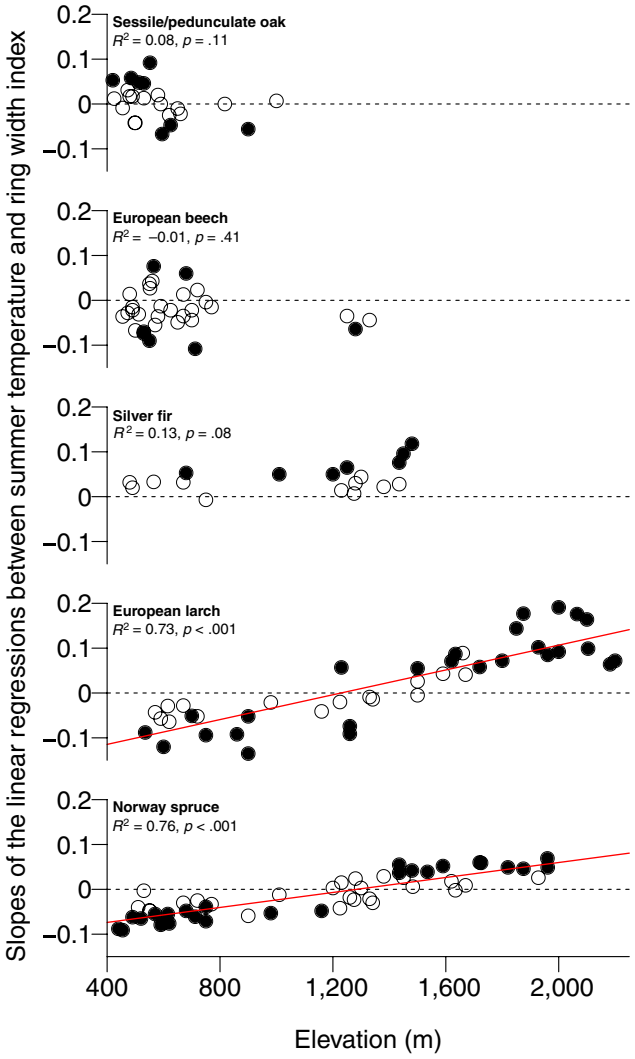

FIGURE 5 Slopes of the linear regressions between summer air temperature (May–August, 1930–2016) and tree-ring width chronology for each site in relation to elevation. Black dots correspond to significant slopes at $p < .05$. Significant linear regression lines ($p < .05$) are represented in red

4 | DISCUSSION

Extreme drought events are expected to increase in Europe in both magnitude and frequency (Ballester et al., 2010), while the risk of damaging spring frosts on major tree species remains uncertain for the future, but should persist in Europe or even increase in some regions due to earlier spring phenology (Ma, Huang, Hanninen, & Berninger, 2019). To provide a solid basis for decision-making regarding the future selection of species and provenances matching the changing environment, there is an urgent need to assess their specific responses to both drought and spring frost. Using tree-ring width series from 2,844 trees growing under a wide range of climatic conditions in central Europe, our results reveal strong disparities in the species resilience to both extreme events. An impact of spring frosts on tree growth was only detected for the two broadleaved species (beech and oak) with a magnitude that often exceeded the effects of extreme drought events. Nevertheless, both species quickly recovered after such damaging frosts. More importantly, our analysis allows comparing the resilience of the focal species to extreme droughts of similar magnitude. While oak, fir, and to a lower extent beech could moderately cope with severe droughts, spruce and larch poorly resisted and recovered after such events.

4.1 | Damaging spring frosts

Damaging spring frosts are assumed to cause growth reduction due to the shortening of the growing season and the cost of additional carbon resources to produce new leaves (Augspurger, 2009). Our study highlights the lower resistance of angiosperms to late frosts compared to gymnosperms (including deciduous species such as larch). This result could be due to differences in their coupling between leaf and wood phenology, in intra-annual nonstructural carbohydrate (NSC) dynamics, or in their different growing degree-days requirement. More particularly, (a) evergreen gymnosperms carry multiple needle generations and older needles are generally more resistant to frost than new needles in spring (but see Bachofen, Wohlgemuth, Ghazoul, & Moser, 2016 for pines), and can therefore compensate for photosynthesis when the new needles are damaged (except for the deciduous larch); (b) beech is characterized by stronger dependence of radial growth to leaf photosynthesis rather than to stored stem NSC, showing low growth rates until leaves are fully developed (Michelot, Simard, Rathgeber, Dufrêne, & Damesin, 2012). However, a strong contribution of stored carbon to early wood growth has been postulated for beech in other studies (Helle & Schleser, 2004; Skomarkova et al., 2006). In contrast to evergreen coniferous species, which mainly use NSC from old needles to produce the new flush, deciduous trees rely on stem and branch NSC for leaf development (Egger et al., 1996), and thus, a preferred allocation of carbon from these storage pools for leaf repair or to a second leaf flush might strongly compete with radial stem growth. (c) Finally, the two studied conifer species are known to have quite an early (larch) and late (spruce) budbreak (Bigler & Bugmann, 2018). Larch could therefore be more exposed to spring frosts but has a higher freezing resistance (LT50 of ~−7°C, Bigler & Bugmann, 2018; Taschler & Neuner, 2004) whereas spruce may largely avoid late spring frosts as it requires higher growing degree-days to develop new needles (Vitasse, Schneider, et al., 2018). Our method that uses the accumulation of degree-days from midwinter to the last potentially damaging frost as a proxy for the frost risk proved to be reliable as it shows an abrupt decline of radial growth when this accumulation exceeds ~200 degree-days for both angiosperm species. This threshold seems sufficient to trigger leaf out of many European broadleaved species (Fu et al., 2015; Vitasse, Schneider, et al., 2018), although short photoperiod in early spring may prevent too precocious leaf out for some species such as beech (Fu et al., 2019). Furthermore, our results identified 1957 and 1981 as the 2 years with the highest meteorologically defined risk of spring damaging frost during the study period across all sites, which is consistent with the damage reported in orchards in the Swiss weather archive from MeteoSwiss (annual reports available at https://www.meteoswiss.admin.ch/home/climate.html).

Interestingly, our results show no carry over effect of the impact of damaging frost for the two broadleaved species on radial growth of the next 2 years, as also found recently for beech in Germany after local spring frosts (Príncipe et al., 2017). This is likely because trees are able to produce a new cohort of leaves during the same growing season, allowing to refill carbon reserve later in autumn (Zohner, Rockinger, & Renner, 2019). However, a secondary bud flush later in the same growing season may cause a depletion of plant carbon reserves at a time when water and nutrient availability is generally lower, which may weaken tree defenses against diseases and insect pests (McDowell et al., 2011), an aspect that has remained largely unconsidered so far.

4.2 | Extreme spring droughts

Our results suggest that spruce, larch, and to a lower extent beech exhibit rather low resistance and resilience to extreme spring droughts whereas oak and fir are more tolerant. Although the link between radial growth and tree vitality is not straightforward, severe droughts can induce negative plant water potentials that inhibit cell division and expansion resulting in cessation of xylogenesis and longer periods of stomatal closure (Ryan, 2011). Severe droughts can further lead to hydraulic failure caused by xylem embolism if the tension in the xylem water becomes too high (Choat et al., 2012) and the loss of hydraulic conductivity versus the ability to regain functional xylem might affect species-specific recovery (Yin & Bauerle, 2017). NSC storage has been shown to be maintained under lower carbon availability at the expense of biomass accumulation in various tree species (Weber, Gessler, & Hoch, 2019) thus offering an explanation for reduced radial growth. Moreover, both hydraulic and carbon constraints (Herms & Mattson, 1992; McDowell et al., 2011) can lead to general metabolic limitations as indicated by impaired carbon transport from sources to sinks (Ruehr et al., 2009) or reduced allocation to defense compounds (McDowell et al., 2008) and the consequences thereof might strongly determine the recovery trajectories. Our findings are in agreement with recent dendroecological studies showing a higher vulnerability of spruce and larch to drought than fir (Lévesque et al., 2013; van der Maaten-Theunissen, Kahle, & Maaten, 2012; Vitali, Buntgen, & Bauhus, 2017), which is also in line with studies showing a high sensitivity of spruce to elevated VPD (Sanginés de Cárcer et al., 2018) and the inability of its root system to access deep water layers during summer drought (Brinkmann, Eugster, Buchmann, & Kahmen, 2019). Our study also confirms that sessile and pedunculate oaks are able to cope with severe hot drought, as previously suggested in a study focusing on its water status and photosynthesis during the extremely hot drought in 2003 (Leuzinger, Zotz, Asshoff, & Körner, 2005).

4.3 | European tree species under global warming

Our results demonstrate contrasting resistance and resilience of major European tree species to ECEs with spruce and larch exhibiting the highest vulnerability to severe droughts. Thus, if the frequency of ECEs increases, competition among tree species may change, resulting in structural and functional changes within forest ecosystems (McDowell et al., 2018). Besides, our results underline that spruce and larch are not only constrained by severe spring droughts but also by warmer summer temperatures resulting in a strong dependency of tree growth to mean summer temperature in relation to elevation. Over the past decades, warmer summers enhanced the radial growth of these two species above ~1,300 m but reduced it below this elevation. In contrast, we found that warmer summers had neutral to beneficial effects on the radial growth of silver fir, even at low elevation sites. In addition, fir is the only species for which the SPEI calculated over the summer months was on average across sites negatively correlated with tree-ring width chronologies indicating increased growth under drier conditions (Figure S1). This surprising result may be related to its deep-rooting system, which allows to profit from high temperatures often associated with drier conditions in summer without substantial water limitation, and to its early growth in spring (Vitasse et al., 2019). Our study area, however, is situated in the core of the species distribution and different results might be expected at warmer and drier sites. For example, silver fir has been reported to decline at the southern margin of its distribution in the Spanish Pyrenees, likely as a consequence of the cumulative effect of very dry years that have followed the exceptionally warm and dry summer of 2003 (Gazol et al., 2015; Linares & Camarero, 2012).

Although the time window from March to June was best correlated with the tree-ring index (Figure S1) and encompasses the beginning of tree radial growth, species may have different periods of drought sensitivity. For instance, in some regions, radial growth of silver fir has been shown to be sensitive to previous summer–autumn conditions and radial growth of beech to previous summer conditions (Pasho, Camarero, Luis, & Vicente-Serrano, 2012; Vicente-Serrano, Camarero, & Azorin-Molina, 2014). Our results are still relevant to show how extreme spring droughts affect radial growth of different species but do not account for previous winter or summer conditions. Biotic factors that were not considered in this study, such as the occurrence of mast years and insect outbreaks, may also strongly affect radial growth and their frequency could also change under future warmer climate. For example, recent studies highlighted a strong radial growth reduction during and after mast years for beech (Hacket-Pain et al., 2018) or during and after larch budmoth outbreak for larch (Peters, Klesse, Fonti, & Frank, 2017). Although we cannot rule out the influence of mast years in our study, the influence of larch budmoth outbreak should not affect our result concerning the impact of spring droughts for this species as critical climatic water balance was found only at low-elevation sites where the larch budmoth is absent.

Because global warming is increasing the frequency and magnitude of drought events and advancing spring phenology, the probability that a damaging frost would occur in the same year as an extreme drought is likely to increase in the next decades. Besides, the resilience to ECEs may quickly decline if their frequency reaches a critical level. Hence, more investigations are necessary to assess the cumulative and cascading long-term effects of damaging frost and spring/summer drought on tree vigor

if they occur within the same year or in consecutive years as they may deplete tree carbon reserves and promote favorable conditions for pests and pathogens.

5 | CONCLUSIONS

Our results allow for a robust comparison of the vulnerability of major European tree species to spring frosts and droughts. While the two broadleaved species, oak and beech, are less resistant to late spring frosts than coniferous species, they are still highly resilient to frost. However, as for the other species, they show lower resilience to extreme drought, likely because drought affects the hydraulic integrity of the xylem while late spring frost affects mainly leaves. Among conifers, larch and spruce showed the strongest growth reduction in response to severe droughts while fir and oak showed higher resistance and resilience to such events. Providing that the frequency of damaging frost does not increase, deciduous oak species and fir seem better adapted to the projected warmer and drier climate conditions in lowlands of central Europe and should therefore be promoted on suitable sites to ensure healthy forests providing multiple ecosystem services.

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ORCID

Yann Vitasse https://orcid.org/0000-0002-7454-505X
Alessandra Bottero https://orcid.org/0000-0002-0410-2675
Maxime Cailleret https://orcid.org/0000-0001-6561-1943
Christof Bigler https://orcid.org/0000-0003-3757-6356
Patrick Fonti https://orcid.org/0000-0002-7070-3292
Arthur Gessler https://orcid.org/0000-0002-1910-9589
Mathieu Lévesque https://orcid.org/0000-0003-0273-510X
Brigitte Rohner https://orcid.org/0000-0003-3768-092X
Andreas Rigling https://orcid.org/0000-0003-1944-4042
Thomas Wohlgemuth https://orcid.org/0000-0002-4623-0894

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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