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Bark traits and their influence on thermal resistance to wildfires: an experimental study across six tree species common in Central Europe

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Abstract

Climate change is increasing the probability of wildfires in the non-fire-prone forests of Central Europe. Systematic knowledge on tree resistance to fire would help to improve the future management of forests to ensure their long-term adaptation to climate change impacts. However, a systematic classification of the fire resistance of tree species occurring in Central Europe remains largely unexplored. While observations from surface-fire-dominated ecosystems show that bark constitutes an important interface between fire and tree physiology, the influence of bark traits remains an open question, due to conflicting study results. To address this gap, we conducted heating experiments on stem discs with intact bark, assessing bark thermal conductivities of six tree species common in Europe (the native species *Abies alba*, *Fagus sylvatica*, *Larix decidua*, *Picea abies*, *Pinus sylvestris*, and the non-native *Pseudotsuga menziesii*). By applying generalised additive models, we further investigated the influence of bark traits (thickness, moisture content, density), relative height along the tree stem, and tree species identity on insulation capability. Our results indicate that bark thickness may be the most robust predictor for assessing bark-related resistance to surface fires (i.e. insulation capability). A decrease in thermal resistance was observed with increasing relative height of the sample along the tree stem. Further, we found evidence for decreasing thermal resistance with increasing bark moisture content, but no significant effect of bark density on bark insulation capability. We identified significant interspecific differences in bark insulation capability between the investigated tree species, particularly in combination with species-specific patterns of bark investment. Accordingly, our results suggest higher resistance to fire for *L. decidua*, *P. menziesii*, and *P. sylvestris*, while *A. alba*, *P. abies*, and especially *F. sylvatica* may be associated with lower fire resistance. Our results underscore the need to incorporate diverse tree species' characteristics into assessments of disturbance resistance in the face of climate change.

Keywords Bark insulation, Bark thermal conductivity, Bark trait, Forest fire, Insulation capability, Wildfire resistance

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Resumen

Antecedentes El cambio climático está incrementando la probabilidad de ocurrencia de incendios de vegetación en bosques de Europa central que no son propensos al fuego. El conocimiento sistemático de la resistencia de árboles al fuego podría mejorar el futuro manejo de esos bosques para asegurar su adaptación a los impactos del cambio climático a largo plazo. Sin embargo, una clasificación sistemática de la resistencia al fuego de las distintas especies de árboles de Europa Central no ha sido aún explorada. Mientras que las observaciones sobre incendios que ocurren en ecosistemas dominados por fuegos superficiales muestran que la corteza de los árboles constituye una interfase importante entre el fuego y la fisiología de los árboles, la influencia de las características de la corteza aparece como una pregunta abierta, debido fundamentalmente a resultados conflictivos de varios estudios. Para estudiar este vacío en el conocimiento, condujimos experimentos aplicando calor a discos de troncos de árboles con corteza intacta, determinando la conductividad térmica de seis especies comunes de Europa (las especies nativas *Abies alba*, *Fagus sylvatica*, *Larix decidua*, *Picea abies*, *Pinus sylvestris*, y la exótica *Pseudotsuga menziesii*). Mediante la aplicación de modelos aditivos generalizados, investigamos luego la influencia de las características de la corteza (grosor, contenido de humedad, densidad), la altura relativa a lo largo del tronco, y la identidad de la especie y su capacidad de aislación al fuego.

Resultados Nuestros resultados indican que el grosor de la corteza puede ser el predictor más robusto para determinar la resistencia de la corteza a fuegos superficiales (capacidad de aislación). Un decrecimiento en la resistencia térmica fue observado en el tronco al incrementarse la altura de la muestra. Además, encontramos evidencias de una reducción en la resistencia térmica al aumentar la humedad de la corteza, aunque no encontramos efectos significativos de la densidad sobre la aislación de la corteza. Identificamos diferencias inter-específicas en la capacidad de aislación de las cortezas entre las especies de árboles investigadas, particularmente en combinación con los patrones especie-específicos sobre cuánto cada especie invierte en la formación de su corteza.

Conclusiones De acuerdo con ello, nuestros resultados sugieren una mayor resistencia al fuego para *L. decidua*, *P. menziesii*, y *P. sylvestris*, mientras que *A. alba*, *P. abies* y especialmente *F. sylvatica* pueden ser asociadas con una baja resistencia al fuego. Nuestros resultados subrayan la necesidad de incorporar diversas características de especies de árboles en la determinación de la resistencia a los disturbios en el contexto del cambio climático.

Background

Fire is a natural disturbance factor in many ecosystems, with important regulatory impacts in numerous vegetation zones worldwide (Johnson and Miyanishi 2001; Bond et al. 2005; Pausas and Keeley 2019; Kraus et al. 2022). In fire-dominated ecosystems, plants – including trees – have developed various adaptive strategies to endure fire disturbances. These include, for example, resprouting, regeneration through heat- or smoke-induced germination, or the development of thick and heat-resistant bark (Schwilk and Ackerly 2001; Keeley et al. 2011; Pellegrini et al. 2017). It is plausible that climate change will increase the climatic probability of wildfires in the currently non-fire-prone forests of Central Europe (Khabarov et al. 2016; Grünig et al. 2023; Patacca et al. 2023; Miller et al. 2024). Consequently, fostering systematic knowledge concerning the resistance and resilience of native tree species towards forest fires is crucial for managing forests and ensuring their long-term adaptation to climate change impacts, thus safeguarding important forest ecosystem services (Schelhaas et al. 2010; Seidl et al. 2014; Thom and Seidl 2016; Gehring et al. 2019; Lecina-Díaz et al. 2024; Strith et al. 2024).

Depending on their intensity, wildfires potentially affect a variety of physiological processes in trees, which can cause direct lethality or induce a variety of secondary detrimental effects (Hood et al. 2018b; Bär et al. 2019; Dickman et al. 2023). For example, it has been shown that stem char from surface fires leads to growth reductions even when foliage is not affected (Seifert et al. 2017). However, the exact physiological mechanisms remain unclear regarding the major causes of heat-induced tree mortality resulting from surface fires (Ryan and Frandsen 1991; Midgley et al. 2011; Michaletz et al. 2012; Bär et al. 2018; Partelli-Feltrin et al. 2021). Generally, heat-induced cellular necrosis is considered complete at a temperature of 60 °C (Rosenberg et al. 1971; Michaletz and Johnson 2007), although this threshold can vary among species, across seasons, and with tissue age (Fuller et al. 2025). Further, even sub-lethal temperatures (i.e. below a 60 °C threshold) can induce detrimental physiological stress responses in trees (Kelsey and Westlind 2017), especially when sustained over longer durations (Dickinson and Johnson 2004; Subasinghe Achchige et al. 2021; Fuller et al. 2025).

Given the vulnerability of cambial cells to heat-induced stress responses and necrosis, bark plays a key role in protecting individual trees, forming the interface between environmental influences and tree physiology (Keeley et al. 2011; Bär et al. 2019). The importance of bark as an insulator against fire-induced heat, and the associated bark thermal conductivity, is evident as an adaptation within ecosystems dominated by surface fires. Many tree species in fire-prone regions are characterised by thick bark (Keeley et al. 2011; Pausas 2014; Pellegrini et al. 2017). Beyond its role as a fire-adaptive tissue, bark fulfils multiple functions, including the translocation and storage of assimilates by the inner bark and mechanical protection against biotic and abiotic stressors by the outer bark (Rosell 2019). Bark diversity among and within tree species, such as variation in the ratio of inner to outer bark (Graves et al. 2014; Varner et al. 2022), may result from trade-offs and functional coordination among these functions rather than from a single adaptive response to fire (Rosell et al. 2014; Rosell 2016).

The identification of factors relevant to bark insulation, dependent on both the material's thermal conductivity and its thickness, has been the subject of numerous studies with standing trees within field experiments (van Mantgem and Schwartz 2003; Lawes et al. 2011; Sheppard et al. 2016), experimental heating applied to stem discs (Odhambo et al. 2014), and laboratory experiments utilising loose bark samples (Bauer et al. 2010; Bär and Mayr 2020). In this context, a widely used approach for quantifying the bark insulation capability is to measure the time span during which the lethal temperature threshold of 60 °C is reached (τ_{60}) within the vascular cambium (Dickinson and Johnson 2001; Odhambo et al. 2014; Bär and Mayr 2020). Many studies have demonstrated that bark thickness is the main characteristic that promotes greater fire resistance of trees (Hengst and Dawson 1993; Pinard and Huffman 1997; van Mantgem and Schwartz 2003; Bauer et al. 2010; Lawes et al. 2011; VanderWeide and Hartnett 2011; Brando et al. 2012; Odhambo et al. 2014; Bär and Mayr 2020), with a greater material thickness at a given material conductivity logically providing a higher insulation capability (Peterson and Ryan 1986; Dickinson and Johnson 2001).

Beyond bark thickness, the influence of other bark-specific properties on thermal conductivity, such as moisture content, density, or even interspecific factors, remains poorly understood. In previous studies, conflicting results have been reported regarding the role of bark moisture content, with some authors describing an increase in bark insulation capability with decreasing (Lawes et al. 2011; VanderWeide and Hartnett 2011; Odhambo et al. 2014) and others with increasing bark moisture content at the individual

species level (Bauer et al. 2010; Bär and Mayr 2020). A potential dual role of bark moisture content, i.e., water as a coolant in the periderm and as a conductor to the vascular cambium, was proposed by Wesolowski et al. (2014). In parallel, a number of investigations have suggested that lower bark density enhances the protection against lethal overheating of the vascular cambium (Hengst and Dawson 1993; Bauer et al. 2010; Bär and Mayr 2020; Nolan et al. 2020), while other experimental studies have failed to demonstrate this effect (Pinard and Huffman 1997; VanderWeide and Hartnett 2011; Brando et al. 2012; Wesolowski et al. 2014). The influence of bark surface roughness on heat transfer remains poorly understood, yet it likely exerts a strong effect through boundary layer dynamics (O'Brien et al. 2018). Surface irregularities can alter airflow, modify convective heat exchange, and affect the retention or dissipation of thermal energy, suggesting that even small-scale variations in bark texture may modulate the insulation properties of the bark (O'Brien et al. 2018). There is evidence for an increase in the protective effect of bark with both increasing rugosity (Bauer et al. 2010) and increasing surface smoothness (Bär and Mayr 2020).

Beyond the above factors, Odhambo et al. (2014) observed decreasing bark insulation capability with increasing sampling height along the tree, potentially reflecting species-specific allometric strategies that enhance the protection of stem sections near the ground (Graves et al. 2014; Hammond et al. 2015). In addition, interspecific differences in bark insulation effects have been found in several studies (van Mantgem and Schwartz 2004; Odhambo et al. 2014; Bär and Mayr 2020), but these differences have not been fully confirmed (Lawes et al. 2011).

Taken together, these uncertainties indicate the need to better understand the factors that contribute to the insulation capability of bark across tree species, and how the importance of these factors differs across regions with different levels of fire-proneness. Although bark insulation is an important trait beyond protection from fire-induced damage (e.g., mitigating sun-induced damage; Sheppard et al. 2016), few studies have focused on this aspect within Central Europe (Bauer et al. 2010; Bär and Mayr 2020). In addition, further efforts are required to provide empirical data on species-specific bark thermal properties (e.g., bark thermal conductivity) for use in the mechanistic heat transfer models (Dickinson and Johnson 2001; O'Brien et al. 2018) typically used for vulnerability assessments in relation to forest fires (Peterson and Ryan 1986; Dickinson and Johnson 2001; Schumacher et al. 2006; Dupire et al. 2019).

To help address these gaps, we investigated the bark characteristics of six commercially important tree species

growing in the traditionally less fire-prone region of Central Europe. Our specific aim was to establish corresponding functions for assessments of the vulnerability of the selected tree species to surface fires. Three research questions guided our investigation:

- I. What are typical value ranges of bark thermal conductivity for important tree species in Central Europe?
- II. Which bark traits influence its insulation capability against the heat from surface fires?
- III. How do interspecific differences influence the bark insulation capability and the vulnerability of individual tree species?

Methods

Investigated tree species and samples

The bark insulation capability of six tree species common in Europe was investigated, namely silver fir (*Abies alba*, ABAL), European beech (*Fagus sylvatica*, FASY), European larch (*Larix decidua*, LXDC), Norway spruce (*Picea abies*, PCAB), Scots pine (*Pinus sylvestris*, PISY), and Douglas-fir (*Pseudotsuga menziesii*, PSMN). These six tree species represent approximately 75% of the total growing stock of Germany, according to the fourth German national forest inventory (Federal Ministry of Food and Agriculture 2024), with similar percentages reported for Switzerland (Strauss and Fischer 2025), Austria (BMLUKV 2023), and the Czech Republic (Pulkrab et al. 2015). Douglas-fir was included in this study as a commonly planted non-native tree species in Europe that exhibits fire adaptation traits in its native range in western North America, from the Pacific Northwest and Rocky Mountains to northern Mexico (Hood et al. 2018a). The selected species were sampled in two mixed-species forests in southwestern Germany, located in the municipalities of Bernau (47°46′27.5″N, 8°01′01.6″E) and Emmendingen (48°06′20.7″N, 7°53′41.1″E). Samples were collected in August and September 2021 under similar weather conditions; a brief site and stand description is given in Supplementary Information B.

Following the protocol by Odhiambo et al. (2014), all measurements were conducted on freshly harvested

stem sections with a sectional height of approx. 20 cm. In total, 129 stem discs were randomly sampled from 26 individual trees (Table 1). All samples were collected from bole sections with intact bark because xylem wetness was presumed to affect heat conduction. To include a wide variety of bark thicknesses and to achieve a representative sample size, sampling was performed at distinct positions along the stem. The sampling position along the stem (relative height, H_{rel}) was recorded (for details on relative and absolute sampling positions see Supplementary Information B). Immediately after sampling in the stand, each stem disc was placed in an airtight package and stored at approx. 4 °C to prevent moisture loss, and was removed prior to the experiment to allow acclimatisation to ambient air temperature.

Heating experiments

Experimental setup for the determination of τ_{60}

Heat was applied to the bark surface using a commercial 2200-W heat gun (Steinel 2020e, Steinel GmbH, Herzebrock-Clarholz, Germany), comparable to that used in other studies (Odhiambo et al. 2014; Bär and Mayr 2020). The hot air flow acting on the samples was spatially confined by a circular opening (45 mm in diameter) in a fibre-reinforced gypsum board (Fig. 1). An experimental temperature of 215 °C was set via the digital control panel of the heat gun. The mean experimental temperature (T_{out}) acting at the bark surface was 212.3 °C (± 5.2 °C, $n = 321$). This temperature is comparable to typical heat effects of low- to moderate-intensity surface fires and to the experimental temperatures in the two previous Central European studies (Bauer et al. 2010; Bär and Mayr 2020), while also preventing unwanted ignition or charring of the samples.

To record the temporal temperature development during heating, a three-channel temperature measuring device (Testo 735–2; Testo SE & Co. KGaA, Titisee-Neustadt, Germany) was used in combination with two thermocouples installed in the vascular cambium and at the bark surface (Fig. 1). The temperature acting at the bark surface was measured with a thermocouple (Type K, RS Components GmbH, Germany) placed on the bark surface.

Table 1 Number of sampled trees, sampled stem discs, and conducted heating experiments (considered for analysis) per species. A detailed characterisation of the samples is provided in Supplementary Information B

Species	<i>Fagus sylvatica</i> (FASY)	<i>Picea abies</i> (PCAB)	<i>Abies alba</i> (ABAL)	<i>Pinus sylvestris</i> (PISY)	<i>Larix decidua</i> (LXDC)	<i>Pseudotsuga menziesii</i> (PSMN)	All species
No. of trees	5	5	3	4	6	3	26
No. of stem discs	27	22	15	21	21	23	129
No. of measurements	63	47	33	65	50	63	321

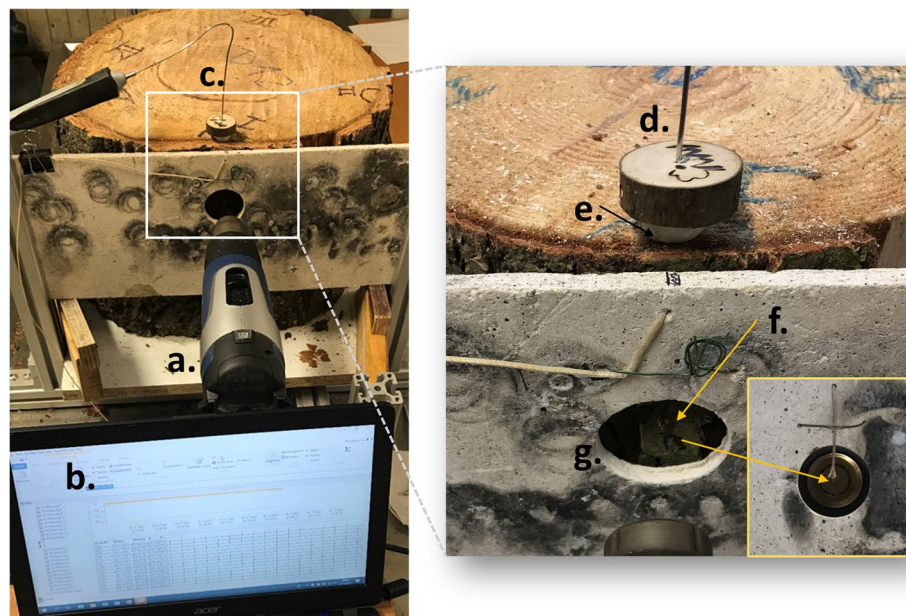


Fig. 1 Heating experiment on one of the prepared stem discs. Heat (212.3 ± 5.2 °C at the bark surface, $n = 321$ test series) was applied using a heating gun (a). Data were recorded with a laptop coupled to a three-channel temperature-measuring device (b), which was connected to a thermocouple inserted into a borehole behind the bark at the cambium–bark interface (c, d) and to a thermocouple placed on the bark surface (f). Hot air flow acting on the samples was confined by a circular opening in a fibre-reinforced gypsum board (g). During the experiments, the borehole was sealed with a rubber compound (e)

To determine the vascular cambium temperature, a thermocouple (Type K, accuracy class 1 (EN 60584–2), Testo SE & Co. KGaA, Germany) was installed immediately adjacent to the vascular cambium region of each stem disc. This was carried out by drilling a hole (5 mm in diameter, 65 mm in length) in the outermost annual ring of the stem disc, tangential to the vascular cambium. In total, 356 measuring points were prepared across the 129 stem discs (Table 1). During the heating experiments, the top of the borehole was sealed with a rubber compound to prevent heat exchange by convection (Fig. 1e).

The initial temperatures at the bark surface (T_{surface}) and in the vascular cambium (T_{start}) were measured shortly before the start of each heating experiment. The mean temperature acting at the bark surface during heating (T_{out}) was measured as a further experimental control variable. As soon as the temperature measured in the vascular cambium exceeded the defined threshold of 60 °C, measurements were stopped and the time (τ_{60}) was determined. To allow long measurement series for samples with thick bark, no temporal termination criterion was defined (in contrast to Bauer et al. 2010; Bär and Mayr 2020). No standardisation was performed in terms of the bark structure of the heating target, i.e., ridge vs. furrow.

As a final step, the bark at the measurement location was removed to determine the deviation (d_{sensor})

of the borehole tip (i.e. where the thermocouple was placed within the stem disc) compared with an optimal positioning in the vascular cambium, measured using a digital caliper. Measurements with d_{sensor} outside a range of ± 2.5 mm were excluded to ensure that the thermocouple was positioned in a meaningful range around the cambium–bark interface, as larger deviations were observed with altered heating patterns during the experiments. In total, 35 test series were excluded, resulting in $n = 321$ test series considered for the analysis.

Characterisation of sample traits

Bark thickness (BT; comprising both inner and outer bark) was determined at individual measurement points, whereas bark density (ρ), moisture content (MC), and stem disc diameter (d_{sample}) were measured at the stem disc level. BT was determined as the arithmetic mean of two measurements made with a digital caliper in the close vicinity of the heat exposure location. BT was determined before heating to avoid potential bias due to heat-induced swelling or shrinkage effects (Butler et al. 2005).

Two bark samples were detached from the stem discs prior to the heating experiment to assess MC and ρ . To determine MC, the fresh bark samples were first weighed (m_{fresh}) using a laboratory scale (Mettler PM 4600 DR,

resolution 0.01 g; Mettler-Toledo International Inc., Columbus, Ohio, USA), then oven-dried at 105 °C until they reached an equilibrium moisture content, and finally weighed again to determine the dry mass (m_{dry}). The relative MC of each bark sample was calculated as the difference between the fresh mass and the dry mass, divided by the dry mass.

Bark density ρ was determined using the Archimedean principle, following Seifert and Seifert (2014), based on dry mass and fresh volume (for details see Supplementary Information A.2). The fresh bark samples were used to determine the reference volume, to avoid overestimation of bark density due to potential shrinkage processes during drying (VanderWeide and Hartnett 2011).

A detailed characterisation of the investigated samples is provided in Supplementary Information B.

Analysis

Bark thermal conductivity k

A one-dimensional heat transfer model was applied (Peterson and Ryan 1986; Dickinson and Johnson 2001; Bär and Mayr 2020) to determine bark thermal conductivity k ($\text{Wm}^{-1} \text{K}^{-1}$) for each individual measurement series i (Eq. 1).

$$k_i = \frac{BT_i^2}{4 * \tau_{60,i} \left(\text{erf}^{-1} \left(\frac{T - T_{\text{out},i}}{T_{\text{out},i} - T_a} \right) \right)^2 * \rho_i * c_{b,i}} \begin{cases} c_{b,i} = c_{dr} + c_w * MC_i + 1227 * MC_i, MC_i \leq 0.27 \\ c_{b,i} = c_{dr} + c_w * MC_i + 348, MC_i > 0.27 \end{cases} \quad (1)$$

Here, T corresponds to the temperature in the vascular cambium (60 °C), which is reached after time τ_{60} at a temperature T_{out} acting on the bark surface. T_a is the ambient temperature (assumed to be constant at 20 °C). c_b is the specific heat capacity of bark, which depends on the heat capacity of dry bark c_{dr} ($1,196.72 \text{ Jkg}^{-1} \text{K}^{-1}$ at 20 °C; Martin 1963). c_w corresponds to the specific heat capacity of water ($4,185.1 \text{ Jkg}^{-1} \text{K}^{-1}$ at 20 °C; Schmidt 2019). Sample bark parameters BT , ρ and MC are also included (Table 2). Values for the inverse Gaussian error function (erf^{-1}) were determined by using the *pracma* package (Borchers 2021) in R version 4.3.1 (R Core Team 2021) in the R Studio environment (Posit team 2023).

A Welch analysis of variance (ANOVA; $\alpha=0.05$) was applied to test for species-specific differences between modelled thermal conductivities k , as this method is insensitive to potential violations of the normal distribution assumption (Kubinger et al. 2009; Rasch et al. 2011). Furthermore, a Games–Howell post-hoc test was applied to identify the locations of differences between all 15 combinations of species pairs. The calculated p -values were modified using the Bonferroni–Holm correction, keeping the overall probability of committing alpha-errors $\leq 5\%$ (Holm 1979). Statistical analysis of

Table 2 Overview and description of the experimentally determined parameters. It is indicated which parameters were used for the calculation of the bark thermal conductivity k and which parameters were used for the modelling of τ_{60} as a dependent variable in a generalised additive model (GAM). Please note that the parameters d_{sample} and T_{surface} were determined but not used as model parameters

Parameter	Unit	Description	Used within...	
			Calculation of bark thermal conductivity k	Generalised additive model GAM
τ_{60}	s	Time span during which the lethal temperature threshold of 60 °C is reached within the vascular cambium; measured from the beginning of the heating experiments	x	x (dependent variable)
β_{species}	–	Tree species identity; <i>Fagus sylvatica</i> (FASY), <i>Abies alba</i> (ABAL), <i>Pinus sylvestris</i> (PISY), <i>Picea abies</i> (PCAB), <i>Pseudotsuga menziesii</i> (PSMN) and <i>Larix decidua</i> (LXDC)	x	x
BT	mm	Bark thickness	x	x
MC	–	Relative bark moisture content, calculated as the difference between the fresh mass and dry mass, divided by the dry mass	x	x
ρ	g cm^{-3}	Bark density	x	x
H_{rel}	–	Relative height along the tree stem, i.e. sampling position along the stem measured from the ground surface	x	x
d_{sample}	cm	Diameter of stem disc		
d_{sensor}	mm	Deviation of the borehole tip (i.e. where the thermocouple was placed within the stem disc) compared with an optimal positioning in the vascular cambium		x
T_{start}	°C	Temperature of the vascular cambium before the start of the heating experiment		x
T_{surface}	°C	Temperature of the bark surface before the start of the heating experiment		
T_{out}	°C	Mean temperature acting on the bark surface during the heating experiment	x	x
tree_id	–	Unique identifier for each sampled tree		x

thermal conductivities was carried out utilising the *ggbetweentstats* package (Patil 2021) in R.

Generalised additive models (GAMs)

Generalised additive regression models (GAMs) were applied to assess the impact of bark traits (BT, MC, ρ , H_{rel}), tree species identity ($\beta_{species}$), and experimental settings (T_{start} , T_{out} , d_{sensor}) on bark insulation capability (τ_{60} ; Table 2).

By fitting GAMs, the potential non-linearity of predictor variables was addressed upfront by modelling a non-parametric smoothing term $s(x_i)$ for each variable (Zuur et al. 2009) (Eq. 2):

$$y_i = \alpha + s(x_i) + \varepsilon_i \text{ with } \varepsilon_i \sim N(0, \sigma^2) \quad (2)$$

The central outputs of a GAM are smoothing terms for all significant terms, which allow conclusions about the degree and strength of the correlations and the form of the influence of each variable. To avoid overfitting the model due to high spline flexibility, and to increase the ability to interpret general trends, the maximum flexibility per smoothing term was limited to three dimensions.

Pearson correlation coefficients and variance inflation factors (VIF) were determined prior to model construction to avoid multicollinearity between individual variables (Zuur et al. 2009; Murray et al. 2012). To avoid multicollinearity, $T_{surface}$ was subsequently excluded from the modelling procedure due to high VIF values ($VIF > 3$, see Supplementary Information E.1) and a strong correlation with T_{start} ($r = 0.81$, $p < 0.001$). In addition, d_{sample} was excluded due to a strong negative correlation with H_{rel} ($r = -0.72$, $p < 0.001$) and a strong positive correlation with BT on the individual species level (see Supplementary Information D for all Pearson correlation coefficients). k was also excluded from modelling to avoid structural multicollinearity (Daoud 2017).

The full model, constituting the starting point for further model selection, was defined as follows (3):

all predictors were significant ($p < 0.05$) in the GAM, the smoothing term with the highest p -value was removed from the model in each step (Zuur et al. 2009). The candidate models were assessed using the adjusted coefficient of determination R^2_{adj} and the Akaike information criterion (AIC; see Supplementary Information E.2.1). Graphical residual-based model diagnostics were used for model validation, i.e., to ensure that the normal distribution assumption of the residuals was met and to rule out heteroscedasticity (Zuur et al. 2009; Fahrmeir et al. 2016). In addition, concavity between the splines was assessed to ensure that none of the modelled smoothing terms could be approximated by another smoothing term (Wood 2017).

As the validation of a first GAM revealed a tendency towards heteroscedasticity (see example in Supplementary Information E.2.1.1), τ_{60} was natural-log ($\ln$) transformed for further analysis (Eqs. 3 and 4). During iterative backward selection, ρ was removed from the final GAM ($F = 0.006$, $p = 0.937$). Further, the final GAM was fitted without the initially included random term of $tree_id$, as it was not significant ($F = 0.491$, $p = 0.053$) and did not improve model performance ($\Delta AIC = 2.25$; adj. $R^2 = 94.8$ vs 94.7%; see Supplementary Information E.2.1).

GAMs were modelled and visualised using the packages *mgcv* and *gratia* (Wood 2017; Simpson 2024) in R.

Predictions for τ_{60} based on species-specific bark allometries

The final GAM was used to derive predictions for τ_{60} from species-specific bark allometries, which were developed for the German National Forest Inventory (Kublin 2003; Vonderach et al. 2021). Species-specific predictions for BT based on diameter at breast height (DBH; stem diameter 1.3 m above ground) were modelled using the package *rBDAT* (Vonderach et al. 2021) in R. For MC, species-specific means as observed in this study were used (see Supplementary Fig. 6), while T_{start} , T_{out} , and d_{sensor} were assumed to be constant across species (for all settings see Supplementary Information E.3.2).

$$\ln(\tau_{60}) = \alpha + s_1(BT_i) + s_2(MC_i) + s_3(\rho_i) + s_4(H_{rel,i}) + s_5(T_{start,i}) + s_6(T_{out,i}) + s_7(d_{sensor,i}) + s_8(tree_id_i, bs = "re") + \beta_{species_i} + \varepsilon_i \text{ with } \varepsilon_i \sim N(0, \sigma^2) \quad (3)$$

Here, the full model considered the bark traits (BT, MC, ρ , H_{rel}) and experimental settings (T_{start} , T_{out} , d_{sensor}), $\beta_{species}$ and the intercept α . A random effect $s_8(tree_id_i, bs = "re")$ was included to account for potential non-independence of measurements originating from the same tree.

Iterative backward selection based on the p -values of the predictors was performed for model selection. Until

Results

Across all observations, experimentally measured values for τ_{60} ranged from a few seconds to several hours. A positive non-linear relationship between τ_{60} and BT was observed (Fig. 2a), with particularly long durations observed for thick-barked species such as LXDC, PSMN, and PISY (Fig. 2b). The close relationship was further indicated by the strong correlation between BT

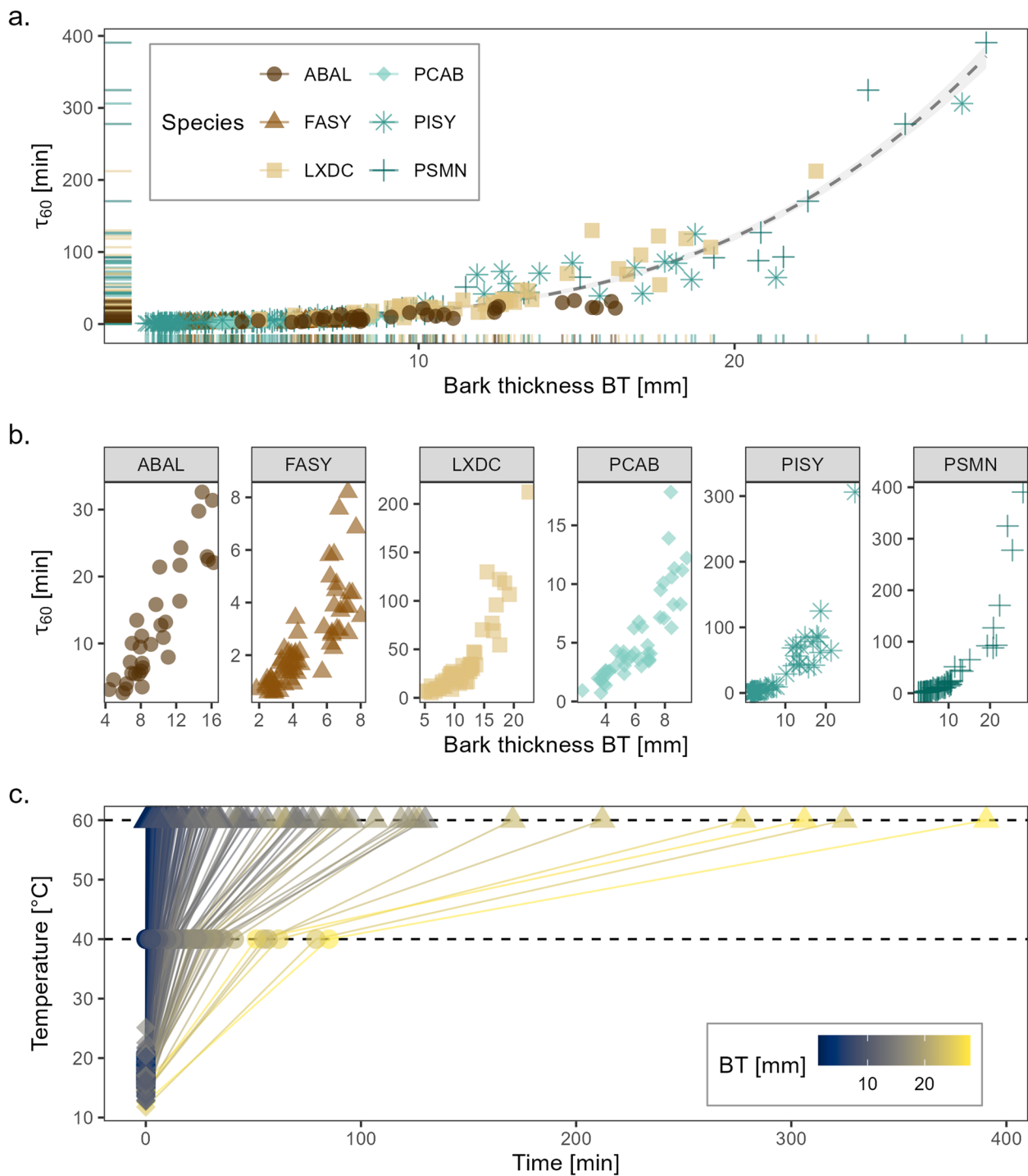


Fig. 2 **a** Time required to reach the lethal temperature threshold of 60 °C in the cambium (τ_{60}) plotted against bark thickness (BT) for $n=321$ test series (across all species). The dashed line represents the fit of a simplified generalised additive model (GAM; $\tau_{60} \sim s(BT)$, adj. $R^2=0.87$). **b** τ_{60} plotted against BT, separated by investigated tree species. **c** Linearly interpolated time-temperature profiles between the initial temperature of the vascular cambium T_{start} and 40 °C (lower dashed line), and between 40 °C and 60 °C (upper dashed line) for all heating experiments. Species codes refer to *Fagus sylvatica* (FASY), *Abies alba* (ABAL), *Pinus sylvestris* (PISY), *Picea abies* (PCAB), *Pseudotsuga menziesii* (PSMN), and *Larix decidua* (LXDC)

and $\ln$ -transformed τ_{60} (across all observations: $r=0.93$, $p<0.001$), which ranged from $r=0.87$ (FASY; $p<0.001$) to $r=0.95$ (PSMN; $p<0.001$) at the species level (Supplementary Information D).

Notably, the observed non-linear trend between τ_{60} and BT (Fig. 2a) was also reflected in an inverse relationship between the mean heating rate in the vascular cambium and BT (Supplementary Information C.1), with heating rates converging to zero for high values of BT. In addition, mean heating rates in the vascular cambium decreased over the course of the experiments, i.e., the heating rate between the initial temperature T_{start} and a threshold of 40 °C was observed to be higher than that between the interval between 40 °C and 60 °C (Fig. 2c). This effect was particularly pronounced in samples with thick bark, such as those for LXDC (Supplementary Information C.1).

Bark thermal conductivity (k)

In ascending order, the mean values for bark thermal conductivity (k) were 0.03 W m⁻¹ °C⁻¹ for PISY, 0.04 W m⁻¹ °C⁻¹ for LXDC, 0.08 W m⁻¹ °C⁻¹ for PSMN, 0.11 W m⁻¹ °C⁻¹ for PCAB, 0.12 W m⁻¹ °C⁻¹ for ABAL, and 0.16 W m⁻¹ °C⁻¹ for FASY (Fig. 3). Individual observed k values for FASY, ABAL, and PSMN showed a large variability around their respective means, whereas the distributions for LXDC and PISY were considerably narrower.

Differences between the species-specific k values were significant ($F_{\text{Welch}}=119.94$, $p<0.001$), whereas homogeneity of variance was not given ($F_{\text{Levene}}=23.25$, $p<0.001$). The Games–Howell post-hoc test revealed significant differences among 13 of 15 species pairs (Fig. 3), for example, between FASY and ABAL ($p=0.013$). No significant differences were found between the k values of the barks of PCAB and ABAL ($p=0.836$) and of PISY and LXDC ($p=0.836$).

Generalised additive models (GAMs)

The final GAM (Eq. 4) explained 94.7% (R^2_{adj}) of the observed variance of the dependent variable $\ln(\tau_{60})$ and was also preferred in comparison to the full and base (minimal) GAMs, having the lowest AIC value of 232.67 (Table 3; see also Supplementary Information E.2).

Information E.3.1). In addition, no concavity between the splines in the final GAM was detected (Supplementary Information E.3.1).

Effects of bark traits

Visualisation of the non-parametric smoothing functions shows the type and form of the influence of the investigated bark traits on the bark insulation capability (Fig. 4a, c, e). Here, a strong positive increase in the dependent variable $\ln(\tau_{60})$ can be seen with increasing BT, with a non-linear relationship becoming visible through the decreasing curve slope with increasing BT (Fig. 4a). Based on Fig. 4c, it is also evident that $\ln(\tau_{60})$ was negatively affected by increasing MC. Although the smoothing term for MC was determined to be non-linear ($df=1.65$), a straight line drawn through the 95% confidence interval would suggest that the observed effect could also be adequately characterised by a linear smoothing term. Moreover, an additional significant explanation for the behaviour of $\ln(\tau_{60})$ was provided by H_{rel} (Fig. 4e). With increasing values of H_{rel} , the associated spline $s(H_{\text{rel}})$ described a linear ($df=1.00$) negative trend for $\ln(\tau_{60})$.

Effects of experimental control variables

In general, the effects of the experimental control variables – already indicated by Pearson correlation coefficients (Supplementary Information D) – were confirmed by the modelled smoothing terms (Fig. 4b, d, f). $\ln(\tau_{60})$ decreased with increasing T_{start} (Fig. 4b) and simultaneously increased with increasing d_{sensor} (Fig. 4d) into the xylem.

A nonlinear ($df=1.90$) smoothing term was fitted for T_{out} (Fig. 4f), according to which $\ln(\tau_{60})$ initially increased with increasing T_{out} and culminated at 215 °C. After this point, the spline $s(T_{\text{out}})$ showed a slightly decreasing tendency again. Furthermore, $\ln(\tau_{60})$ tended to increase with increasing T_{out} .

The direct comparison of all smoothing terms underlines the importance of BT when assessing the protective effect against lethal overheating of the vascular cambium, as the most powerful spline was modelled for this vari-

$$\ln(\tau_{60}) \sim s(BT) + s(T_{\text{start}}) + s(MC) + s(d_{\text{sensor}}) + s(H_{\text{rel}}) + s(T_{\text{out}}) + \beta_{\text{species}} \quad (4)$$

In total, 14.52 estimated degrees of freedom (df) were used, 6.0 of which were accounted for by the parametric terms and, in decreasing order, by the smoothing terms s_i for BT ($df=1.98$, $p<0.001$), T_{out} ($df=1.90$, $p<0.001$), MC ($df=1.65$, $p<0.001$), and H_{rel} ($df=1.00$, $p=0.003$). For both d_{sensor} and T_{start} , the approximated smoothing terms were linear (each with $df=1.00$, $p<0.001$). The final GAM was validated by visual plot diagnostics (Supplementary

able. MC and H_{rel} , on the other hand, had comparatively small effects when considered individually. However, in combination with other parameters, they contributed to a notable effect.

Effects of tree species identity

Species effects were modelled as parametric terms β_{species} within the final GAM (Table 3), with FASY serving as

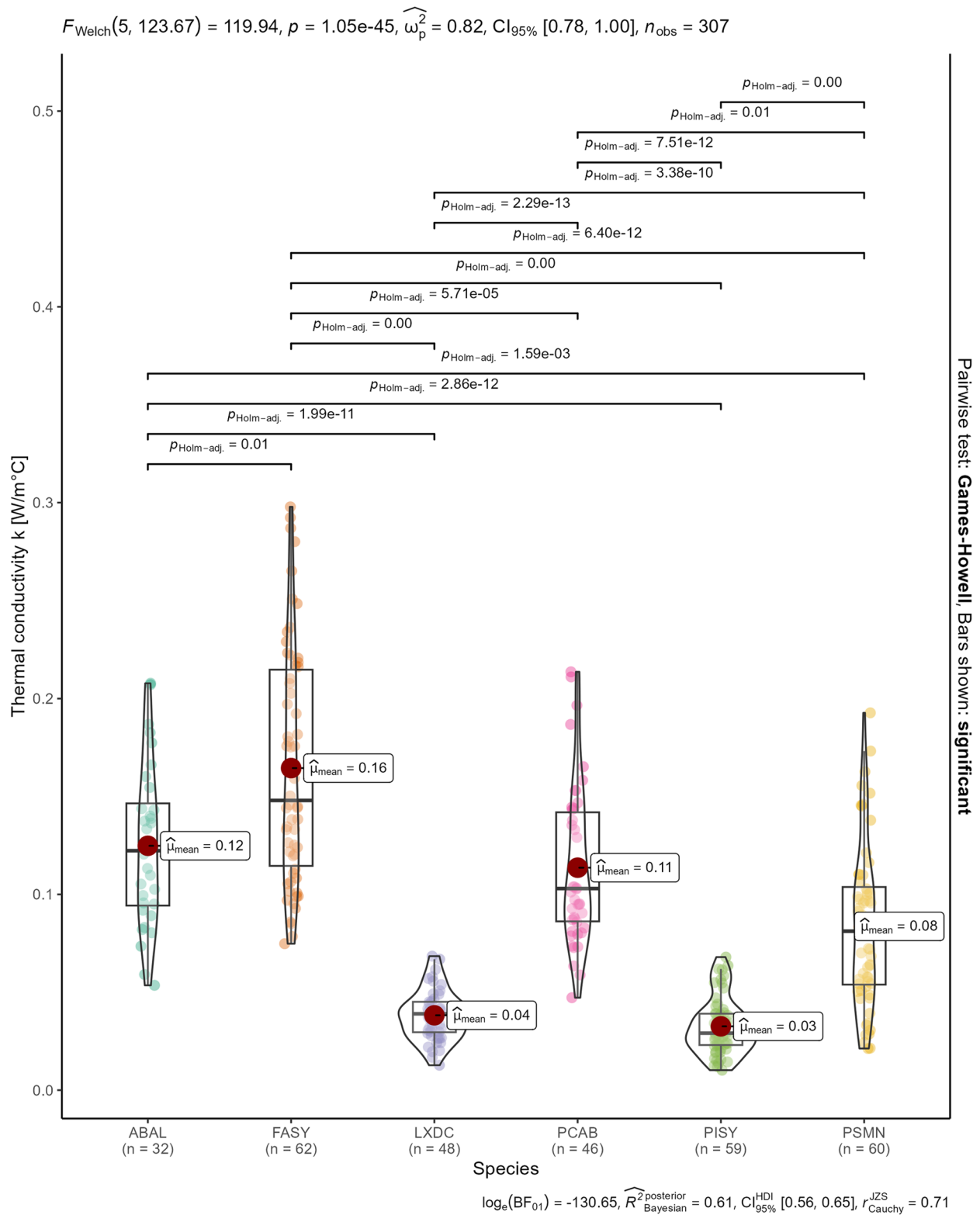


Fig. 3 Violin plots of species-specific thermal conductivity (k) of bark. Significant differences between the investigated species were identified by the Games–Howell post-hoc test following a Welch analysis of variance (ANOVA). To avoid alpha-error accumulation, the presented p -values were corrected according to Holm (1979). k was calculated using a one-dimensional heat transfer model (Dickinson and Johnson 2001). In total, 14 observations were identified as outliers (Tukey 1977) and excluded from analysis. Species codes refer to *Fagus sylvatica* (FASY), *Abies alba* (ABAL), *Pinus sylvestris* (PISY), *Picea abies* (PCAB), *Pseudotsuga menziesii* (PSMN), and *Larix decidua* (LXDC)

baseline ($\beta_{FASY} = 0$). All other species corresponded to significantly higher values for $\ln(\tau_{60})$, in the following order: ABAL ($\beta_{ABAL} = 0.22$), PISY ($\beta_{PISY} = 0.44$), PCAB ($\beta_{PCAB} = 0.52$), PSMN ($\beta_{PSMN} = 0.61$), and LXDC ($\beta_{LXDC} = 0.68$).

To allow intuitive interpretation of the identified species effects, the predictors representing all the remaining terms besides species effects were re-transformed, so that the species-specific regression parameter $\beta_{species}$ could be interpreted as multiples of $\tau_{60,FASY}$, modelled for FASY (Supplementary Information E.3). Exemplarily, for comparable bark characteristics (BT, MC, H_{rel}) and experimental conditions, the re-transformed proxy τ_{60} for LXDC compared with FASY was higher by a factor of 1.98. The comparatively low bark insulation capability of FASY was consistent with its high thermal conductivity (Fig. 3) and with the high heating rates observed during the experiments (Supplementary Information C.1).

Predictions for τ_{60} based on species-specific bark allometries

Across all investigated tree species, predicted values for τ_{60} increased with increasing DBH (Fig. 5), generally reflecting the corresponding species-specific allometric relationship between DBH and BT (see Supplementary Information E.3.2). Notably, LXDC showed a progressive DBH-dependent increase in bark insulation capability, with high τ_{60} values already reached at small diameters. Compared to LXDC, PISY and PSMN showed a similar but less pronounced pattern, i.e., a strong but more gradual increase in τ_{60} with DBH. ABAL and PCAB showed intermediate relationships, achieving high τ_{60} values only at larger diameters (DBH > 70 cm). In contrast, FASY exhibited the lowest DBH-dependent investment in bark insulation capability, with comparatively low τ_{60} values even at high DBH values.

Table 3 Final generalised additive model (GAM) formulation for the explanation of the behaviour of τ_{60} (time required to reach the lethal temperature threshold of 60 °C in the cambium). The model run for *Fagus sylvatica* (FASY) serves as the baseline for the determined species-specific parametric terms $\beta_{species}$. Abbreviations refer to bark thickness (BT), bark moisture content (MC), bark density (ρ), sample position of the stem disc along the tree stem (relative height, H_{rel}), initial temperature of the vascular cambium before heating (T_{start}), average temperature at the bark surface while heating (T_{out}), and positional deviation of the thermocouple positioned in the vascular cambium (d_{sensor}). Asterisks refer to significance levels ($p < 0.05$ *, $p < 0.01$ **, $p < 0.001$ ***). Species codes refer to *Fagus sylvatica* (FASY), *Abies alba* (ABAL), *Pinus sylvestris* (PISY), *Picea abies* (PCAB), *Pseudotsuga menziesii* (PSMN), and *Larix decidua* (LXDC)

Smoothing terms	Final GAM		
	Estimated degrees of freedom df	F	p
$s(BT)$	1.979	417.419	< 0.001***
$s(T_{start})$	1.000	15.548	< 0.001***
$s(\rho)$	–	–	–
$s(MC)$	1.645	9.564	< 0.001***
$s(d_{sensor})$	1.000	48.429	< 0.001***
$s(T_{out})$	1.899	10.690	< 0.001***
$s(H_{rel})$	1.000	8.706	0.003**
$s(tree_id, bs = "re")$	–	–	–
Parametric terms	Coefficient	Standard error	p
Intercept	5.52143	0.05625	< 0.001***
β_{PSMN}	0.61129	0.08846	< 0.001***
β_{PCAB}	0.51596	0.09116	< 0.001***
β_{PISY}	0.44374	0.07202	< 0.001***
β_{LXDC}	0.68149	0.08624	< 0.001***
β_{ABAL}	0.22051	0.09209	0.0172*
No. of observations n	321		
REML	135.15		
Akaike Information Criterion AIC	232.6675		
R^2	0.949		
R^2_{adj}	0.947		

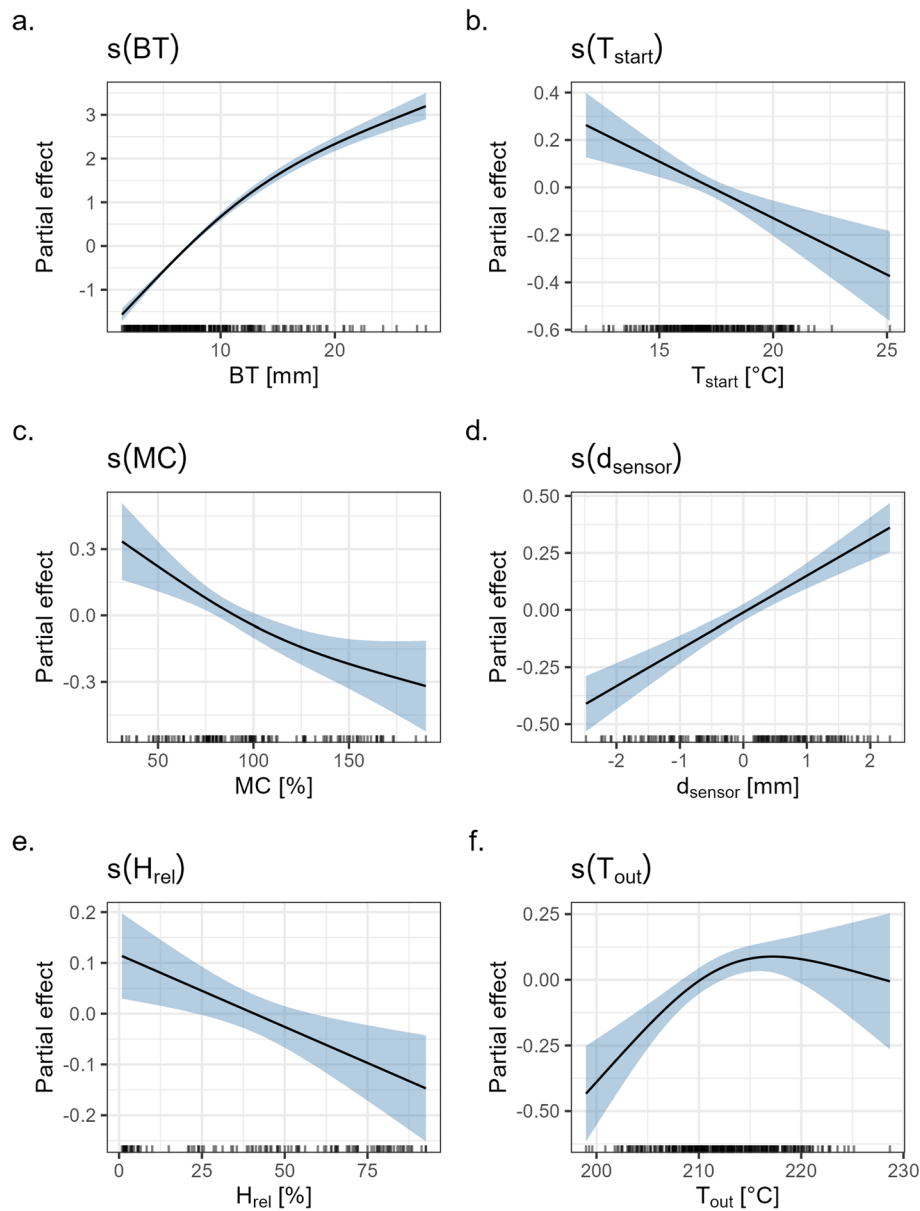


Fig. 4 Smoothing terms describing the experimentally observed behaviour of τ_{60} (ln-transformed) in the final generalised additive model (GAM). Visualised partial effects refer to **(a)** bark thickness (BT), **(b)** initial temperature of the vascular cambium before heating (T_{start}), **(c)** bark moisture content (MC), **(d)** positional deviation of the thermocouple positioned in the vascular cambium (d_{sensor}), **(e)** sample position of the stem disc along the tree stem (relative height, H_{rel}), and **(f)** average temperature at the bark surface while heating (T_{out}). Please note the different scaling of the y-axis for the different panels, with the strongest relationship occurring for bark thickness (BT; a)

Discussion

A key objective of this work was the identification of relevant bark traits for the resistance to heat-induced damage of the vascular cambium, which can result from light to moderate surface fires. For this purpose, our experimental design focused on τ_{60} , a well-established proxy for fire resistance (van Mantgem and Schwartz 2003; Bauer et al. 2010). Bark thickness emerged as the primary determinant

of insulation against surface fires, with thermal resistance additionally decreasing at greater heights along the tree stem and at higher bark moisture contents (see Fig. 4). Further, pronounced interspecific differences emphasized the need to consider species-specific traits (see e.g. Fig. 3), especially in combination with bark allometries that vary among investigated tree species (see Fig. 5).

Effects of bark traits

Bark thickness (BT) was found to be a key determinant for the protection against lethal overheating of the vascular cambium. With BT as the single predictor for τ_{60} , a good model fit was already obtained (Supplementary Information E.2, Base GAM: $R^2_{adj} = 0.903$). Thus, our results concur with previous studies that have identified BT as an important protective factor against surface fire (van Mantgem and Schwartz 2003; Bauer et al. 2010; Lawes et al. 2011; Odhiambo et al. 2014; Bär and Mayr 2020). This result is also supported by the geographic coherence of thick-barked tree species with surface-fire regimes (Keeley et al. 2011; Pausas 2014; Pellegrini et al. 2017).

Our findings further indicate a decrease in the insulation effect with increasing bark moisture content (MC), supporting the results of VanderWeide and Hartnett (2011), Lawes et al. (2011) and Odhiambo et al. (2014). Physically, the observed trend is likely to be based on the higher thermal conductivity of water ($k_{water} \approx 23.4 * k_{air}$; Tipler and Mosca 2014) compared with the determined species-specific bark thermal conductivities (e.g., $\bar{k}_{PSMN} = 0.08 \text{ W m}^{-1} \text{ } ^\circ\text{C}^{-1} \approx 0.13 * k_{water}$). Accordingly, we found no evidence for a positive correlation between bark insulation capability and MC (Bauer et al. 2010; Bär and Mayr 2020). Thus, the theory that higher MC leads to greater protection, due to the high specific heat capacity of water, is not supported by our results. Instead, our

observations show that effects of the high thermal conductivity of water might represent the main causal effect of MC on bark insulation.

The differences between our results and those presented by Bauer et al. (2010) and by Bär and Mayr (2020), who also focused on tree species in Central Europe, may partially reflect the respective methodological procedures applied. In both of these previous studies, bark samples detached from the wood were utilised, resulting in an increase in surface area that facilitated direct moisture exchange. This may have led to increased evaporation during the course of the experiment run time, meaning that the expended evaporation enthalpy (i.e. evaporative cooling; see also Wesolowski et al. 2014) would have exceeded the typical conditions on intact stems. Usually, the inherent bond between bark and wood provides a physical barrier to evaporation, while moisture transport from inner bark layers to the atmosphere is reduced by impermeable periderm layers (Meyer et al. 1981), which is why we carried out the experiments on stem discs (Odhiambo et al. 2014). These differences in the experimental conditions between the previous studies and ours might explain the ambivalent conclusions about the direction of the effect of MC on bark insulation capability. The relationship observed here of decreasing resistance caused by increasing MC is particularly relevant regarding seasonal and weather-related variations in MC

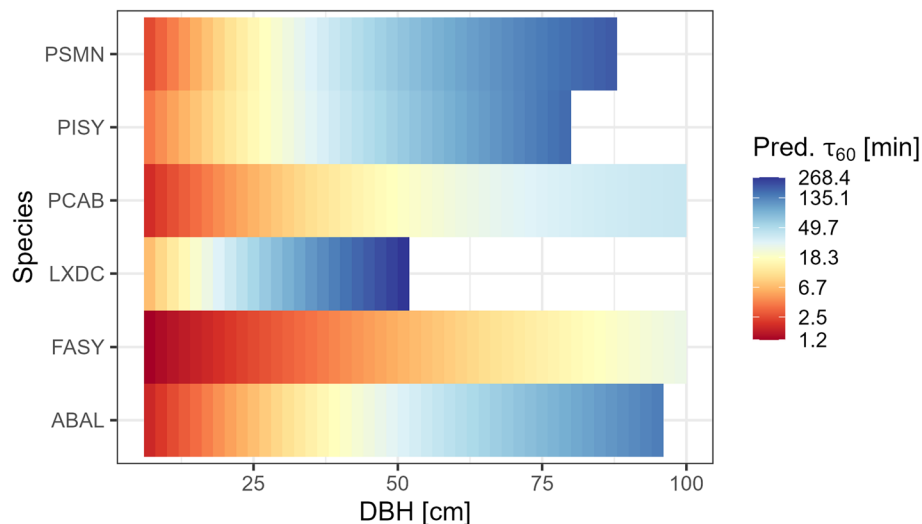


Fig. 5 Predicted behaviour of τ_{60} as a function of diameter at breast height (DBH; stem diameter 1.3 m above ground), derived from the final generalised additive model (GAM). Predictions are based on species-specific allometric relationships between DBH and bark thickness (BT; 1.3 m above ground), using the package *rBDAT* (Vonderach et al. 2021) in R (R Core Team 2021). Species codes refer to *Fagus sylvatica* (FASY), *Abies alba* (ABAL), *Pinus sylvestris* (PISY), *Picea abies* (PCAB), *Pseudotsuga menziesii* (PSMN), and *Larix decidua* (LXDC). See Supplementary Information E.3.2 for details on the assumptions regarding species-specific bark allometries, initial temperature of the vascular cambium before heating (T_{start}), bark moisture contents (MC), positional deviation of the thermocouple positioned in the vascular cambium (d_{sensor}), relative height along the tree stem (H_{rel}), and average temperature at the bark surface while heating (T_{out}). Please note the ln-scaling of the colour scale. Further note that displayed values for τ_{60} were filtered to match the observed range of BT values within this study

in real forest settings (Hengst and Dawson 1994; O'Brien et al. 2018). Consequently, seasonal differences in cambium-related vulnerability to surface fires might occur.

In this study, we found no evidence for a significant effect of ρ on bark insulation capability (i.e. τ_{60}), in contrast to the results reported by Bauer et al. (2010) and by Bär and Mayr (2020). This was already apparent in the correlation coefficients between ρ and τ_{60} determined at the species level (Supplementary Information D), which demonstrated moderate and positive correlations between τ_{60} and ρ for ABAL and PSMN only. These findings contradict the theory-based premise that k decreases with decreasing ρ and consequently that the proxy τ_{60} tends to increase with increasing ρ (Dickinson and Johnson 2001). The reasons for these differences may be methodological, since ρ was determined based on the fresh volume in this study, to avoid species-specific differences in swelling or shrinking behaviour upon heating (Butler et al. 2005) and potential drying-related biases in density values (Meyer et al. 1981; VanderWeide and Hartnett 2011).

It is reasonable to consider that the theoretical effect of ρ on bark insulation properties is represented by the major contributions of MC, as well as individual tree species effects. Specifically, in our study, Pearson correlation coefficients determined at the species level indicated a close negative correlation between ρ and MC (Supplementary Information D; e.g. for ABAL: $r_{MC-\rho} = -0.71$, $p < 0.01$). This can be interpreted as a decrease in MC with increasing ρ due to smaller intercellular spaces. A similar relationship was described by Wesolowski et al. (2014) for *Eucalyptus* species; these authors found ρ to be inversely proportional to MC, resulting in a stabilisation of thermal diffusivity. Our findings therefore support the view that potential effects of ρ are outweighed by the effects of variations in MC. Lastly, this result is in line with the findings of other studies which indicated no significant explanatory contribution of ρ with respect to fire resistance (Pinard and Huffman 1997; Lawes et al. 2011; VanderWeide and Hartnett 2011; Brando et al. 2012; Wesolowski et al. 2014).

It must be noted that we determined ρ across the entire bark fraction of the sampled material, for experimental reasons. Considering characteristic variations in ρ and MC over the cross-sectional profile of the bark (Reifsnyder et al. 1967; Meyer et al. 1981; Rosell 2019), it seems possible that density gradients at a smaller scale might contribute to the explanation of the observed interspecific differences.

The effect of decreasing bark insulation capability with increasing relative height along the tree stem (H_{rel}), described by Odhiambo et al. (2014), was confirmed in

our study. An explanatory factor here may be the variation in bark structure along the tree stem due to differences in cambial age, as is particularly visible in Scots pine with its characteristic orange-red bark colouration at greater stem heights. Bauer et al. (2010) found evidence for an influence of bark structuring on the bark insulation effect. However, Bär and Mayr (2020) described the opposite effect of bark structure, with a decreasing protective effect with increasing rugosity and fissures potentially acting as weak points within the bark. Such effects can be attributed to bark roughness, ranging from centimetre-scale fissures to millimetre-scale surface heterogeneity, influencing surface area, boundary layer dynamics, and the associated heating and thermal transfer (O'Brien et al. 2018). Therefore, we recommend investigating the role of bark structure on the insulation effect in more detail, for instance via a three-dimensional assessment of the micro-relief and the specific bark surface (O'Brien et al. 2018; Sioma et al. 2018). A more pragmatic alternative may be the visualisation of heat development on differently structured bark surfaces using thermographic methods (O'Brien et al. 2018; Majdák et al. 2021; Frey et al. 2023).

In addition to bark structure, height-specific variations in the allocation of bark tissues (Graves et al. 2014; Hammond et al. 2015), as described in fire-prone ecosystems (Pausas 2014), might explain the observed effect of H_{rel} . Whether the modelled decrease in bark insulation capability with increasing H_{rel} is ecologically relevant, or whether only the thick bark at ground level provides sufficient protection, depends on the prevailing fire regime and intensity (Keeley et al. 2011; Pellegrini et al. 2017). Nevertheless, the observed decrease in bark insulation capability with increasing H_{rel} might be relevant in combination with the effects of bark MC. For all the species investigated in this study (except FASY), a strong positive relationship between MC and H_{rel} was observed (Supplementary Information D), reflected in Pearson correlations ranging from 0.74 (LXDC, $p < 0.01$) to 0.92 (PCAB, $p < 0.001$). This is consistent with findings from previous studies (Meyer et al. 1981; Hytönen et al. 2018). One plausible reason for this pattern is the increasing share of phloem with increasing height along the tree stem (Eberhardt 2013; Graves et al. 2014). Thus, our observations of decreasing bark insulation capability with increasing H_{rel} and distribution gradients of MC also suggest that a stem section close to the ground would tend to be more protected than expected based on BT alone. This might also explain the distinct underestimation of τ_{60} from models with BT as the sole predictor compared with our observations (Supplementary Information C.2).

Effects of experimental set-up

Experimental control variables were assessed to detect outliers and ensure data quality. For example, the parameter d_{sensor} was used to exclude measurements where the thermocouple was not positioned accurately in the vascular cambium. The suitability of the restriction of d_{sensor} to less than ± 2.5 mm is demonstrated by the fact that the influence of d_{sensor} on τ_{60} was significant but causally explainable.

Due to our experimental design, the cooling effect of assimilate and water transport in the phloem and xylem (O'Brien et al. 2018; Frey et al. 2023) remained unconsidered, which might lead to lower cambium mortality under real forest fire conditions. An indication for this effect may be the cambium temperature before heat exposure (T_{start}), which was initially collected to document constant experimental conditions. The observed effect of decreasing bark insulation capability (i.e. τ_{60}) with increasing initial cambial temperature can be causally explained by the reduced thermal buffer capacity of the inner stem, as less additional heat energy is required to reach critical temperatures when starting from higher initial temperatures (Chatziefstratiou et al. 2013). Although Brando et al. (2012) discussed a potential effect of cambial temperature, this parameter was neglected in previous experimental studies (van Mantgem and Schwartz 2003; Bauer et al. 2010; Lawes et al. 2011; Brando et al. 2012; Odhiambo et al. 2014; Bär and Mayr 2020). Considering the close linkage of inner stem temperatures to ambient conditions (Rossi et al. 2007; Cuny and Rathgeber 2016; Maclauchlan and Brooks 2017; Schaberg et al. 2017), our observations support the assertion that there are climatic, seasonal, weather-related, and even diurnal variations in the fire resistance of individual trees (Dupire et al. 2019).

The mean experimental temperature T_{out} acting on the bark surface was 212.3 ± 5.2 °C over all measurement series. Despite this narrow range, increasing values for τ_{60} with increasing experimental temperatures were found. At first, this pattern does not seem to be causally explainable, and it may rather reflect experimental constraints or collinearities which could not be identified during data exploration and model validation. However, based on the energy-dependent evaporation rate of water, higher T_{out} values might reduce the MC in outer bark areas faster. In addition, Butler et al. (2005) observed an increase in radial bark swelling with increasing temperatures for PSMN, which may lead to a heat-induced increase in bark insulation capability. Since T_{out} was not varied in a systematic or intentional way in our study, the two suggested explanations remain speculative. Even if this observed effect was shown to be causally explainable, in nature, increasing fire temperatures imply an increase in the risk for destructive

crown fires (Xanthopoulos and Athanasiou 2018). Thus, the role of fire intensity may outweigh a potential heat-induced optimisation of bark insulation. Nevertheless, investigating changes in radial bark thickness under heat exposure, as described by Butler et al. (2005), would be an interesting aspect for further characterisation of direct fire response mechanisms at the tree species level.

Thermal conductivity and modelled species effects

In our experiment, thermal conductivity (k) differed between the tree species: 13 of the 15 pairwise comparisons indicated significant differences, with k ranging from $0.03 \text{ W m}^{-1} \text{ °C}^{-1}$ (PISY) to $0.16 \text{ W m}^{-1} \text{ °C}^{-1}$ (FASY). Compared with more general reference values, the experimentally determined k values are within a plausible spectrum (Dickinson and Johnson 2001; Niemz 2007; Pásztor and Ronyecz 2013). Considering that the reciprocal of k corresponds to thermal resistance, the bark of FASY has the lowest thermal protection effect among the investigated tree species, whereas PISY and LXDC are more resistant (Bär and Mayr 2020).

The observed differences in k confirm reports of inter-specific differences from other studies (van Mantgem and Schwartz 2003; Odhiambo et al. 2014; Bär and Mayr 2020), while further evidence for species-specific differences is provided by the GAM in our study. At the individual species level, FASY had a relatively low bark insulation capability, confirming the findings of Bär and Mayr (2020), potentially contributing to the high fire sensitivity of this species (Maringer et al. 2016; Conedera et al. 2017). The GAMs indicated significantly higher values for τ_{60} for all the other investigated tree species, with values differing by a factor of up to 2 (LXDC compared with FASY). The causes for this may lie in species-specific bark morphologies, which were not considered in this study. For instance, species-specific gradients of MC and ρ within the bark (Reifsnyder et al. 1967; Meyer et al. 1981) may lead to different heat transfer rates towards the cambium. An indication for this lies in the species-specific ratios of outer to inner bark (Bär and Mayr 2020), as inherently different ρ and MC values are associated with these different bark compartments (Winter 2020). Consequently, this explanation shows parallels with the previously described resistance gradient as a function of H_{rel} (Odhiambo et al. 2014), which may also interact with the possible effects of bark structuring (Bauer et al. 2010).

It must be noted that this investigation did not account for an intraspecific differentiation of bark development stages, although considerable structural and morphological changes in the bark are possible with tree development (Michel et al. 2011). For example, the typical bark structures with corked periderm layers in PSMN form only with progressive diameter development. These

structures are largely responsible for characteristic swelling reactions upon heat exposure (Butler et al. 2005), contributing to the higher fire adaptation of large PSMN individuals (Hood et al. 2018a). The neglect of bark developmental stages might explain why PSMN did not differ substantially from the other investigated species within our study. Thus, we recommend a differentiation of k and modelled species effects, based on e.g. diameter classes or bark development stages, for future studies, to be able to elaborate interspecific effects in a more detailed and meaningful way.

Previous studies have observed considerable interspecific and ontogenetic variations in bark allocation patterns, i.e. tree species differing in the timing and distribution of bark investment along the stem (Jackson et al. 1999; Varner et al. 2022). To account for this, we combined the final GAM with species-specific allometric relationships for DBH and BT (Kublin 2003; Vonderach et al. 2021), allowing for a straightforward interpretation of our results (see Fig. 5). Accordingly, the species PSMN, PISY, and especially LXDC showed a progressive, DBH-dependent increase in their bark insulation capability, supporting their classification as highly fire-adapted tree species (Hille and Ouden 2004; Moris et al. 2017; Fréjaville et al. 2018; Hood et al. 2018a). ABAL and PCAB showed slower increases in bark insulation capability with increasing DBH, reflecting generally higher sensitivity to fire of these species (Wallenius et al. 2005; Conedera et al. 2017; Fréjaville et al. 2018). In contrast, the thin-barked FASY maintained low bark insulation capability across all diameter ranges, supporting observations that fire can cause severe damage for FASY, especially when coupled with secondary stressors (Conedera et al. 2010; Maringer et al. 2016, 2021).

Outlook

Our results provide further insights on the prevailing mechanisms of bark insulation capability and species-specific differences. In addition, they have several implications for further comprehensive research, as well as for forest management. First, species-specific k values could be applied within established heat-transfer models (Peterson and Ryan 1986; Dickinson and Johnson 2001). Second, the presented GAM could be directly implemented in the context of modelling forests' vulnerability to wildfires (Schumacher et al. 2006; Dupire et al. 2019), offering an alternative approach to existing models of bark insulation capability (Supplementary Information C.2). A third field of application might be the inclusion of the presented models (see e.g. Fig. 5) as a sub-indicator within indicator-based disturbance predisposition assessment systems, aiming for decision support in long-term forest planning (Thrippleton et al. 2023; Mutterer et al.

2025). Here, temporal or seasonal factors, such as variability in bark moisture content, may be included in future research efforts in order to identify periods of increased vulnerability.

It is important to note that further factors beyond bark insulation capability are relevant for characterising the resistance of trees to forest fires (O'Brien et al. 2010, 2018; Fréjaville et al. 2018; Cansler et al. 2020), including aspects of flammability (Fréjaville et al. 2013; Pausas et al. 2016; Varner et al. 2022). At the stand level, for example, vertical fuel connectivity determines whether surface fires can develop into stand-destroying crown fires (Pollet and Omi 2002; González et al. 2007; Neumann et al. 2022). Capabilities such as resprouting (Clarke et al. 2013; Pausas and Keeley 2014), self-pruning (Schwilk and Ackery 2001; Keeley et al. 2011), and root system extension (Hood et al. 2018a) are additional adaptive mechanisms at the individual tree level which might be important to consider. Finally, we call for further research to refine the temperature threshold at which cambial injury occurs. While 60 °C is widely cited as a critical value (Rosenberg et al. 1971; Dickinson and Johnson 2004; Michaletz and Johnson 2007), empirical evidence suggests that stress responses can manifest at lower temperatures or under prolonged exposure (Kelsey and Westlind 2017; Subasinghe Achchige et al. 2021; Fuller et al. 2025). As the heating rates observed here were dependent on the considered temperature thresholds (Fig. 2c and Supplementary Information C.1), we emphasise the need for controlled experiments to quantify species-specific and context-dependent thermal limits of cambial viability.

Conclusion

In this experimental study, we investigated the influences of several bark traits on bark insulation capability for protection against the thermal effects of surface fires of six tree species common in Europe (*Abies alba*, *Fagus sylvatica*, *Larix decidua*, *Picea abies*, *Pinus sylvestris*, and *Pseudotsuga menziesii*).

Overall, bark thickness was identified as the central and causally explainable predictor for bark insulation capability, consistent with previous studies. However, our results also suggest that other bark traits contribute to bark insulation capability. Notably, bark insulation capability decreased with increasing relative height along the tree (H_{rel}), suggesting that lower stem sections may provide higher resistance to fire than bark thickness (BT) alone would predict. Increasing bark moisture content (MC) was associated with reduced insulation capability, likely due to increased thermal conductivity outweighing the potential buffering effect of water's high specific heat capacity. In addition, the observed effects of MC and initial vascular cambium temperature suggest that

trees' bark insulation may vary with weather conditions. Contrary to theoretical expectations, no significant effect of bark density (ρ) on the bark insulation capability was found in this study, potentially due to an overlapping effect of MC.

Additional interspecific differences suggest that bark insulation is influenced by traits beyond those directly measured in this study: among the investigated tree species, *F. sylvatica* had the lowest species-specific bark insulation capability, whereas a significantly higher resistance was identified for *P. sylvestris*, *P. menziesii*, and especially *L. decidua* – likely due to species-specific gradients of ρ and MC along the bark cross-section, as well as effects of bark structure. Species-specific differences were also observed for bark thermal conductivity (k), with *P. sylvestris* and *L. decidua* exhibiting the lowest k values, followed by *P. menziesii*, *A. alba*, *P. abies*, and *F. sylvatica*. These differences accumulate particularly in connection with species-specific bark allometries, which reflected higher diameter-related investments in bark insulation for *L. decidua*, *P. sylvestris*, and *P. menziesii*, while *P. abies*, *A. alba*, and especially *F. sylvatica* showed lower investments in bark insulation.

An important direction for future research is to investigate how other traits, such as bark morphology or tree developmental stage, contribute to the bark insulation capability – ideally utilising alternative experimental methods and field observations. Since trees' resistance to fire depends on multiple traits beyond bark insulation, developing a systematic classification of fire resistance and resilience for common tree species in Central Europe remains a significant challenge.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42408-025-00438-4>.

Supplementary Material 1.

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Authors' contributions

SM: Conceptualisation, Methodology, Formal analysis and investigation, Writing (original draft preparation); TS: Conceptualisation, Methodology, Writing (review and editing), Resources, Supervision; JS: Writing (review and editing); UK: Writing (review and editing), Supervision.

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Data availability

The data that support the findings of this study are available from the authors on reasonable request.

Declarations

Competing interests

The authors declare no competing interests.

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