

European beech resistance to false spring is associated with small-vessel xylem conductivity

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ABSTRACT

Climate warming advances spring phenology in temperate forests, increasing exposure of early leaf-out species such as European beech (*Fagus sylvatica* L.) to late frost defoliations (LFDs). Leaf-out timing, a key factor in determining the exposure to spring frosts, may be partially associated with wood anatomical traits. Trees with a higher fraction of narrow conduits exhibit limited xylem embolism during winter, which would promote high xylem conductance in spring, enabling trees to rapidly develop a new canopy. This study aims to determine whether intraspecific variation in xylem vessel traits formed during the preceding growing season predicts individual level susceptibility to spring-frost growth reductions in European beech. Four stands were sampled along elevation gradients: two in the Apennines (Italy) and two in the Pyrenees (Spain). Tree-ring analyses identified negative pointer years linked to validated LFDs. Frost resistance was related to a set of vessel traits: theoretical hydraulic conductivity (Ks), conductivity from small (18–30 μm wide) vessels (Ks_{18–30}), mean hydraulic diameter (Dh), and relative conductive area (RCA). Despite representing only $\approx 0.6\%$ of total Ks, Ks_{18–30} was the only xylem trait significantly associated with higher vulnerability to LFD in the linear mixed-effects models. Most variation was attributable to site-, elevation-, and event-specific factors, while Ks_{18–30} explained only a limited portion of the residual individual-level variability. This result was consistent across alternative model formulations and sensitivity analyses, suggesting that Ks_{18–30} may represent a robust anatomical correlate of spring-frost vulnerability and a potential link between xylem anatomy and tree phenological responses to extreme spring climatic events.

1. Introduction

Trees' spring phenology, which includes processes like budburst and leaf-out, is advancing due to climate warming (Chamberlain and Wolkovich, 2021; Mantovani et al., 2026). This shift has significant implications for plant productivity, forest dynamics, and ecosystem functioning (Fridley 2012; Zohner et al., 2021). While advanced phenology may extend the growing season and enhance plant productivity, earlier leaf-out increases the vulnerability of deciduous species to late frost defoliations (LFD), which can damage emerging leaves, limit growth, affect tissue traits, and ultimately reduce forest productivity (Schwartz et al., 2006; Hufkens et al., 2012; Qiu et al., 2024; Wang et al., 2025). A false spring is an extreme meteorological event with unusually

early spring warm weather that prompts precocious leaf phenology and followed by a rapid temperature drop leading to freezing conditions (i.e. growing-period frost). This compound event is critical because it enhances the likelihood of frost damage and the ecological consequences of climate-driven phenological changes. Major tree species of high ecological and economic importance such as European beech (*Fagus sylvatica* L.), are highly susceptible to false springs, suffering severe defoliation that can reduce forest growth (Gazol et al., 2019; Baumgarten et al., 2023; Rubio-Cuadrado et al., 2025; Vitasse et al., 2025). The timing of bud break and leaf-unfolding strongly influences vulnerability to LFDs; when they occur earlier, triggered by warm spells associated with false springs, the risk of frost injury rises substantially. Nonetheless, not only warm temperature regulates beech spring

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phenological responses.

Budburst timing in European beech is a complex interplay of photoperiod, temperature and chilling requirements (Vitasse and Basler, 2013; Kramer et al., 2017). Consequently, in mountainous regions, leafing occurs earlier at lower elevations compared to higher ones (Cufar et al., 2012). However, the chilling requirement makes these differences less pronounced in beech trees compared to other tree species (Vitasse et al., 2009; Fu et al., 2015). As a result, LFDs can have varying effects in mountain areas depending on the elevation of the forest stands (Sangüesa-Barreda et al., 2021; Tonelli et al., 2023). Certain spring frosts may affect forests only at higher elevations, as extreme temperatures are typically lower there. Instead, frosts associated with thermal inversions may cause damages downslope. Sometimes, frost damage primarily affects forests at low or mid elevations, while the uppermost areas remain largely unaffected because budburst occurs later. During this period, buds exhibit substantially greater resistance to freezing temperatures compared to newly unfolded leaves (Vitasse et al., 2014; Menzel et al., 2015; Lenz et al., 2016), explaining the reduced frost impact at higher altitudes.

Defoliation rates do not depend solely on elevation gradients. Variation in tree phenology can occur among individual trees of the same stand and species (Malyshev et al., 2022). European beech trees exhibit substantial stand-level variation of freezing tolerance, likely driven by asynchronous leaf-out, whereby earlier emitted leaves are disproportionately vulnerable to frost damage (Kunert and Gebhard, 2026). Thus, alongside fully defoliated trees, may be found neighbouring individuals unaffected by the LFD (Fig. 1a). Population-level phenological dynamics are crucial because these differences reflect variation in onset timing

and damage severity, yet the role of inter-individual variation within stands remains comparatively understudied (Malyshev et al., 2022). Individual beech trees consistently maintain their early-leaving phenological rank across years, and these stable differences are strongly linked to their growth (Delpierre et al., 2017). Although inter-individual differences in budburst have been linked to microsite heterogeneity and genetic variation (Müller et al., 2015), evidence suggests that neither microclimate nor genotype can fully explain the remarkable variation in leaf-unfolding dates observed among individual trees (Delpierre et al., 2024). Additional traits with potential effects on tree phenology include social status and ontogenetic stage (Vitasse, 2013; Gressler et al., 2015).

Yet, the physiological mechanisms underlying inter-individual differences in leaf-out timing remain incompletely understood. Among the traits that may contribute to this variability, wood anatomy has been proposed as a potential correlate of leaf-out timing because xylem vessel traits influence hydraulic transport capacity during spring (Panchen et al., 2014; Savage et al., 2022). In temperate deciduous forests, xylem vessel traits have likewise been shown to predict both spring and autumn leaf phenology (Yin et al., 2016). Trees featuring narrow conduits generally exhibit lower vulnerability to embolism during winter and drought periods (Scholz et al., 2013; Lens et al., 2022; Isasa et al., 2023). This promotes greater hydraulic functionality at the onset of the growing season (Grícar et al., 2020; Savage et al., 2022). In contrast, trees with wider conduits are likely more vulnerable to embolism and must delay leafing out until new functional conduits are formed through xylogenesis. It has been observed that, at leaf-out, trees rely on xylem formed during the preceding growing season, and species with wider vessels generally exhibit later leaf-out (Savage et al., 2022). Also, because conduit size is positively correlated with tree height (conduit widening, Olson et al., 2021), taller trees are more susceptible to conduit embolism in the basal stem (Zambonini et al., 2024) and may exhibit delayed leaf-out under false spring conditions relative to smaller individuals. Younger (and also smaller) trees tend to resume cambial activity earlier than older, taller ones, as shown in studies of age-dependent xylogenesis documented in several conifer species (Rossi et al., 2008). These differences in anatomical traits may contribute to explain the variable leaf-out timing observed among trees of different structure and ontogenetic phase. Although previous studies have linked xylem anatomy to hydraulic functioning and phenology, whether intraspecific variation in vessel traits is associated with individual resistance to false-spring events remains unresolved.

In this study, we employed a single-tree sampling design to investigate growth anomalies associated with false spring events in European beech. Specifically, we tested whether variation in xylem vessel formed during the preceding growing season influences the susceptibility to ring-width constriction. This approach is based on the assumption that xylem functionality declines substantially during winter due to embolism (Wang et al., 1992; Sperry et al., 1994). Accordingly, we hypothesize that variation in the contribution of small-diameter conduits to hydraulic conductivity is associated with differences in individual susceptibility to false spring-induced growth reductions. Predisposing hydraulic traits, measurable through quantitative wood anatomy (QWA), may amplify the impact of late frost damage by influencing phenological timing. To evaluate these predictions, we analysed four pure beech forest stands located in two climatically contrasting mountain range conditions: wet-cool in the Italian Apennines vs. continental in the Spanish Pyrenees.

2. Material and methods

2.1. Study sites

We studied four sites (Fig. 1b) located two in the Central Apennines (Italy) and two in Central Pyrenees (Spain). All fall within the continuous distribution range of European beech (Pott, 2000) and host beech

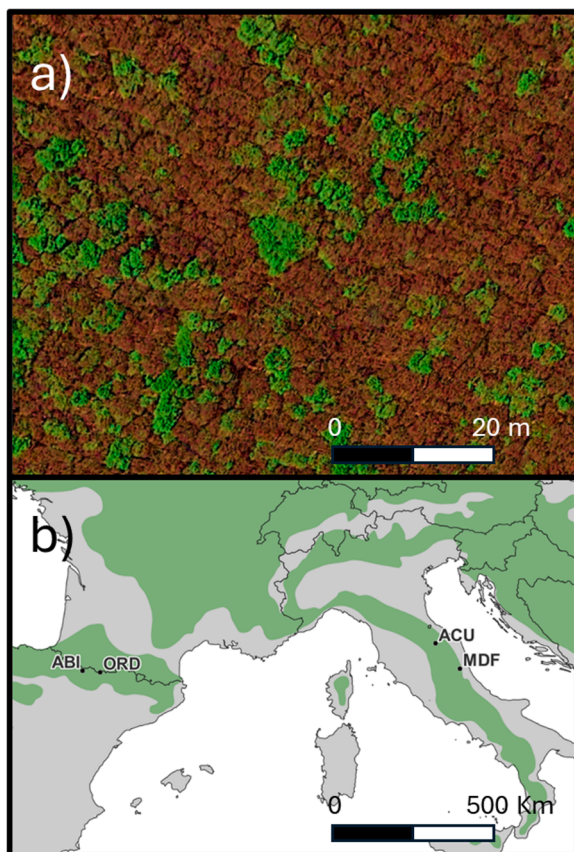


Fig. 1. (a) Aerial view of a pure beech forest (MDF, Italy) showing tree-specific damage caused by a late frost event occurred in the spring of 2016 (Google Earth image, May 22, 2016). (b) Location of the four study sites (ACU, MDF, ABI and ORD) and distribution range of the European beech across southern Europe (green area) (Pott, 2000).

forests extending with no interruption for at least 300–400 m of elevation from mid-slope to the upper forest line. Monte Acuto (ACU) and Montagna dei Fiori (MDF) populations in the Apennines display distinct forest structures characteristics. ACU is located on a limestone massif, with pure beech high forests on lower slopes and transitioning coppices at higher elevations. MDF features unmanaged broadleaf stored coppices in a temperate sub-Mediterranean climate. The two sites in the Pyrenees are Hayedo de Abi (ABI) and Valle de Pineta (ORD). ABI is situated within the Western Valleys Natural Park in Aragón and displays a geomorphological framework shaped by karstic and glacial processes. The surroundings are temperate montane forests mainly composed of beech, silver fir (*Abies alba* Mill.) and Scots pine (*Pinus sylvestris* L.). ORD is located in the “Ordesa y Monte Perdido” National Park and exhibits limestone formations and geomorphic features largely shaped by Pleistocene glacial activity. Forests are also mainly of mixed conifers and broadleaves.

2.2. Recent false spring events

False-spring episodes have affected all the study areas repeatedly in recent decades, causing defoliation of varying intensity across elevation gradients. The two Apennines sites correspond to those analysed in a previous study (Tonelli et al., 2023), whereas the Pyrenees sites have been selected after reports of severe LFD (e.g., 2010, 2017) from local forest managers and technicians. All cited LFD events (Table 1) are cited in previous studies (Bascietto et al., 2018; Nolè et al., 2018; Sangüesa-Barreda et al., 2021; Olano et al., 2021; Tonelli et al., 2023) and validated through four independent sources of evidence/proxies: dendrochronological data, climatic records, field observations of defoliation, and satellite imagery (Sentinel-2 and Landsat).

In the central Apennines, LFD events occurred when temperatures abruptly dropped below 0 °C between late April and early May. Major episodes were recorded in 1957, 1991, 2001, 2016, and 2017, with minimum temperatures reaching approximately −3.9 °C (Bascietto et al., 2018; Nolè et al., 2018; Sangüesa-Barreda et al., 2021; Tonelli et al., 2023), well below the temperature at which beech leaves lose half of their functional capacity (Kunert and Gebhard 2026). These frost snaps were all preceded by winter chilling and anomalously warm springs, with high accumulated degree-days (ADD) (Sangüesa-Barreda et al., 2021; Tonelli et al., 2023). Such conditions advanced leaf unfolding, leaving newly emerged beech foliage highly vulnerable to returning freezing temperatures.

The Pyrenean region experienced very few LFD events before 1990, but their frequency and spatial extent have increased in recent decades (Sangüesa-Barreda et al., 2021). Tree-ring records reveal regional and synchronous growth reductions across sites during major frost years, particularly 1997, 2010, 2013, and 2017 (Olano et al., 2021; Sangüesa-Barreda et al., 2021). As observed in the Apennines, these episodes were preceded by unusually warm early-spring conditions, suggesting that accelerated phenology increased exposure to subsequent cold spells.

2.3. Sampling design and tree-rings data

Because LFD events vary in severity across elevations, we examined their recent impacts by sampling pure beech stands distributed along

Table 1

List of Late Frost Defoliation (LFD) events associated to false springs examined in this study.

Region	Site	LFD years
Apennines	ACU	2017, 2016, 1991, 1957
	MDF	2016, 2001, 1957
Pyrenees	ABI	2017, 2013, 2010, 1997
	ORD	2017, 2013, 2010, 1997

low, mid, and high-elevation belts at each site (Table 2). Within each elevation belt, we selected five dominant trees for QWA analysis, and increment cores were extracted at breast height (1.30 m) using a 10-mm borer. We also measured the total height of each sampled tree with a hypsometer. Additionally, fifteen additional individuals were sampled using a 5-mm increment borer, resulting in 20 trees per each elevation belt and 60 trees per site. All cores were mounted on wooden supports and polished with progressively finer sandpaper. Tree-ring widths were measured to 0.01 mm using a semi-automatic system (LINTAB). Each series was visually cross-dated and verified with COFECHA software (Holmes, 1983). All series pass minimum COFECHA thresholds of less than 40% “problem segments”, and greater than 0.35 Mean Series Inter-correlation.

To obtain reliable estimates of tree size at each false spring event, tree-ring series were used to retrospectively adjust measured diameters by subtracting the corresponding annual increments from the values recorded on each survey date.

Severe LFD usually limits significantly the cambial activity of trees, resulting in the formation of narrow growth rings. To identify these anomalies along the elevation gradient, we conducted a pointer-year analysis (Schweingruber et al., 1990) on tree-ring series for years with proved LFD events (Table 1). We applied the ‘Normalization in a Moving Window’ method (Cropper 1979) to all tree-ring series using the PointRes package in R (van der Maaten-Theunissen et al., 2015). This technique generates Cropper values (zi) by normalizing ring-width data within a five-year moving window (1).

$$z_i = \frac{X_t - \bar{X}_t^{(n)}}{sd_t^{(n)}} \text{ with } \begin{cases} \bar{X}_t^{(n)} = \frac{1}{2n+1} \sum_{k=-n}^n X_{t+k} \\ sd_t^{(n)} = \sqrt{\frac{1}{2n} \sum_{k=-n}^n (X_{t+k} - \bar{X}_t^{(n)})^2} \\ n = 2 \end{cases} \quad (1)$$

Years with zi values equal to or lower than −0.75 were classified as negative event years. A negative pointer year was assigned when the same event year occurred in at least 50% of the series within the same altitudinal belt. This analysis proved which elevation belts were impacted by documented LFD events.

Then, to assess the individualistic tree-level resistance to late frost defoliations (LFD_Rt) in affected elevational belts, we used the following equation (2) (Lloret et al., 2011).

$$LFD_Rt = \frac{Ring\ width_t}{\frac{1}{5} \sum_{i=1}^5 Ring\ width_{t-i}} \quad (2)$$

LFD_Rt was derived from 10-mm cores (five per elevational belt per site), which served as the basis for extracting anatomical traits. The five-year window was initially selected to provide a stable baseline for evaluating tree resistance.

To account for potential multi-year lagged growth responses and to test the sensitivity of our results to the choice of baseline period, we repeated the resistance analysis using alternative pre-disturbance windows of three and seven years. In addition, to reduce the influence of anomalous growth years within the baseline period (e.g. droughts, late frost events or masting), we compared the conventional formulation based on the arithmetic mean of pre-disturbance ring widths with an alternative index based on the median.

Finally, for the seven-year window, we further evaluated a robust estimation approach by computing the Tukey's biweight robust mean, a method commonly used in dendrochronology to minimize the influence of outliers in chronology construction (Cook and Kairiukstis, 1990).

2.4. Anatomical slide preparation and analysis

The 10-mm wood cores (n = 60) were first divided in 4-cm-long

Table 2

Geographic characteristics of the study sites and their elevation ranges along the gradient.

Region	Site code	Latitude (°N)	Longitude (°E)	Slope aspect	Elevation (m a.s.l.)		
					Low	Mid	High
Apennines	ACU	43.4767	12.6757	NW	1080	1245	1375
	MDF	42.7886	13.5877	NE	1159	1423	1584
Pyrenees	ABI	42.7320	-0.5905	W	1428	1471	1562
	ORD	42.6860	0.0677	SE	1314	1597	1738

wood sections with oblique cuts, so that each contiguous piece shared one or more tree-rings with the following one. Wood samples were then boiled in water and glycerol solution for 30 minutes to soften the wood and avoid damage to cell structures during cutting. Anatomical micro-sections of 10–12 μm thickness were cut with a rotary microtome (Leica RM2245/ Leica Histocore). Permanent slides were prepared staining with safranin and astrablue. The slide preparation procedure requires sections dehydrating using ethyl alcohol and permanent sections fixing between glass slide and a cover glass with the Eukitt® mounting medium. Slides were sandwiched between PVC strips with a magnet placed on the top of the slides and a metal plate below to keep the microsection flat and avoid air bubbles formation during drying. High-resolution digital images of anatomical sections were captured using slide scanners (D-Sight, A. Menarini Diagnostics srl or Axioscan 7, Carl Zeiss AG) at 100x magnification.

Scanned images were then analysed with the ROXAS v3.0.1 tool and the image-processing software Image-Pro Plus v6.1 to extract vessel and tracheid features (von Arx and Carrer, 2014) and dated using the tree-ring measurements previously obtained. To address the hypothesis, four anatomical traits were computed for each tree-event combination, from the tree-ring formed in the year preceding the investigated events (Table 1): xylem-specific hydraulic conductivity assuming a tube length of one meter (K_s), the fraction of K_s ensured only by small-diameter vessels (K_{s18-30}), hydraulically weighted mean vessel diameter (D_h) and relative conductive area (RCA). K_s was calculated as the ratio between the theoretical hydraulic conductivity as approximated by Poiseuille's law and the total ring area (Scholz et al., 2013). The computation of K_{s18-30} refers exclusively to the hydraulic conductivity provided by conduits with diameters ranging between 18 and 30 microns. These thresholds were selected because an 18-mm diameter allows for the distinction between the lumens of fibres and those of vessels (Sass and Eckstein 1995), while a 30-mm diameter represents a threshold below which greater resistance to embolism is supposed (Davis et al., 1999). Finally, D_h was calculated following Sperry et al., (1994) and RCA as the ratio between conductive area and total examined ring area.

2.5. Statistical modelling

This study employed Linear Mixed-Effects Models (LMMs) to account for both fixed and random sources of variability in resistance to late frost defoliations (LFD_{Rt}) in elevation belts where pointer years occurred (i. e., populations affected by late frost events). Site was treated as a fixed effect in the main analyses, allowing us to control for site-specific differences without estimating a poorly supported random variance component.

The response variable (LFD_{Rt}) was Box–Cox transformed to improve normality using the powerTransform function from the car package in R (Fox and Weisberg, 2018). Prior to model fitting, all continuous predictors were standardized to zero mean and unit variance to facilitate the comparison of effect sizes, improve model convergence and ensure comparability among variables measured on different scales.

Our hypothesis was that resistance to late frost events is influenced by xylem anatomical traits, particularly by the contribution of small vessels (18–30 μm diameter) to hydraulic conductivity. Accordingly, the main anatomical model (Model A) was specified as:

$$LFD_{Rt} \sim K_{s18-30} + D_h + RCA + DBH + Site + (1|Site : Belt : Year) \quad (3)$$

where K_{s18-30} , D_h and RCA were pre-frost anatomical traits and DBH the retrospectively estimated diameter. A random intercept for Site:Belt: Year was included to account for repeated measurements within the same site, belt, and year combination.

The robustness of Model A was assessed through a series of sensitivity analyses. First, we tested the consistency of results across the different definitions of resistance used, which varied according to the width of the pre-disturbance temporal window (3, 5 and 7 years) and calculation methods for the baseline (mean, median, and biweight mean). Second, we performed a sensitivity analysis to evaluate how the definition of small vessels (18–30 μm) affected the selected model. The Model A was repeatedly refitted while increasing the upper vessel-diameter limit from 20 to 50 μm in 1- μm steps. The lower bound was fixed at 18 μm to avoid including fibres.

To evaluate whether alternative representations of hydraulic functioning influenced the observed relationships, an additional model (Model B) was fitted in which the anatomical predictors D_h and RCA were replaced by K_s :

$$LFD_{Rt} \sim K_{s18-30} + K_s + DBH + Site + (1|Site : Belt : Year) \quad (4)$$

Model B represents an alternative functional hypothesis whereby resistance is associated with whole hydraulic efficiency rather than directly with its anatomical determinants. Because K_s is intrinsically derived from xylem anatomical properties and is therefore strongly linked to D_h and RCA, these variables were not included simultaneously in the same model to avoid interpretational issues arising from their functional dependence.

Finally, the sensitivity of model results to the representation of spatial variability was evaluated by replacing Site with alternative fixed-effect structures. First, elevation belt was used as the spatial grouping factor (Model C) to evaluate whether elevation had a significant effect independently of the site structure:

$$LFD_{Rt} \sim K_{s18-30} + K_s + DBH + Belt + (1|Site : Belt : Year) \quad (5)$$

Second, all combinations of Site and Belt were treated as distinct populations (Model D), allowing the assessment of stand-specific responses while maintaining a consistent random-effects structure:

$$LFD_{Rt} \sim K_{s18-30} + K_s + DBH + Site \times Belt + (1|Site : Belt : Year) \quad (6)$$

All models were fitted using Restricted Maximum Likelihood (REML) with the lmer() function from the lmerTest package, which provides degrees of freedom and p-values based on Satterthwaite's approximation (Kuznetsova et al., 2017). Multicollinearity among predictors was assessed using the Variance Inflation Factor (VIF). Residual normality was primarily evaluated through visual inspection of Q–Q plots and additionally verified using the Shapiro–Wilk test. Homoscedasticity was assessed through residual-versus-fitted plots and further examined using the Breusch–Pagan test.

Exploratory analyses were conducted to visualize patterns associated with predictors retained in the final model. For each significant predictor, a non-parametric bootstrap procedure (10,000 resamples) was

used to estimate the sampling distribution of mean values within two resistance classes: unaffected trees ($LFD_Rt > 0.75$) and affected trees ($LFD_Rt < 0.75$). These distributions were visualized using violin plots and further stratified by region, site and elevation belt to evaluate context-dependent patterns. Differences between resistance classes were assessed using Welch's two-sample t-test, selected for its robustness to unequal variances and sample sizes.

3. Results

3.1. Frost-induced growth limitation across elevations

The mean age of the sampled trees is consistent across all sites and elevation belts, averaging approximately 70 years (Table S1). However, notable deviations are observed in the lower belt at ACU and, more prominently, in the upper belt at ORD, where the mean age reaches 208 years. Regarding radial growth, the average ring width exhibits a general inverse relationship with elevation across most sites, with growth rate declining upwards (Fig. 2). An exception to this trend is observed at the ABI site, where altitude range is smaller and no variation in mean growth is detected along the elevational gradient.

Most populations show an abrupt growth decline related to false springs (Fig. 2). The percentage of affected individuals varied between elevation belts and years, with sites in the Pyrenees generally showing higher proportions of affected trees (Fig. 3, Table S2). The 1957 event at the ACU site had a severe impact across all populations along the elevational gradient, with over 90% of individuals exhibiting a negative event year. During the other events, the impacts varied depending on elevation. However, there is no clear relationship between population elevation and the percentage of affected trees. The ACU site experienced two sequential events (2016 and 2017) that impacted distinct altitudinal

belts of the slope. In 2016, defoliation was more pronounced at higher elevations, whereas in 2017 the mid-slope belt was the most affected.

In affected elevation belts, mean LFD_Rt values are generally below 0.5 in both the Pyrenees and Apennine stands (Fig. S1). The analysis of resistance further indicates that interquartile ranges are broader in Apennine sites compared to those in the Pyrenees (Fig. S1). On average resistance progressively decreased as elevation increased (Fig. S1). Among the studied sites, MDF exhibited the highest resistance values, whereas ACU displayed the lowest ones, highlighting pronounced spatial heterogeneity in trees responses to false spring stress. The alternative resistance metrics produced highly comparable estimates, with strong positive correlations observed among all methods used to define resistance (Fig. S2).

3.2. Pre-frost variation in xylem vessel traits

Vessel traits formed during the year preceding the false-spring event show strong site-specific contrasts and a clear influence of elevation (Fig. 4). K_s reveals pronounced differences among sites: ORD and ABI Pyrenean sites show markedly higher median K_s values and greater variability, particularly within high belts, whereas ACU and MDF Apennine sites display lower K_s values. K_{s18-30} follows a different spatial pattern with MDF consistently showing elevated values. ORD exhibits the highest values of RCA, especially in the old-growth population located at high elevation. ABI also exhibits relatively high RCA values, whereas ACU and MDF maintain lower medians. Dh mirrors the trends observed for RCA: ORD shows higher values and variability, while ACU and MDF exhibit more constrained values. Dh values show a clear increasing trend along the elevational gradient in ACU (Fig. S3).

To explore the relationships among vessels traits, we computed Pearson correlation coefficients for K_s , K_{s18-30} , RCA, and Dh, assessing

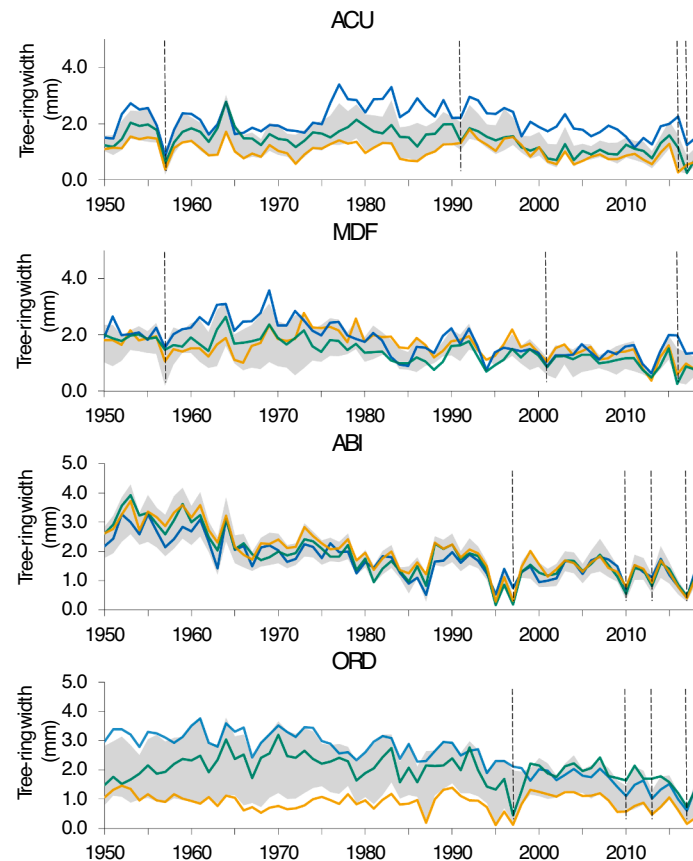


Fig. 2. Mean tree-ring widths across the three elevation belts (Low:blue, Mid:green, High:orange) in the period 1950–2018. The grey shading represents the annual interquartile range of tree growth at each site (60 trees). Vertical dashed lines indicate LFD events (see Table 1).

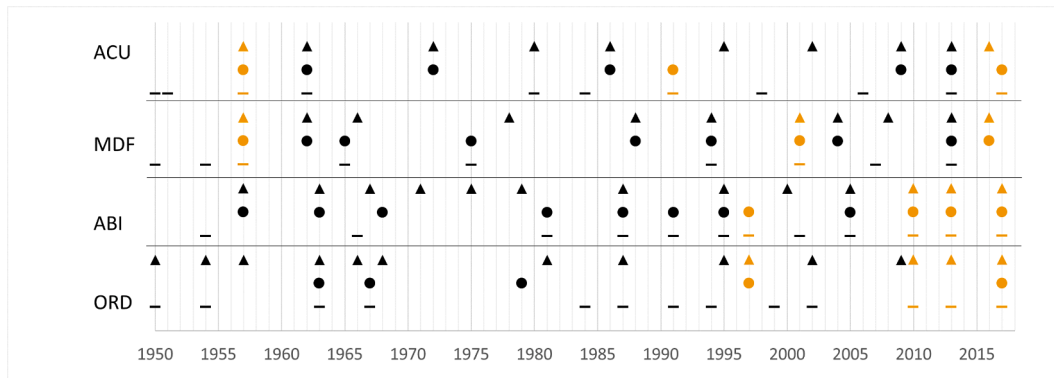


Fig. 3. Negative pointer years detected at high (▲), mid (●) and low (–) elevation belts of the four study sites in the period 1950–2019. In orange the negative pointer years with concomitant LFDs.

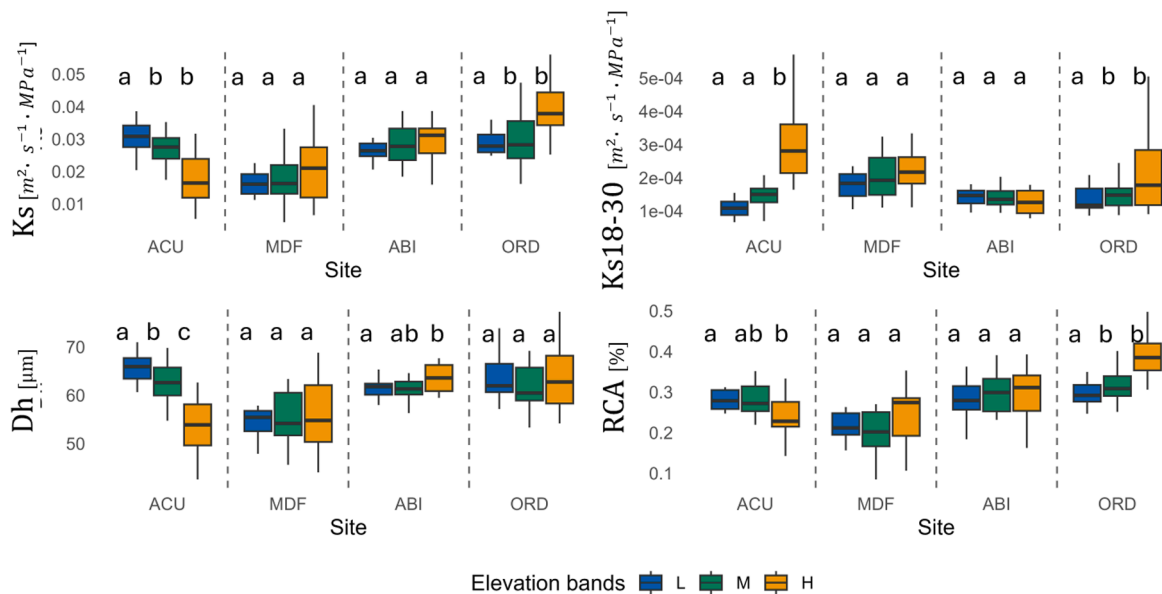


Fig. 4. Distribution of four hydraulic parameters (K_s , K_{s18-30} , D_h , and RCA) in the year preceding LFDs across four study sites (ACU, MDF, ABI, and ORD), stratified by affected elevation belts (H, high; M, mid; L, low). Different letters indicate statistically significant differences among elevation belts within each site (ANOVA followed by Tukey's HSD test, $\alpha = 0.05$; groups sharing the same letter are not significantly different). Boxes represent the interquartile range (IQR), horizontal lines indicate median values, and whiskers extend to $1.5 \times IQR$.

both the strength and statistical significance of these associations (Table S3). The strongest correlations are observed between K_s and RCA ($r \approx 0.89$) and between K_s and D_h ($r \approx 0.81$), both highly significant ($p < 0.001$). K_{s18-30} accounts for only 0.4–0.9% of total stem conductivity (Fig. S4) and was negatively correlated with K_s ($r \approx -0.39$, $p < 0.001$). K_{s18-30} also shows a negative correlation with D_h ($r \approx -0.60$, $p < 0.001$), whereas its correlation with RCA was weak and not statistically significant ($p \approx 0.054$). Finally, D_h and RCA showed a positive correlation ($r \approx 0.54$, $p < 0.001$).

3.3. Vessel trait variation as a driver of late-frost resistance

Box-Cox analysis indicates that all the resistance metrics (LFD_Rt) required transformation prior to modelling. Estimated transformation parameters were highly consistent across resistance definitions, ranging from 0.278 to 0.312 (Table S4), indicating very similar distributional properties among the alternative resistance metrics.

Model A yields highly consistent results across all resistance metrics considered in the sensitivity analysis (Tables S5–S11). In every model, the conductivity contributed by small vessels (K_{s18-30}) was the only anatomical trait significantly associated with late-frost resistance, with

standardized coefficients ranging from -0.13 to -0.14 ($p = 0.010$ – 0.021). By contrast, neither hydraulically weighted vessel diameter (D_h), relative conductive area (RCA), nor tree size (DBH) shows significant effects under any resistance definition.

The magnitude and direction of the K_{s18-30} effect remain remarkably stable regardless of the pre-disturbance reference period (3, 5, or 7 years) or baseline estimator (mean, median, or biweight mean), indicating that the observed relationship is not sensitive to the method used to calculate resistance. Similarly, model performance shows little variation among resistance metrics, with marginal R^2 values ranging from 0.07 to 0.12 and conditional R^2 values consistently close to 0.42. Consequently, the resistance metric calculated using a 5-year pre-disturbance window and mean baseline growth was selected as the reference metric for subsequent analyses to simplify result presentation and interpretation.

Although resistance calculated using a 7-year reference period identified significantly lower resistance in ABI compared with MDF (Tables S7, S10 and S11), the relationship between K_{s18-30} and LFD_Rt remains consistent across sites (Fig. 5). The similar slopes observed among sites indicate that spatial differences primarily affected mean resistance levels rather than the strength or direction of the association

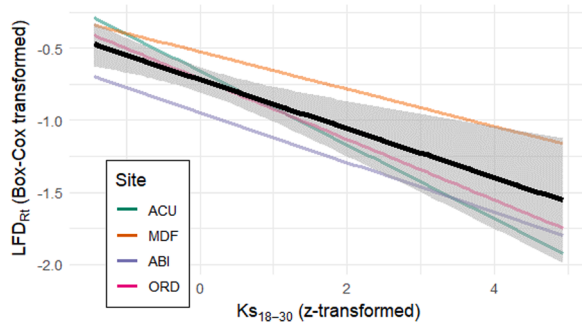


Fig. 5. Observed relationship between specific conductivity contributed by vessels between 18 and 30 μm in diameter (K_{s18-30} , standardized values) and late-frost resistance (LFD_{Rt} , Box-Cox transformed). The black line represents the overall linear relationship estimated across all observations, with the shaded area indicating the 95% confidence interval. Colored lines show site-specific linear trends (ACU, MDF, ABI, and ORD).

between K_{s18-30} and LFD_{Rt} (Fig. 5).

The predictive effect of vessel-specific conductivity progressively declined as the upper diameter threshold increased (Fig. 6). K_s remained a significant predictor ($p < 0.05$) for all diameter windows with an upper bound below 33 μm , indicating that conductivity provided by vessels between 18 and $\sim 32 \mu\text{m}$ reliably explained variation in late-frost resistance. When the upper limit exceeded 32 μm , the predictor became non-significant, and its contribution to model performance weakened.

In Model B, replacing the anatomical predictors D_h and RCA with total K_s does not alter the main result (Table S12). Conductivity contributed by small vessels (K_{s18-30}) remains significantly and negatively associated with late-frost resistance ($\beta = -0.13$, 95% CI = -0.21 to -0.04 , $p = 0.006$), whereas overall hydraulic conductivity (K_s) shows no significant relationship with resistance. Model performance was nearly identical to that of the Model A (marginal $R^2 = 0.091$, conditional $R^2 = 0.432$).

In Model C, replacing “Site” with elevation “Belt” as a fixed effect yields results largely consistent with those obtained for Model A (Table S13). K_{s18-30} remains significantly and negatively associated with late-frost resistance ($\beta = -0.10$, 95% CI = -0.19 to -0.01 , $p = 0.033$), while overall hydraulic conductivity (K_s) and tree size (DBH) show no significant relationships with resistance. Among elevation belts, trees from the high-elevation belt show significantly lower resistance than those from the reference low belt ($\beta = -0.37$, $p = 0.037$), while differences associated with the middle belt are not significant.

In Model D, treating each Site $\times$ Belt combination as a distinct

population substantially increases the explanatory power of the models (marginal $R^2 = 0.197$; conditional $R^2 \approx 0.50$; Table 3). The effect of conductivity contributed by small vessels remains consistent with previous analyses. Several Site $\times$ Belt combinations differ significantly from the reference population (low belt in MDF). Significant differences are observed primarily for high-elevation populations, suggesting an altitudinal component to the observed spatial variability. Nevertheless, the direction and magnitude of the K_{s18-30} effect remain remarkably stable across all model formulations.

The bootstrap mean of the K_{s18-30} parameter calculated for trees with $LFD_{Rt} < 0.75$ (affected trees) is significantly higher ($\alpha=0.05$) than that calculated for the rest of the population (Fig. 7, Table S14). The difference is also significant at the regional scale (Apennines and Pyrenees).

Table 3

Linear mixed-effects model (Model D) results for European beech resistance to late frost defoliations (LFD_{Rt}). The model includes K_{s18-30} , K_s , DBH and Site $\times$ Belt combinations as fixed effects. All continuous predictors were z-transformed. A random intercept was fitted for Site:Belt:Year. Estimates are reported with 95% confidence intervals (CI) and p-values. Variance components (residual variance σ^2 and random intercept variance τ_{00}), intraclass correlation coefficient (ICC), and marginal/conditional R^2 values, accounting for the variance explained by fixed and fixed plus random factors, are reported to describe model fit. ICC=0.38, $N_{\text{Belt}}=3$, $N_{\text{Site}}=4$, $N_{\text{Year}}=8$, Observations=182. Marginal $R^2 = 0.197$, Conditional $R^2=0.499$.

Fixed effects			
Predictors	Estimates	CI	p
(Intercept)	-0.06	-0.59 – 0.47	0.818
K_s	-0.07	-0.18 – 0.05	0.238
K_{s18-30}	-0.10	-0.19 – -0.00	0.040
DBH	0.03	-0.11 – 0.18	0.646
MDF_M	-0.75	-1.44 – -0.06	0.034
MDF_H	-0.73	-1.44 – -0.03	0.041
ACU_L	-0.43	-1.18 – 0.31	0.253
ACU_M	-0.52	-1.17 – 0.13	0.115
ACU_H	-0.96	-1.74 – -0.19	0.015
ABI_L	-0.88	-1.58 – -0.18	0.014
ABI_M	-0.81	-1.48 – -0.14	0.018
ABI_H	-0.91	-1.59 – -0.23	0.009
ORD_L	-0.54	-1.27 – 0.19	0.146
ORD_M	-0.53	-1.20 – 0.14	0.119
ORD_H	-0.83	-1.59 – -0.07	0.033
Random effects			
Term	Variance		
σ^2	0.21		
τ_{00} Site:Belt:Year	0.12		

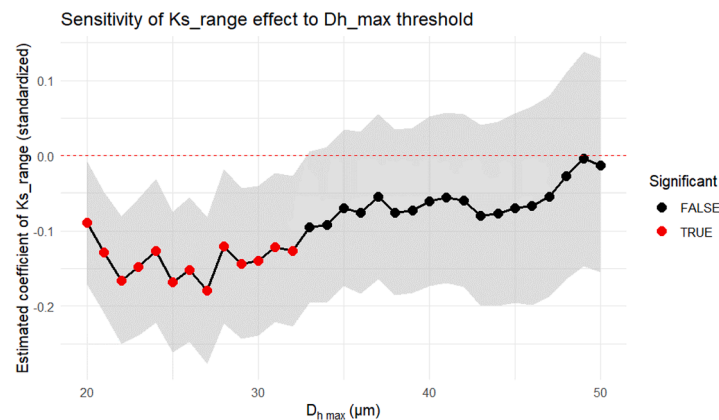


Fig. 6. Sensitivity of the relationship between late-frost resistance and vessel-specific hydraulic conductivity to the definition of the small-vessel size class. The lower vessel-diameter threshold was fixed at 18 μm , whereas the upper threshold was progressively increased from 20 to 50 μm . Points represent standardized regression coefficients (β) for vessel-specific conductivity (K_{s_range}) obtained from Model A, and shaded areas indicate 95% confidence intervals. Red points denote significant ($p < 0.05$) effects.

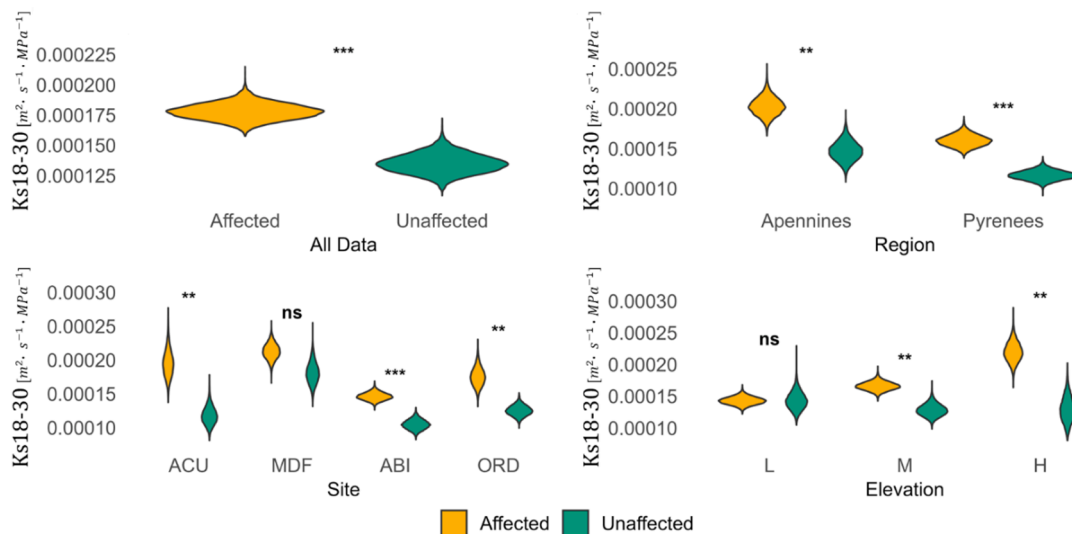


Fig. 7. Bootstrap distributions (10000 replicates) of mean K_{s18-30} values comparing frost “Affected” (orange) and “Unaffected” (green) trees. Panels show overall status differences (upper left), differences within biogeographic regions (upper right), within sites (lower left), and within elevation classes (lower right). Significance was assessed using Welch’s two-sample t-tests, with codes defined as: ns ($p \geq 0.05$), * ($0.01 \leq p < 0.05$), ** ($0.001 \leq p < 0.01$), and *** ($p < 0.001$).

At the site level, it remains significant except for the MDF site. When individuals from different sites are grouped by altitudinal belts, differences in K_{s18-30} are significant only in the mid- and high-elevation belts (Fig. 4). Trees damaged by LFD events (Affected) show K_{s18-30} values 31.8% higher than those of undamaged trees (Unaffected). The percentage increase is comparable between the Apennines and the Pyrenees but reaches its maximum at the ACU site (+65.4% in Affected trees) and in the high-elevation belts (+69.7% in Affected trees).

4. Discussion

4.1. Impacts on growth of late frost defoliations

Our results confirm that late frost defoliations (LFDs) substantially reduce forest productivity by constraining annual stem radial increment, consistent with previous dendroecological evidence for European beech (e.g. Rubio-Cuadrado et al., 2021; Dittmar et al., 2006; Príncipe et al., 2017). However, no anatomical injuries typically associated with frost rings were observed in our wood sections, indicating that spring frost events generally affect newly developed leaves and shoots rather than directly damaging the cambium or the developing xylem.

Severe and long defoliation periods during early spring directly limit carbon assimilation and cambial activity, resulting in narrow rings during event years (D’Andrea et al., 2019; 2020; Baumgarten et al., 2023). Mature beech trees can draw on stored carbon reserves to produce a second cohort of leaves after LFD, whereas seedlings often lack sufficient reserves and may die following severe events (Muffler et al., 2024). Also, mature trees can partially offset spring frost damage by extending autumn productivity (Zohner et al., 2019). These findings indicate that although mature beech trees show considerable resilience to late-frost defoliation, false springs still constitute a significant climate stressor for deciduous forests under ongoing climate warming (Martínez del Castillo et al., 2022).

Despite clear growth impacts, the frequency of LFD events and the proportion of affected trees did not show a consistent elevational pattern across sites, as observed in Lenz et al., (2013). This apparent lack of pattern suggests that, within a given elevational belt, the occurrence of frost events is broadly comparable. At the regional scale, Pyrenean beech forests on average exhibited higher proportions of frost affected trees compared with Apennine ones. This pattern is consistent with earlier studies reporting a greater sensitivity of Pyrenean beech forests to late spring frosts (Sangüesa-Barreda et al., 2021). The more

continental climate of the Pyrenees, with larger temperature variations and a higher probability of abrupt cold spells after early spring warming, is likely to enhance the severity and spatial coherence of LFD events. Conversely, the more buffered climatic conditions of the Apennines (wetter and cloudier) may reduce the spatial synchrony of frost damage and contribute to increase the observed interquartile ranges in resistance.

Nevertheless, we observed wide variability among trees within the same elevation belt and event year. This pronounced inter-tree variability indicates that elevation alone cannot fully explain resistance to LFDs and points to the role of individualistic predisposing traits that modulate vulnerability.

4.2. Predisposition to false springs: the role of xylem anatomy

We found that variation in resistance to false spring events is significantly associated with xylem anatomical traits, specifically the hydraulic specific conductivity of narrow vessels (K_{s18-30}). This result provides direct empirical support for the hypothesis that individually predisposing hydraulic traits influence the growth impact of LFDs.

Conductivity remained significantly associated with resistance only when calculated from vessels with diameters below approximately 33 μm . Once larger conduits were progressively incorporated into the metric, the relationship weakened and eventually disappeared. This pattern suggests that late-frost impact is not associated with hydraulic efficiency across the entire xylem, but rather with the contribution of a specific vessel-size class.

Narrow xylem conduits are generally more resistant to freeze-induced embolism during winter dormancy (Sperry and Sullivan 1992; Davis et al., 1999; Hacke et al., 2017). Vulnerability to freezing-induced cavitation increases strongly with conduit diameter because larger conduits generate larger gas bubbles during freeze–thaw cycles, increasing the likelihood of embolism formation (Davis et al., 1999). In a comparative study across woody species, Davis et al., (1999) reported little or no freeze–thaw induced cavitation in species with mean conduit diameters below approximately 30 μm , whereas conductivity losses increased sharply in species with conduit diameters above 30–40 μm , identifying a critical cavitation diameter of about 44 μm .

This physiological framework is consistent with observations in diffuse-porous species such as the European beech, where winter embolism, seasonal losses of hydraulic conductivity and subsequent hydraulic recovery have been documented (Magnani and Borghetti, 1995;

Cochard et al., 2001).

During years with favourable early spring conditions, such a strategy is likely advantageous, allowing trees to capitalize on extended growing seasons and enhanced carbon gain (Richardson et al., 2013; Keenan et al., 2014; Zohner et al., 2019). However, in the false spring events we examined here, early warm spells were followed by abrupt returns of sub-zero temperatures. Under these conditions, earlier leaf-out becomes unsuccessful, as newly unfolded leaves are highly vulnerable to frost injury (Dittmar et al., 2006; Vitasse et al., 2014). This mechanism provides a coherent explanation for the negative relationship observed between K_{s18-30} and resistance to LFDs: trees with greater hydraulic efficiency supported by narrow vessels appear predisposed to advance phenology and are therefore more exposed to frost damage when cold snaps recur.

Importantly, these findings align with recent evidence linking wood anatomical traits to leaf-out timing across broad spatial scales (Savage et al., 2022; Yin et al., 2016), reinforcing the idea that xylem structure integrates past growth conditions and constrains future phenological responses. Our results extend this framework by suggesting that such anatomical predisposition may have measurable consequences for growth resistance during extreme spring climate events.

The hypothesized link between resistance and anatomical traits was supported exclusively for K_{s18-30} , the only anatomical trait significantly associated with resistance across all model formulations and sensitivity analyses. Neither hydraulically weighted vessel diameter (Dh), relative conductive area (RCA), overall specific hydraulic conductivity (Ks), nor tree size (DBH) showed comparable explanatory power. In our wood sections Ks, Dh, and RCA are strongly influenced by the largest vessels, which disproportionately contribute to total estimated amounts. However, these wider conduits are also the most vulnerable ones to freeze embolism (Davis et al., 1999) and may become temporarily non-functional following winter freeze-thaw events, as documented in European beech and other diffuse-porous species (Magnani and Borghetti, 1995; Cochard et al., 2001). Therefore, their contribution to effective water transport in early spring may be limited, reducing the relevance of Ks, Dh, and RCA for predicting phenological advancement and frost exposure.

Previous studies reporting later leaf-out in species or individuals with wider vessels usually relied on anatomical measurements from terminal branches (Yin et al., 2016; Savage et al., 2022), where conduit diameters are smaller compared to the main stem. Differently, our measurements were sampled at breast height, where vessel variability is higher and difference between narrow, embolism resistant conduits and large, vulnerable vessels is much more pronounced. Consequently, xylem traits dominated by large vessels (such as Ks, Dh and RCA) may inadequately capture the functional hydraulic state relevant to early spring phenology when derived from classical dendroecological stem samples. Furthermore, estimates of specific hydraulic conductivity (Ks) were derived from idealized theoretical calculations and therefore did not account for vessel tapering, end-wall resistance, or other sources of non-ideal flow (e.g. vessel grouping inter-vessel pitting) (Jupa et al., 2016; Christman and Sperry, 2010; Hacke et al., 2006). As a result, total conductivity may have been biased, particularly in trees exhibiting large variation in vessel dimensions.

In this context, K_{s18-30} appears as a more meaningful ecophysiological proxy of early spring hydraulic functionality, as it isolates the contribution of a restricted range of conduits that are hydraulically resistant to winter embolism, while potentially reducing biases associated with theoretical conductivity estimates based on ideal flow assumptions.

Spatial variability primarily affected average resistance levels rather than the relationship between anatomy and resistance. Resistance estimates calculated using a seven-year reference period identified lower resistance in ABI compared with MDF, and several high-elevation populations differed significantly from the low-elevation MDF reference population (Model D). Nevertheless, the slope of the relationship

between K_{s18-30} and resistance remained remarkably similar among sites and elevation belts.

4.3. Limitations and implications for future research

Although K_{s18-30} emerged as a robust predictor of late-frost resistance, anatomical traits accounted for only a relatively small proportion of the total variance observed. Marginal R^2 values remained low in all model formulations, whereas conditional R^2 values were substantially higher, indicating that spatial and temporal grouping represented by the random-effects structure explained a large fraction of the observed variability. These patterns emphasize that false-spring impacts result from the interaction of anatomical predisposition with environmental factors such as frost severity, microclimatic conditions, topographic position, and the timing of spring development. Also, the lack of fine scale meteorological data at each belt limited our ability to precisely determine event intensity and disentangle temperature minima from frost duration effects (De Frenne et al., 2021).

A second limitation concerns the interpretation of the underlying mechanism. The proposed link between xylem anatomy and frost vulnerability relies on the hypothesis that anatomical traits influence phenological timing through their effects on spring hydraulic functioning. However, neither leaf-out timing, embolism resistance or leaf traits were directly quantified in the present study. Consequently, the relationship between K_{s18-30} and false-spring vulnerability should be viewed as hypothesis-generating rather than as direct evidence of a causal mechanism linking xylem anatomy, phenology, and frost damage. Future studies should jointly quantify hydraulic functioning, spring phenology, and frost damage to test the proposed mechanism.

Sampling was intentionally restricted to dominant trees, reducing within-stand variation in size and potentially limiting the detection of size-dependent effects on resistance. Consequently, the full spectrum of phenological responses associated with tree age and stature may not have been captured. Ontogenetic effects on phenology are increasingly recognized as a key factor modulating climate sensitivity in European beech, with younger individuals leafing out earlier and responding more strongly to temperature than mature trees (Vitasse, 2013; Bigler and Bugmann, 2018). Particularly in ACU, Ks and Dh values show a clear trend along the elevational gradient, a pattern associated with structural differences among stands, where trees at low elevation were taller than at the mid- and high-elevations. Greater variability in resistance may be expected in stands encompassing a wider range of age and size classes.

Despite these constraints, our results suggest that xylem anatomical traits represent one of the factors that could predispose trees to false springs. As false spring events are projected to increase in frequency (Zhu et al., 2019; Chamberlain et al., 2019; Chamberlain and Wolkovich, 2021), incorporating individual level hydraulic traits may improve predictions of forest resistance under climate warming and future extremes (Meyer et al., 2024).

5. Conclusions

Late frost defoliations associated with false spring events consistently reduce radial growth in European beech, but the resistance to these climate extremes is highly variable among individuals, elevation belts and sites. The hydraulic specific conductivity provided by narrow vessels (K_{s18-30}) emerged as a promising predisposing trait, negatively associated with resistance to late frost defoliations. These results support a trait-based interpretation of false spring vulnerability, in which xylem anatomy integrates past growth conditions and constrains leaf phenological and growth responses to compound climate extremes. As climate warming advances spring phenology while maintaining the risk of late frosts, such hydraulic trade-offs are likely to become increasingly important in shaping forest productivity and growth resilience. Future research should aim to directly link anatomical predisposition to observed leaf phenological timing by integrating individual-level

phenological observations and high-resolution microclimatic data, particularly during years characterized by exceptionally warm pre-leaf-out conditions. Expanding analyses across broader ontogenetic classes and multiple species with contrasting xylem architectures would further clarify how these mechanisms could be generalized. Ultimately, incorporating hydraulic traits into process-based phenological models may improve predictions of forest vulnerability to increasing spring climate variability under ongoing climate change.

CRedit authorship contribution statement

Enrico Tonelli: Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **J. Julio Camarero:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Conceptualization. **Marco Carrer:** Writing – review & editing, Supervision, Resources, Methodology, Conceptualization. **Michele Colangelo:** Writing – review & editing, Methodology, Investigation, Formal analysis, Conceptualization. **Alessandro Vitali:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Arianna Orsetti:** Writing – review & editing, Investigation, Data curation. **Fabio Gennaretti:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Carlo Urbinati:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.agrformet.2026.111484](https://doi.org/10.1016/j.agrformet.2026.111484).

Data availability

Data will be made available on request.

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