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Drivers of drought-induced canopy mortality in conifer and broadleaf forests across Luxembourg

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Abstract. Climate change-induced weather extremes are increasing the intensity and frequency of disturbance events, posing a major threat to forests globally. In Central Europe, hotter and drier summers, such as those during the 2018-2020 drought period, have led to widespread forest damage. To adapt forests to a hotter and drier future it is important to identify sites more vulnerable to canopy mortality during drought, but high-resolution tree mortality data across a continuous landscape is still sparse.

This study aimed at filling this research gap by utilising a high-resolution (single-tree-level), spatially continuous dataset covering the entire Central European country of Luxembourg. We used generalized additive models (GAMs) to explore the contribution of biotic and abiotic site characteristics to the observed canopy mortality of conifer and broadleaf forests during the 2018-2020 summer droughts.

Our model explained 44.6% of canopy mortality variation in conifers and 25.3% in broadleaf forests. Clustered mortality patches spreading from one year to the other, typical for bark beetle infestation, were the strongest predictor of canopy mortality in conifer trees. Forest height also emerged as a strong predictor of mortality in both forest types. Surprisingly, we found limited influence of topography on canopy mortality. Our study highlights the potential of using high-resolution canopy mortality data across a national-scale study area to unravel the influence of site characteristics driving spatial variation in forest mortality during drought events.

1 Introduction

The increasing frequency and intensity of disturbances due to climate change-induced weather extremes are affecting forests globally (Altman et al., 2024; Anderegg et al., 2020; Petritan and Schwenke, 2023). Particularly prolonged drought periods alongside high temperatures have emerged as one of the primary disturbance agents of forests in recent decades and drought-related tree mortality has been observed in all forested biomes (Allen et al., 2010; Hammond et al., 2022; Hartmann et al., 2022). For instance, recent summer droughts alongside high temperatures have triggered widespread tree mortality during

2018–2020 in Central European forests (Schiefer et al., 2024; Schwarz et al., 2024). While some trees die directly during droughts, others only die months to years later often due to pest and pathogen outbreaks. This can lead to a highly heterogeneous occurrence of tree death, making it challenging to quantify and attribute mortality causes (Hartmann et al., 2018). In addition, many abiotic and biotic factors can moderate individual tree responses during drought, challenging accurate projections of future forest dynamics.

Tree mortality due to drought has been explored on a variety of sites around the world (Hammond et al., 2022). Many studies have focused on the ecophysiological processes underlying tree mortality and the question why some tree species are more resilient to drought than others (Choat et al., 2012; Hajek et al., 2022; Trugman et al., 2018). Meanwhile, other research has taken a broader perspective, examining drought related tree mortality at the scale of forest plots and even across entire landscapes (Senf and Seidl, 2021; Sturm et al., 2022). Hereby the focus was less on tree species and more on the effect of environmental characteristics, such as topography and stand structure, along with the interactions between various disturbance agents (Breshears et al., 2005). Individual trees within a forest do not uniformly respond to water shortage, causing a heterogeneous response depending on a variety of abiotic and biotic factors (Hartmann et al., 2018; Trugman et al., 2021; Zhai et al., 2022). Part of the variability in trees' responses to water shortage are assumed to relate to site level-differences in water supply, which are partially determined by soil type, topography and competition.

Topographical variables are important drivers of tree mortality during drought, yet their large-scale effects and interactions remain under-explored. Tree mortality typically increases at lower elevations, but how elevation patterns interact with other factors is not completely understood (Cailleret et al., 2014; Paz-Kagan et al., 2017; Rita et al., 2020; Sturm et al., 2022). Slope steepness, while often linked to higher drought vulnerability due to runoff (Bennett et al., 2015; Meddens et al., 2015) could, as some studies suggest, improve resilience through adaptive traits (Paz-Kagan et al., 2017). The impact of slope orientation on drought-related tree mortality remains not fully understood. While most studies report higher mortality on south- and west-facing slopes (Cailleret et al., 2014; Dorman et al., 2015; Paz-Kagan et al., 2017; Socha et al., 2023; Sturm et al., 2022), stakeholders in Luxembourg reported higher mortality on east-facing slopes. Low Topographic Wetness Index (TWI) values correlate with increased drought mortality (Allen and Breshears, 1998; Breshears et al., 2018), but the influence of confounding factors like stand structure and microclimate heterogeneity remains insufficiently studied.

Stand structure and age are additional key factors influencing forest mortality during drought (Bennett et al., 2015; McDowell and Allen, 2015). Taller or older forest stands are often more prone to die during droughts (Dorman et al., 2015; Floyd et al., 2009; Guarín and Taylor, 2005; Paz-Kagan et al., 2017; Socha et al., 2023), likely due to higher vulnerability to hydraulic failure (McDowell and Allen, 2015). There is however evidence that younger forests are more prone to die during climatic extremes, especially hot and dry conditions (König et al., 2025; Luo and Chen, 2013). Higher canopy mortality has also been observed at forest edges (Mann et al., 2023; Sturm et al., 2022), likely caused by a higher evaporative demand resulting in a faster depletion of water reserves (Brun et al., 2020; Buras et al., 2018). Additionally, forest roads create edges inside the forests that can alter the microclimate, providing pathways for wind and pests such as the European spruce bark beetle (*Ips typographus*), and influencing vegetation type and age (Lugo and Gucinski, 2000). The influence of forest roads on tree mortality during drought remains an open question that is greatly underexplored in Europe (Feleha et al., 2025).

Drought-induced stress can also increase the vulnerability of trees to subsequent disturbance agents (Kärvemo et al., 2023). The hot and dry conditions during droughts weaken the tree's defence mechanisms as well as facilitate the proliferation of bark beetles, which was documented at numerous sites across Central Europe (Gilles et al., 2023; Knutzen et al., 2025; Pirtskhalava-Karpova et al., 2024) and other parts of the world (Cervantes-Martínez et al., 2019; Robbins et al., 2022). A key question remains whether the effects of bark beetle infestations can be disentangled from the influence of other site-specific characteristics, as this distinction is crucial for accurately assessing ecosystem responses and management strategies.

These gaps highlight the need for a more integrated understanding of how environmental factors shape drought-induced tree mortality. Addressing mortality drivers requires high-resolution canopy mortality and environmental data with broad spatial coverage. Low-resolution products, such as Landsat's 30×30 m pixels, represent a number of different trees and various micro-topographic situations that cannot be disentangled. As such they will not be able to address smaller-scale, site-specific responses, let alone depict tree mortality with high certainty (Hansen et al., 2013; Senf and Seidl, 2021). While research on smaller forest plots provides valuable insights into the conditions of individual trees (Hülsmann et al., 2016), it may fail to capture broader, landscape-scale patterns of mortality (Dorman et al., 2015; McDowell et al., 2013). High-resolution datasets of canopy mortality can help identify sites more vulnerable to drought, thereby facilitating targeted monitoring or forest management strategies (Anderegg et al., 2013; Brouwers et al., 2013; Clifford and Booth, 2015; Príncipe et al., 2022). This is supported for example by the new initiative deadtrees.org, which underlines the importance of high-resolution canopy deadwood information in order to capture mortality trends (Kattenborn et al., 2025; Mosig et al., 2024). Recent advances in big data science, including increased computational power and the rise of artificial intelligence, now make it possible to address these data gaps by facilitating the acquisition of high-resolution mortality data at the canopy level across entire countries (Schwarz et al., 2024). This detailed canopy mortality data provides means to a better understanding of mortality drivers at the landscape scale.

In this study, we leveraged a previously published high-resolution dataset capturing canopy mortality spanning the entire country of Luxembourg in Central Europe (Schwarz et al., 2024) to explore fine-scale spatial patterns of canopy mortality and identify contributing factors driving the mortality dynamics. The data covers the summers 2017-2020, three of which were characterised by severe drought (Rakovec et al., 2022). The high spatial resolution of the mortality dataset (20 cm/px) and of the environmental variables (50 cm/px) used here allows to study patterns of drought-induced canopy mortality and contributing factors over the whole country of Luxembourg.

We hypothesised that using high-resolution data over a continuous landscape we would find that (1) canopy mortality is greatly modulated by topography, with higher mortality on steeper, south-facing slopes, (2) canopy mortality is linked to forest structure, such as forest height and the distance to the forest edge, with higher mortality in taller stands as well as closer to the forest edge, and (3) canopy mortality patterns in conifers, but not in broadleaf trees show trends consistent with the spread of bark beetle.

100 2 Methods

2.1 Study site

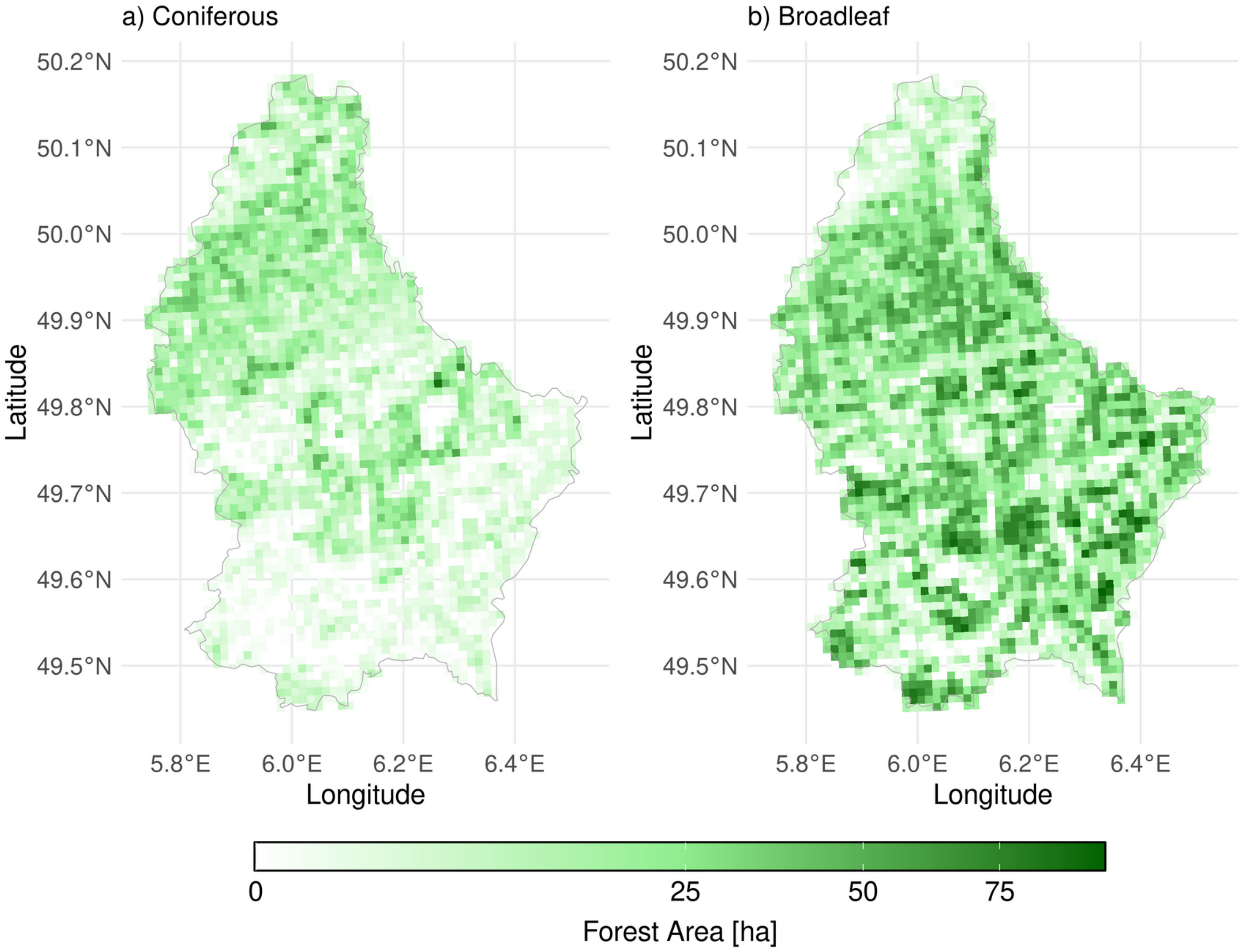

Figure 1: Map of the country of Luxembourg showing forested area. Forest area of a) coniferous and b) broadleaf forests in a 100 ha grid (pixel size). Coniferous forests are more prevalent in the north and center of Luxembourg, while broadleaf forests make up the majority of most forests throughout the rest of the country.

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This study covers all forests of Luxembourg with predominantly temperate coniferous and broadleaf stands, the extent of which are defined by the LIS-L land cover data set (Korzeniowska, 2020). Luxembourg is located in Central Europe (between 49° and 51° latitude and 5° and 7° longitude). It has a forest area of around 900 km², comprising approximately 71% broadleaf, 23% coniferous and 5% mixed forests. Even though the country is one of the smallest in Europe, it is characterised by a diverse landscape, ranging from relatively flat, urban environments in the south (~250 m a.s.l), which are dominated by broadleaf forests to a more hilly, forested, conifer-dominated landscape in the north, reaching elevations of 560 m a.s.l. (Fig. 1).

2.2 Canopy mortality data

Here we used a high-resolution dataset of conifer and broadleaf canopy mortality for the whole of Luxembourg, which was first presented in Schwarz et al., 2024. The dataset covers the drought period between 2018 and 2020 as well as the pre-drought year 2017 and has a ground resolution of 20 cm. It is based on annually collected RGB and Infrared (IR) orthophotos provided by the open data platform of Luxembourg (data.public.lu). Canopy mortality was mapped for conifers and broadleaf trees by employing a Convolutional Neural Network, a deep learning algorithm for image segmentation and classification. Since we used a semantic segmentation model instead of an instance segmentation model to derive the mortality data, the resulting canopy mortality polygons include both free standing dead trees and groups of dead trees.

To identify the drivers of canopy mortality per forest type for the year 2020 (i.e., conifer, broadleaf) we used a Generalized Additive Model (GAM; for explanation see below) (Hastie and Tibshirani, 1986). We focused our analysis on predominantly pure forests with >75% conifer or >75% broadleaf trees as defined by the Lis-L land cover data set (Korzeniowska, 2020). The forest types of both dead and alive canopies were determined by the land cover data. The dataset for 2020 provides 211,461 polygons of dead conifer and 84,698 polygons of dead broadleaf canopies. We created a binary data set of dead and alive canopy data points as follows: we first determined the centroid of each dead canopy polygon and then subtracted the dead canopy polygons from the land cover polygons, which resulted in areas with only alive forest. We then randomly added the same amount of data points throughout the alive forests of each forest type and merged both alive and dead canopy points (Fig. 2a).

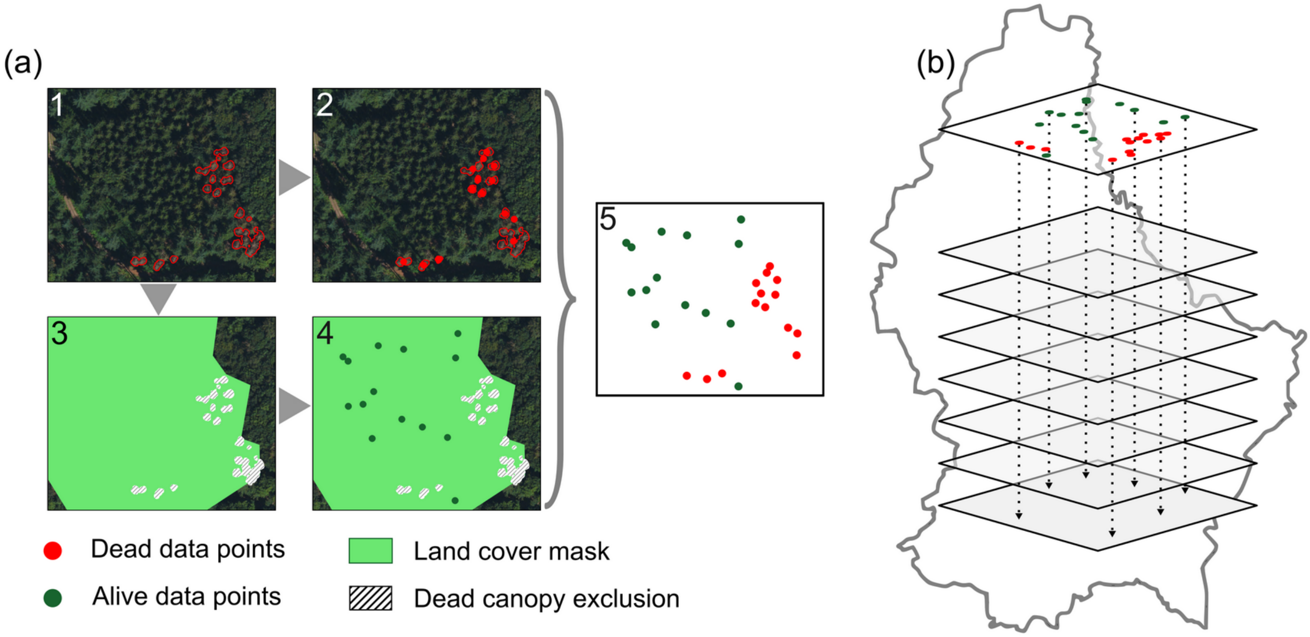

Figure 2: Stepwise data preparation procedures to derive a balanced binary dataset of dead versus alive data points. (a) Step 1-2: Dead canopy points (red) were derived from a data set of dead canopy area in 2020 (Schwarz et al., 2024). Step 3-4: Alive canopy data points (green) were obtained by excluding the dead canopies from a land cover dataset (Lis-L) and randomly distributing data points throughout. Step 5: Dead and alive data points were merged and (b) corresponding values of the environmental variables were extracted to be used in the Generalized Additive Model (GAM).

2.3 Environmental variables

To assess the influence of different environmental drivers in the observed canopy mortality in pure conifer and broadleaf forests during drought we considered 14 variables that were available at a high spatial resolution. All data used for the GAM calculations have a resolution of 50 cm/px, which is highly detailed for such a large spatial data set.

2.3.1 Mortality occurrence and spread

Distance to previously dead canopies was chosen as an indicator to assess a potential influence of bark beetle (I*ps typographus*) spread on tree mortality. We derived the distance of previously dead canopies by calculating the minimum distance of the closest dead canopy of 2019 ($dist_{19}$) to the data points in 2020 using the "Join attributes by location" tool in QGIS. We did the same for the year 2017 ($dist_{17}$) to see if the location of dead canopies before the drought summers had any influence on mortality during the droughts.

Distance to closest (other) dead canopy in 2020 ($dist_{20}$) was calculated using the NN_join tool in QGIS. It represents the distance of the data points to the closest dead canopy in 2020. We selected this variable as a proxy for dead canopy clustering, as bark beetle infestations typically spread from tree to tree in close proximity (Raffa et al., 2008).

Change in dead canopy area (Δarea) was assessed by measuring the extent of dead canopy within a 50 m radius around each data point in 2019 and 2020, and then subtracting the 2019 values from those of 2020. Positive values indicate an increase in canopy mortality due to spreading dieback, negative values reflect a decrease caused by extraction or recovery, and zero values denote no change, either because dead trees remained standing or because no dead canopy was present in the area.

2.3.2 Forest structure

Forest height - A Canopy Height Model was calculated by subtracting the digital terrain model (DTM) from a digital surface model (DSM), which was obtained via a LiDAR sensor and is also provided on the open data platform of Luxembourg. The DSM model includes above ground structures, while the DTM represents the ground.

Distance to forest edges were calculated as the minimum distance to the next forest edge as defined by the Lis-L forest data as a continuous heat map using the gdal proximity tool in QGIS (GDAL/OGR contributors, 2020). We tested two variables (1) $dist_e$ which does not take fragmentation of forests by roads into consideration and only calculates the distance to the outer edges of the forests and (2) $dist_r$ which does include forest edges created by fragmentation due to roads. While forest fragmentation in the rainforests of South America have been extensively researched, studies in Europe remain rare (Feleha et al., 2025). Therefore we chose this approach to test whether the different facets of fragmentation of forest ecosystems have a significant influence on the microclimate of forests during the drought and therefore on the mortality patterns as has been proposed (Dutta and Dutta, 2016).

2.3.3 Topography

Elevation data was derived from the Digital Terrain Model (DTM), provided through the open data platform of Luxembourg. The DTM describes the height above sea level in meters [m] at a resolution of 20 cm per pixel and ranges from 129 to 559 m a.s.l. We resampled the resolution to 50 cm to make the data comparable to the Digital Surface Model (DSM) data we used for the Canopy Height Model. Elevation may influence canopy mortality through changes in temperature and precipitation as well as through exposure to solar radiation and wind.

Slope was calculated from the DTM using the gdal slope function in QGIS (GDAL/OGR contributors, 2020). The data describes the incline of the terrain as difference in elevation between cells of a DTM in degrees. The incline of a slope can influence water run-off, ground depth and radiation exposure.

Northness and *eastness* were calculated from the slope. They represent the components of the aspect variable and describe the direction of a slope on a north-south and west-east axis. Values range from -1 to 1 with negative numbers pointing to south or west facing slopes and positive numbers to north or east facing slopes respectively. The slope direction affects exposition to solar radiation and microclimate. South-facing slopes usually experience more solar radiation, which can lead to higher drought stress, but tree species growing on north-facing slopes may be less adapted to dry conditions and hence more drought prone (Stovall et al., 2019). We chose to also include *eastness*, because discussion with local stakeholders indicated that eastern facing slopes were more affected by canopy mortality between 2018 and 2020 than slopes facing other directions.

Topographic Wetness Index (TWI) was calculated from slope using the "calculate TWI" tool in SAGA GIS (Conrad et al., 2015). TWI uses the slope and contributing upslope area to assess the topographical aspect of water availability (Beven and Kirkby, 1979; Sørensen et al., 2006).

Soil type (soil) - We used a soil type map provided by the Luxembourg open data platform. The data consist of 27 different soil types, categorised by characteristics such as the underlying rock type, describing the soil, for example as "Loamy-stony soils with schist-sandstone material, non-gleyed, with a structural B horizon." (ASTA, 2020; Table S1). An additional code list provides data on drainage and dryness characteristics. Soil type can have a large influence on vegetation and tree mortality as the grain size determines water retention and availability as well as soil nutrient availability.

2.4 Statistical analysis

We used Generalized Additive Models (GAMs) to assess the contribution of the aforementioned environmental covariates to broadleaf and conifer canopy mortality in 2020 as a result of three consecutive drought summers. GAMs are non-parametric linear models used to model non-linear relationships as a sum of linear basis functions (Hastie and Tibshirani, 1986; James et al., 2013). As such they are able to represent more complex relationships between drivers and responses that exist in natural environments. Generally, a GAM consists of a response variable and a number of covariates, expressed as smoothed (non-linear) terms and linear functions.

In this study, we fitted the models using the function bam() provided by the mgcv package (Wood, 2011) in R (V4.2.1, R Core Team, 2022) which is more suitable for very large datasets.

We fitted one model per forest type, i.e. coniferous and broadleaf forest. Due to the binary form of the response variable, referring to dead or alive canopies, we used a binomial distribution and a "logit" link function. A combined smooth of longitude and latitude was added to model spatially structured variation in the data that cannot be attributed to any of the environmental variables. All continuous covariates were added as smooths and *soil type* was added as a categorical term. We used the REML (Restricted Maximum Likelihood) method to automatically adjust the smoothing parameter λ, which controls the wigglyness of the smooth and therefore the flexibility of the model. We kept the parameter $k = 10$, which determines the number of basis functions for the smooth and is reasonably small to achieve interpretable relationships expected for environmental variables.

2.5 Model evaluation

Prior to modelling, variable independence was checked by calculating Pearson's Correlation Coefficient for linear correlations and Spearman's Correlation Coefficient for monotonic relationships, including non-linear trends for each covariate pair (Fig. S1). The degree of correlation between the covariates was low to moderate for almost all variables. The highest correlation was found between the two forest edge variables (~0.8). Due to the large size of the dataset, we consider the statistical power to be large enough to keep both variables in the model and distinguish between different effects of forest fragmentation on canopy mortality. Model assumptions were checked with simulated residuals using the package DHARMa (Hartig, 2022) and revealed no major violations. We report the explained deviance of the model.

To determine the contribution of each variable to the deviance explained per GAM model we calculated partial McFadden's Pseudo-R², along the lines of the implementation in the R-package rsq (McFadden, 1974; Zhang, 2022). Additionally, we quantified the contribution of groups of variables by calculating partial McFadden's Pseudo-R² for topography (*elevation*, *slope*, *TWI*, *northness*, *eastness*), forest structure (*forest height*, $dist_e$, $dist_r$), and indicators of spreading mortality ($dist_{17}$, $dist_{19}$, $dist_{20}$ and $\Delta area$). For each group, a reduced model was fitted excluding all variables in that group, and the resulting McFadden's Pseudo-R² was compared to the full model using Eq. (1).

$$\text{Partial}\,R^2 = 1 - \frac{1-R_F^2}{1-R_R^2} \cdot \frac{n-p_R}{n-p_F} \quad (1)$$

where R_F^2 and R_R^2 represent McFadden's Pseudo-R² for the full and reduced model, respectively, and n the number of total observations. p_R and p_F denote the number of parameters in the reduced and full models, respectively. The formula adjusts for the difference in degrees of freedom between the two models.

225 ## 3 Results

3.1 Canopy mortality distribution in Luxembourg

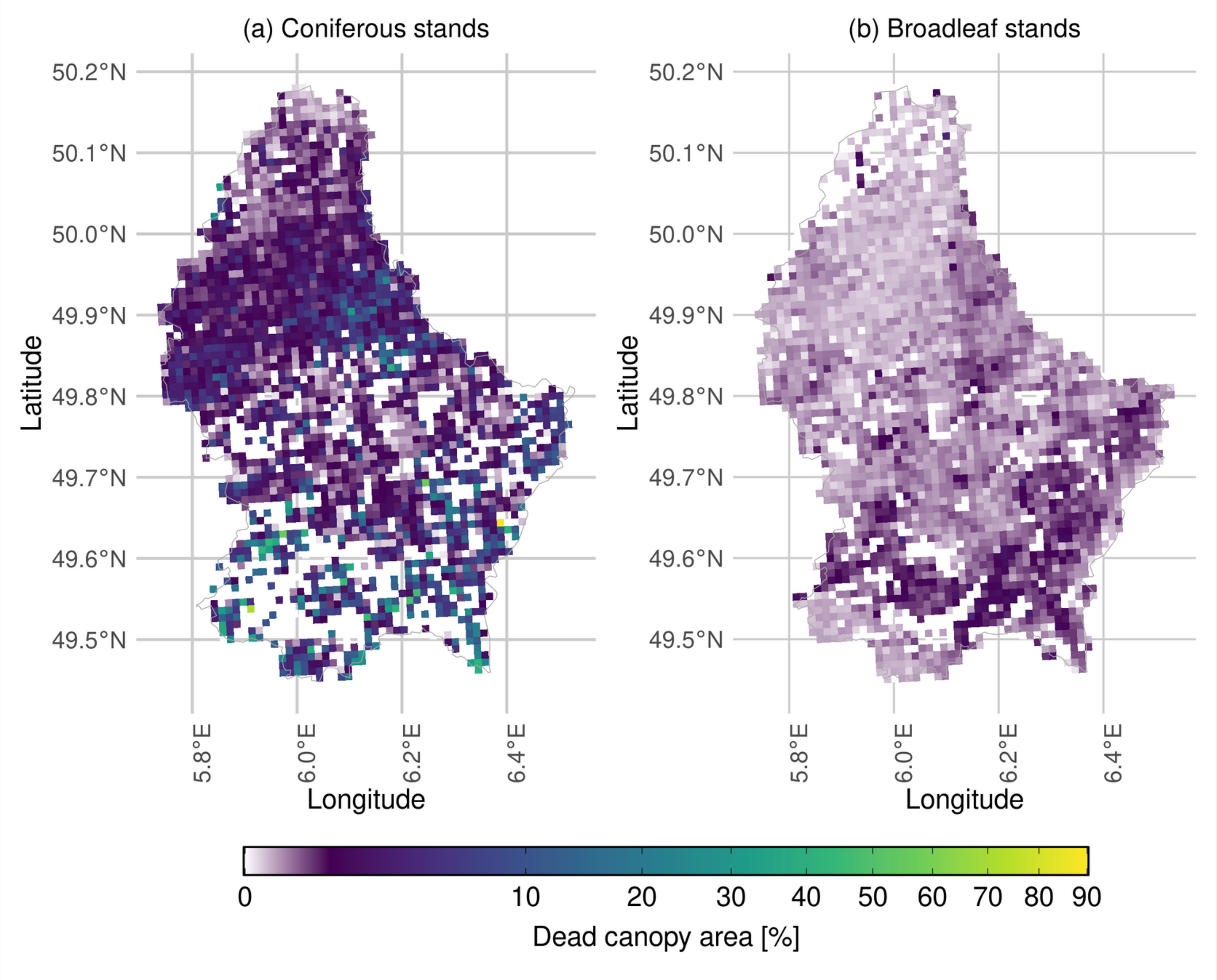

Figure 3: Map of canopy mortality in Luxembourg in 2020. Percent canopy mortality for (a) coniferous and (b) broadleaf forest stands is given. Canopy mortality was derived from convolutional neural network analyses (Schwarz et al., 2024). The distribution of conifer and broadleaf forest stands was attributed based on landcover data (Lis-L) and percentage canopy mortality has been derived in relation to the forested area per pixel (100 ha). 230

Canopy mortality in Luxembourg increased from a total of 64 ha in 2017 to 590 ha in 2020. In 2020, about 420 ha of dead canopies were coniferous and 170 ha were broadleaf. As broadleaf forests dominate in Luxembourg, the disproportionate conifer loss resulted in a higher conifer mortality rate. Hotspots of conifer mortality were observed in the northeast but appeared more scattered across the south (Fig. 3a). In some locations canopy mortality reached almost 90%, although most

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areas experienced mortality rates between 0% and 10%. In broadleaf forests, the mortality rate was generally much lower, particularly in the north of Luxembourg. Isolated areas of higher mortality occurred in the south and southeast but did not exceed 5% (Fig. 3b).

3.2 Relative contribution of environmental variables to canopy mortality

As no distinct large-scale spatial pattern in the distribution of canopy mortality became evident (Fig. 3), we conducted a more detailed analysis of site characteristics contributing to canopy mortality at a much finer spatial scale (50 cm resolution). The relative contributions of the 14 environmental variables to the fit of the broadleaf- and conifer-specific GAM models are summarised in Fig. 4.

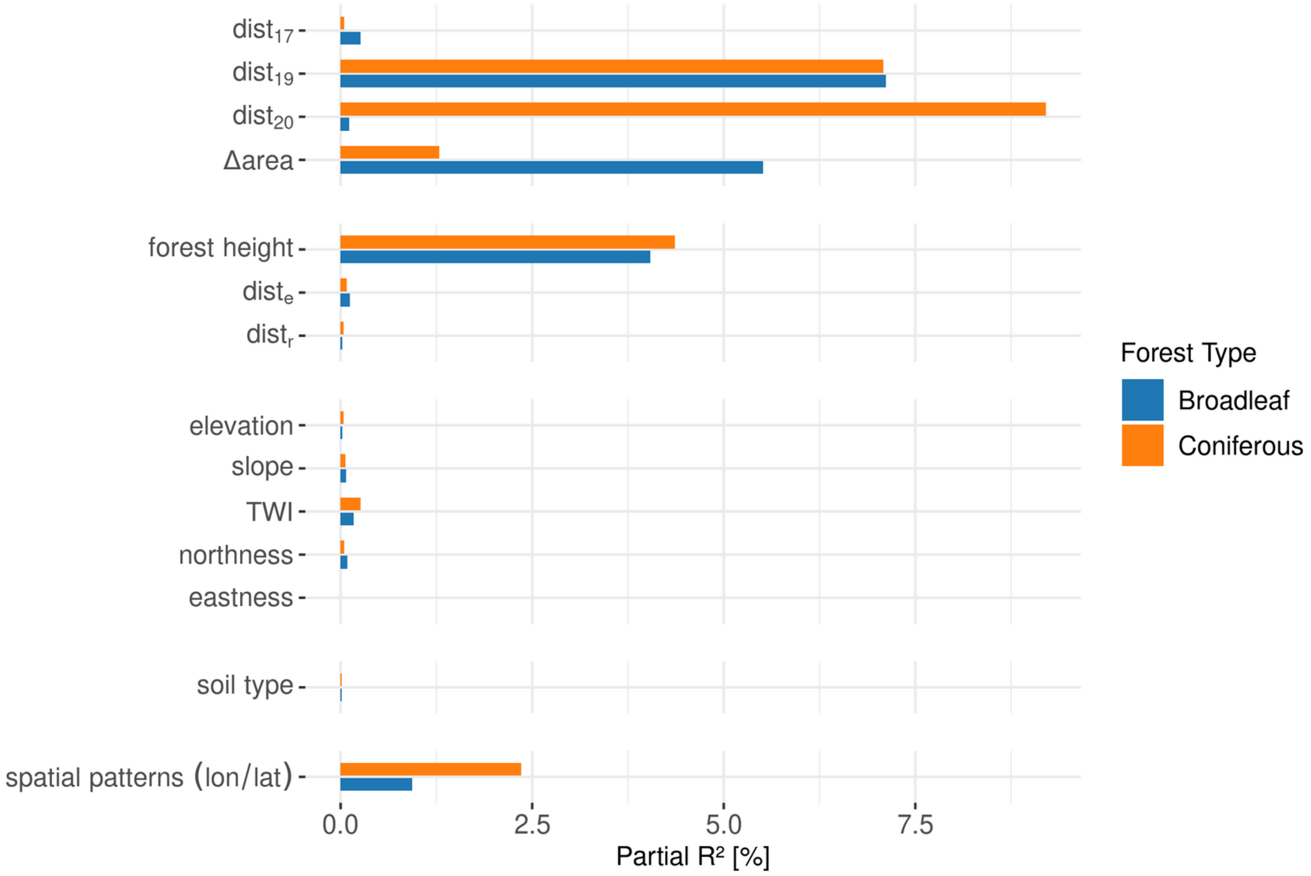

Figure 4: GAM model results presented as partial R² values for all environmental variables for the 2020 canopy mortality in Luxembourg. Partial R² was calculated along the lines of (Zhang, 2022) for broadleaf (blue) and coniferous (orange) forests separately. The values indicate the contribution of each variable in the model's explanation of the observed canopy mortality patterns. The "dist" variables refer to the distance of the closest dead canopy from the previous years 2017 or 2019 and the distance to other dead canopies within the same year 2020. $dist_e$ and $dist_r$ represent the distance to forest edges with and without roads. $\Delta area$ describes the change in dead canopy area between 2019 and 2020 within a 50 m radius around each data point.

Fig. 5 shows the effects of thematic groups of variables on the model's explanatory value. Combined, the variables explained a substantial proportion of the fine-scale spatial distribution of canopy mortality in 2020. For coniferous forests, the GAM accounted for 44.7% of observed mortality, while for broadleaf forests it explained 25.3%. Variables related to the spread of mortality were most important in both forest types (Fig. 4). Taken together they had a partial R² value of 29.43 % in conifers and 14.29 % in broadleaf forests (Fig. 5). Distance to dead canopies in the previous years had a similar effect in both types, but conifers were more likely to die in 2020 when dead canopies occurred close by. In broadleaf forests, mortality was strongly associated with a marked increase in dead canopy area between 2019 and 2020 (*Δarea*). *Forest height* was an important predictor of mortality in both forest types (Fig. 4). In contrast, spatial coordinates (longitude and latitude), included to capture unexplained spatial patterns, contributed little according to partial R² values, and topographic variables as well as *soil type* had minimal influence (Fig. 4,5).

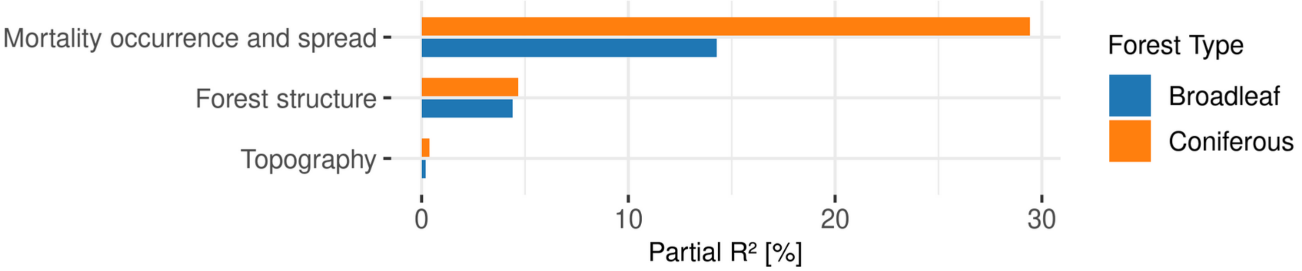

Figure 5: Partial R² values for three groups of environmental variables. Partial R² was calculated along the lines of (Zhang, 2022) for broadleaf (blue) and coniferous (orange) forests separately. The values indicate the contribution of each variable in the model's explanation of the observed canopy mortality patterns.

In order to more closely examine the influence of individual environmental variables on canopy mortality, we used partial effect plots that account for other predictors in the GAMs (Fig. 6). The following subsections explain these effects per group of environmental variables in more detail.

3.3 Self-reinforcing and spreading effects of canopy mortality

In coniferous stands, $dist_{17}$ had no effect on the mortality distribution of conifers, this is not surprisingly given the small partial R² (Fig. 6a). By contrast, proximity to dead canopies in 2019 ($dist_{19}$) was a more influential predictor (Fig. 6b), indicating higher 2020 mortality near trees that had already died in 2019. This pattern was consistent with the observed increase in dead canopy area between 2019 and 2020 (*Δarea*), within a 50 m radius (Fig.6d). The $dist_{20}$ variable was the most important predictor. This indicates that mortality in conifers showed strong spatial clustering, with dead canopies tending to occur in patches within ~20 m of each other (Fig. 6c).

In broadleaf stands, self-reinforcing patterns were also evident. Similar to conifers, 2017 mortality showed no influence on 2020 patterns (Fig. 6e), but 2019 mortality was the most important predictor (Fig. 6f). The increase in dead canopy area (*Δarea*) was also strongly associated with mortality patterns, with local maxima (Fig. 6h). However, unlike conifers, *dist₂₀* did not explain mortality distribution (Fig.6g).

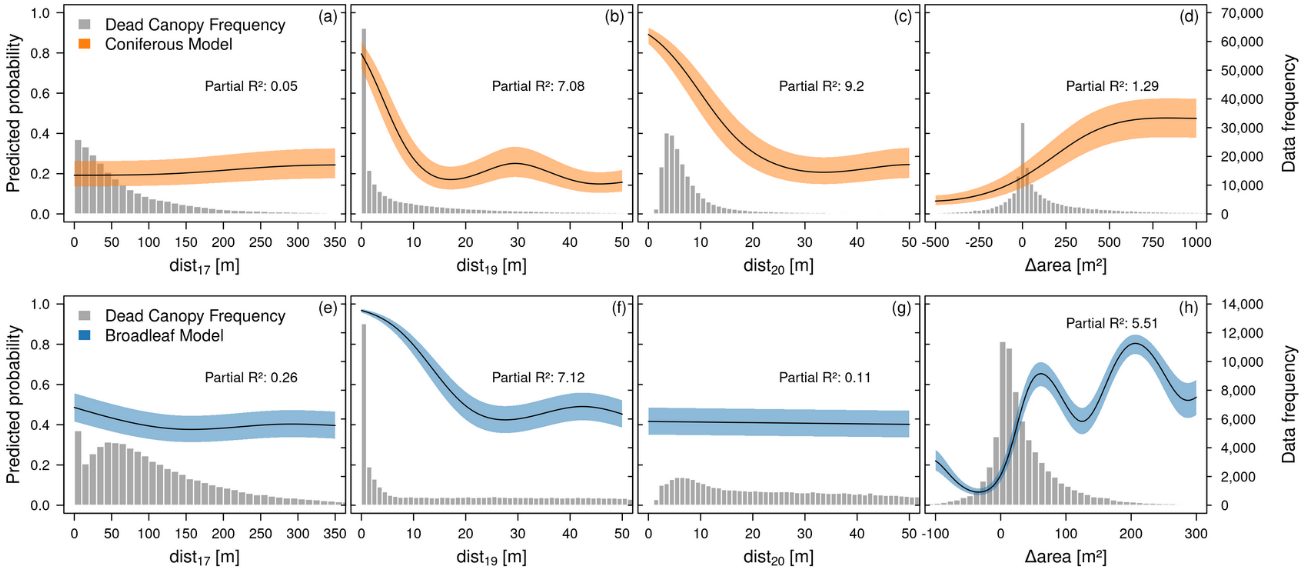

Figure 6: Contribution of environmental variables to the fine-grained spatial distribution and spread of canopy mortality in Luxembourg in 2020. Shown are partial effect plots derived from GAM models for the conifer mortality (upper panels, orange) and broadleaf mortality (lower panels, blue). The "distance" variables describe the distance to the closest dead canopy in the previous years 2017 and 2019 and the distance to other dead canopies in the same year 2020. *Δarea* represents the change in dead canopy area between 2019 and 2020 within a 50 m radius around each data point. The fitted curves describe a smoothed, non-linear relationship between the predictor variable and the response variable, while all other variables in the model are kept at their mean value. The shaded area around the curves represents a 95% confidence interval. The left y-axis represents the predicted probability of the response in relation to the predictor variable. While we might expect average predicted probabilities to be around 0.5 in a balanced binary dataset, the observational and unbalanced nature of our data leads to deviations from this baseline. The histograms (grey) and right side y-axis indicate the frequency of dead canopy observations.

3.4 Effects of forest structure on canopy mortality

We found conifer canopy mortality to increase steeply with forest height >10m and remained high in tall stands (Fig. 7a). In contrast, variables related to forest fragmentation, both outer forest edges (Fig.7b) and inner edges from roads (Fig. 7c) had only minor influence.

In broadleaf stands, the probability of canopy mortality rose steadily with height, leveling off at around 30 m (Fig. 7d). Unlike conifers, broadleaf mortality showed a clearer effect of forest edges, with higher mortality near the forest edge (Fig. 7e), albeit with a low partial R² (Fig.4). This effect is absent for forest roads (Fig. 7f).

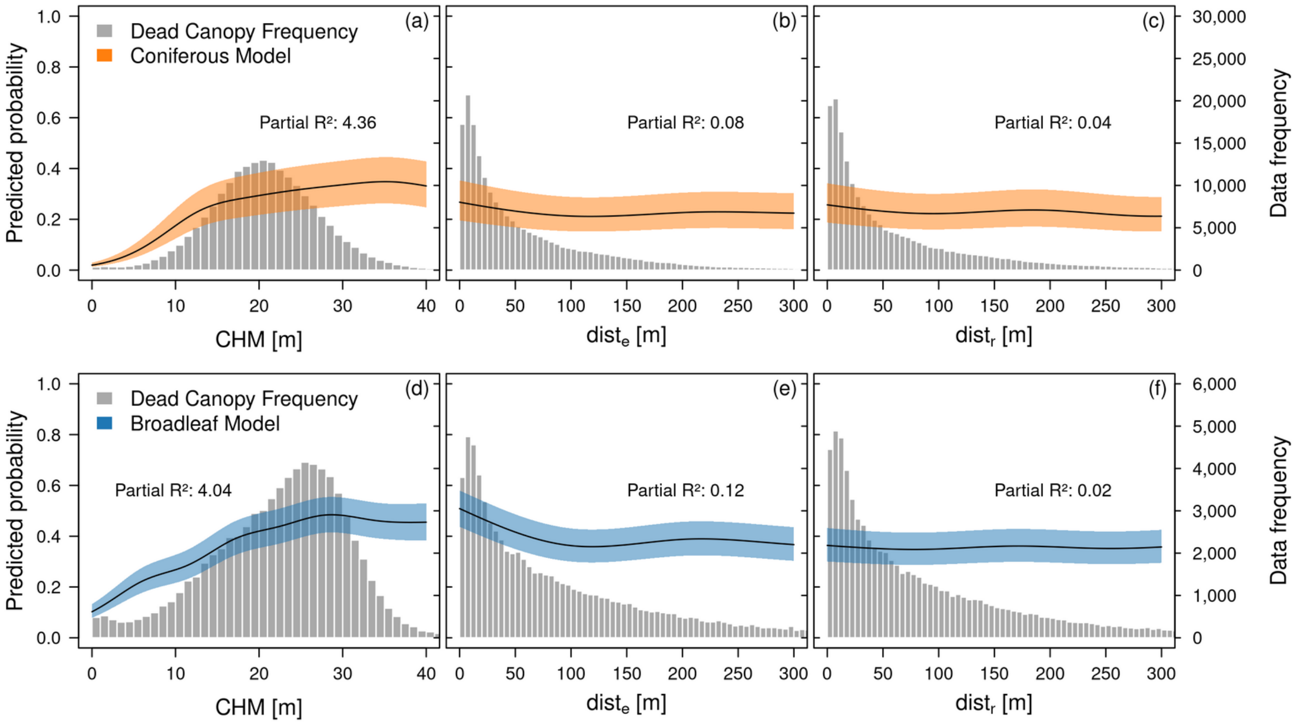

Figure 7: Contribution of environmental variables to the fine-grained spatial distribution and spread of canopy mortality. Shown are partial effect plots derived from GAM models for the conifer mortality (upper panels, orange) and broadleaf mortality (lower panels, blue). Forest Edge describes the distance to the outer edge of each forest, while Forest Edge (roads) describe the distance to the closest edge inside forests, created by fragmentation. The fitted curves describe a smoothed, non-linear relationship between the predictor variable and the response variable while all other variables in the model are kept at their mean value. The shaded area around the curves represents a 95% confidence interval. The left y-axis represents the predicted probability of the response in relation to the predictor variable. While we might expect average predicted probabilities to be around 0.5 in a balanced binary dataset, the observational and unbalanced nature of our data leads to deviations from this baseline. The histograms (grey) and right side y-axis indicate the frequency of dead canopy observations.

3.5 Effects of topography and site conditions on canopy mortality

As shown before, topography played a minor role in explaining canopy mortality patterns for both coniferous and broadleaf stands, with similar responses between forest types (Fig. 4 and 5). Of the tested variables, *TWI* appeared as the most relevant, indicating higher mortality at low TWI values (< 6) for both conifers (Fig. 8c) and broadleaf forests (Fig. 8h).

In conifers, there was no clear effect of *elevation* (Fig. 8a) or *slope* (Fig.8b). Broadleaf mortality increased slightly at elevations above ~250 m (Fig. 8f) and on gentle slopes or plains (Fig. 8g), though these patterns are highly uncertain, reflected in the low partial R² values. Other topographic factors, such as *northness* and *eastness*, showed no discernible trends (Fig.8e,k).

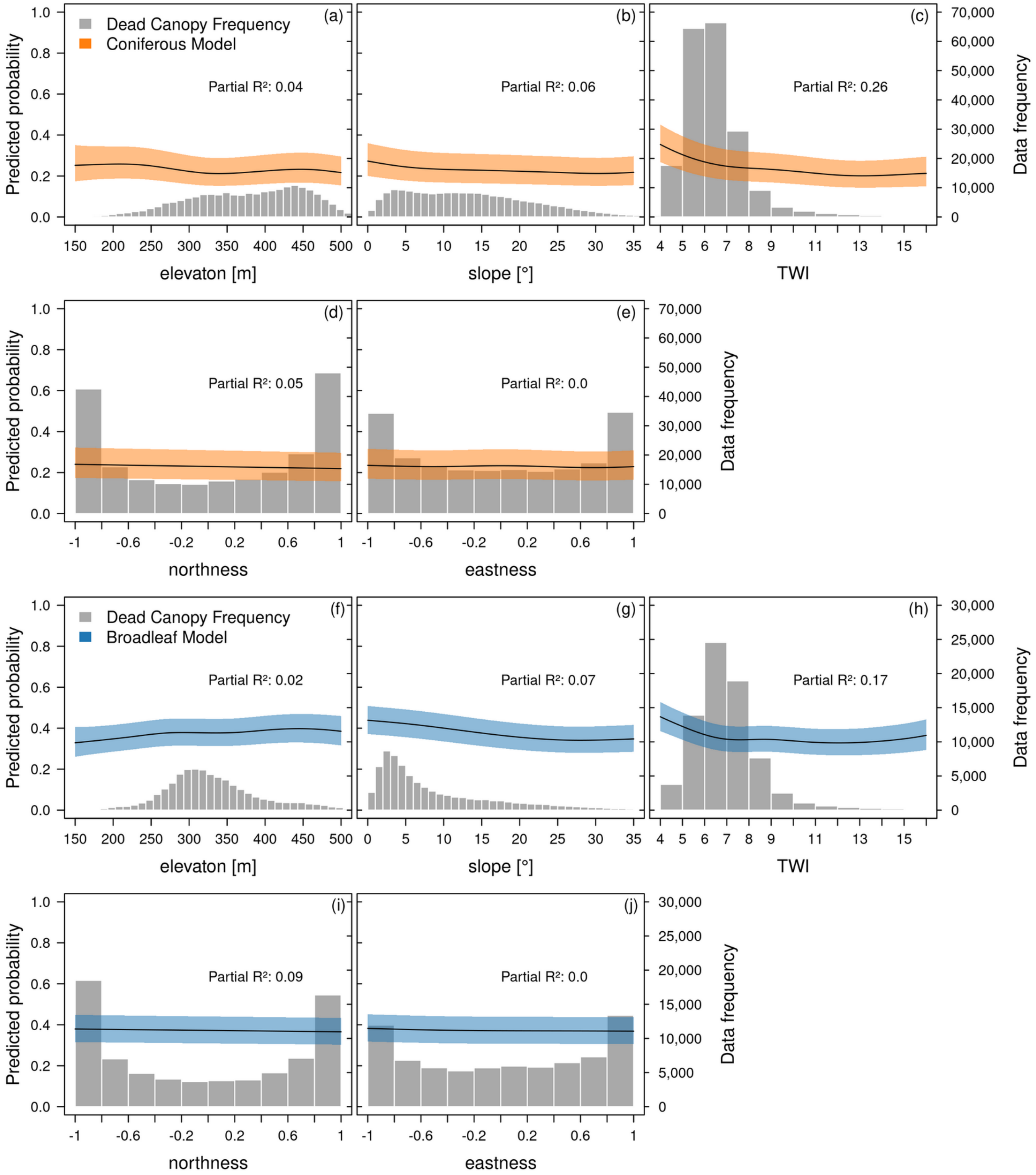
Dead Canopy Frequency
Coniferous Model
(a)
(b)
(c)
Partial R²: 0.04
Partial R²: 0.06
Partial R²: 0.26
Predicted probability
Data frequency
elevaton [m]
slope [°]
TWI
(d)
(e)
Partial R²: 0.05
Partial R²: 0.0
northness
eastness
Dead Canopy Frequency
Broadleaf Model
(f)
(g)
(h)
Partial R²: 0.02
Partial R²: 0.07
Partial R²: 0.17
(i)
(j)
Partial R²: 0.09
Partial R²: 0.0
1.0
0.8
0.6
0.4
0.2
0.0
70,000
60,000
50,000
40,000
30,000
20,000
10,000
0
25,000
15,000
5,000
150
200
250
300
350
400
450
500
0
5
10
15
20
25
30
35
4
5
6
7
8
9
11
13
15
-1
-0.6
-0.2
0.2
0.6
1

Figure 8: Contribution of topographic variables to the fine-grained spatial distribution and spread of canopy mortality. Shown are partial effect plots derived from GAM models for the conifer mortality (upper panels, orange) and broadleaf mortality (lower panels, blue). The *Topographic Wetness Index (TWI)* describes the potential for water accumulation in a landscape based on terrain characteristics. The fitted curves describe a smoothed, non-linear relationship between the predictor variable and the response variable while all other variables in the model are kept at their mean value. The shaded area around the curves represents a 95% confidence interval. The left y-axis represents the predicted probability of the response in relation to the predictor variable. While we might expect average predicted probabilities to be around 0.5 in a balanced binary dataset, the observational and unbalanced nature of our data leads to deviations from this baseline. The histograms (grey) and right side y-axis indicate the frequency of dead canopy observations.

4 Discussion

4.1 Small impact of topography and soil type on canopy mortality

Our findings indicate that topographic variables and *soil type* explained little of the observed canopy mortality in both coniferous and broadleaf forests. Of the six tested variables, *Topographic Wetness Index* emerged as the most important. In contrast, variables such as *slope*, *elevation*, *northness*, *eastness*, and *soil type* had little to no effect on the observed mortality patterns. Luxembourg's relatively low elevation range (150-600 m a.s.l.) may have reduced the effectiveness of *elevation* as a predictor variable. Previous studies that found elevation-related differences in canopy mortality were conducted in regions with significantly higher elevations exceeding 1,500 m a.s.l. (Cailleret et al., 2014; Paz-Kagan et al., 2017; Rita et al., 2020; Sturm et al., 2022). In such situations, climatic differences along the elevation gradients may have more pronounced impacts on potential pest activities as well as precipitation patterns, which both are likely to affect tree mortality. We suggest that in our study, the small elevational gradient together with the country-wide strong effects of the drought possibly overwrote any differences in elevation or slope orientation.

Although high-resolution data are generally advantageous for capturing fine-scale variability (Lannuzel et al., 2021; Pellegrino et al., 2024), they may introduce noise in topographic predictors such as *slope*, *northness*, and *eastness*. This small-scale terrain variability, which may be ecologically irrelevant, could obscure broader topographic patterns (Guillaume et al., 2021; Šilhán et al., 2022). This might explain why variables like *TWI*, which aggregate over broader spatial extents by accounting for upslope contributing area, were less influenced by small-scale terrain features and therefore more effective at capturing relevant hydrological gradients.

Meanwhile, the *soil type* data, comprising 27 classes also showed minimal explanatory value. Although soil moisture is a known driver of drought-induced tree mortality (Belmonte et al., 2022; McDowell et al., 2022), the categorical nature and relatively coarse spatial resolution of the data most likely did not capture the specific soil water holding capacities.

Overall, topographic effects may have been obscured by biotic factors such as bark beetle infestation in conifers and by the overall severe drought conditions. The lack of influence in broadleaf forests, where bark beetles are not a disturbance agent, supports the notion that unaccounted variables, like fine-scaled soil properties or soil water holding capacities played a more important role. However, given the severity and spatial extent of the drought conditions in recent years, it seems plausible that topography played only a minor role across all forest types. This poses a concern for forests in future climate change conditions, as the severity of these hotter drought summers might severely affect even areas thought to be more resilient due to their topographic situations causing even greater forest loss than anticipated (Knutzen et al., 2025).

Our findings largely refute hypothesis (1): topographic and soil variables provided only limited explanatory value for drought-induced canopy mortality, likely due to low regional variability, data limitations, and overriding effects of other factors such as drought severity and biotic disturbances.

4.2 Canopy mortality is higher in tall stands

We found that canopy mortality was related to forest structure and increased in taller stands in both coniferous and broadleaf forests. Taller stands experienced significantly higher mortality rates, consistent with findings from other studies linking forest height to increased vulnerability during drought events (Anderegg et al., 2016; Arend et al., 2021; Stovall et al., 2019; Trugman et al., 2018). Physiologically, tall trees can be more susceptible to hydraulic failure under drought conditions due to longer water transport pathways and higher evaporative demand (Anderegg et al., 2016; Arend et al., 2021; Bennett et al., 2015; Trugman et al., 2018). While trees might not die immediately, the cumulative effects of consecutive drought summers can weaken them over time (McDowell et al., 2022) as for instance reported for beech trees in Switzerland following the 2018 drought (Frei et al., 2022). Additionally, in conifers, increased mortality among taller trees is very likely linked to bark beetles preference for mature hosts with sufficiently thick bark as they are more suitable for the development of bark beetle larvae (Pirtskhalava-Karpova et al., 2024; Raffa et al., 2016).

By contrast, forest edges had negligible effect on observed canopy mortality, suggesting that the severity of the climatic drought conditions extended deep into the forests. While previous research indicates that edge effects can amplify drought stress (Buras et al., 2018; Sturm et al., 2022), our findings show only a minor influence in broadleaf forests and no significant effect in conifers. These findings suggest that the severity of the drought conditions of 2018-2020 might have led to unfavourable conditions even in the forest interior. Similarly, forest fragmentation due to roads had no discernible impact on mortality patterns, consistent with the weak role of edge effects in this study.

These results partially support hypothesis (2): while *forest height* was a strong predictor of mortality, forest edge effects were minimal, likely due to the pervasive severity of the drought across forest interiors.

4.3 Bark beetle infestations is a primary driver of conifer canopy mortality

Our results indicate that bark beetles were a key driver of canopy mortality in conifers, as evidenced by the significant roles of mortality occurrence and spread. Both $dist_{19}$ and $dist_{20}$ were strong determinants of mortality, consistent with the clustered spread characteristic of bark beetle infestations (Zhao et al., 2025). The $\Delta area$ variable, which captured changes in the dead canopy area surrounding our data points, was also important and further supports the interpretation of spreading bark beetle activity as the infestation grows from single trees to large patches of dead trees (Potterf et al., 2019; Stereńczak et al., 2019). *Forest height* emerged as the only other strong predictor, in line with the European spruce bark beetle's preference for larger

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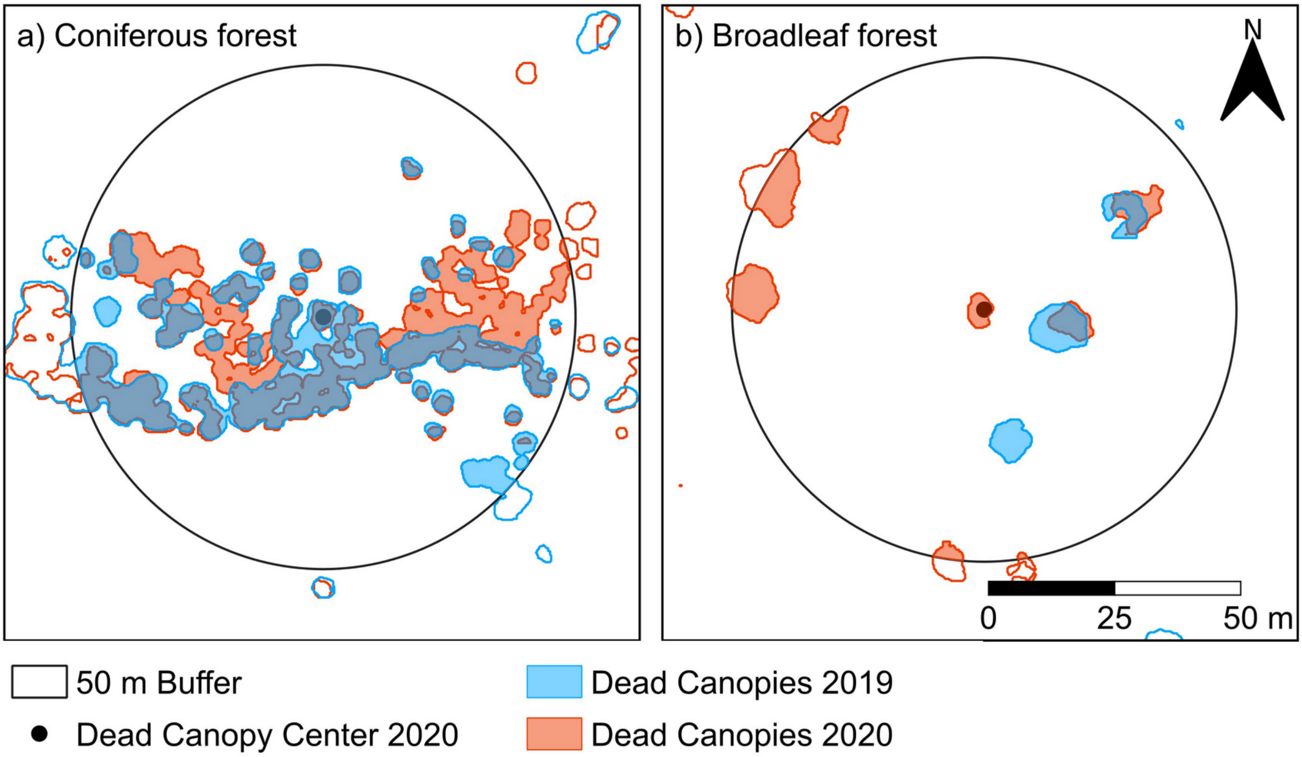
trees with sufficiently thick bark for tunnelling (Raffa et al., 2016). Taken together, these variables clearly reflect bark beetle-driven mortality dynamics in conifers.

While bark beetles likely were a key cause of mortality, their impact appears to be strongly modulated by drought, as confirmed in other studies (Hlásny et al., 2021). Our data reveal little impact of spreading mortality prior to 2018, suggesting that high bark beetle activity only started following the onset of severe drought conditions. This supports existing research indicating that hot droughts can both weaken trees (Rouault et al., 2006) and simultaneously accelerate beetle development, enabling multiple reproductive cycles per year (Fleischer et al., 2016; Lindman et al., 2023; Robbins et al., 2022; Webb et al., 2025). At the physiological level, we assume that the trees exposed to drought suffered from both hydraulic failure due to low water availability and rising vapor pressure deficit (Adams et al., 2017), and carbon starvation as stomata closed to conserve water (Ziegler et al., 2024). Reduced water availability likely also impaired resin flow (Kolb et al., 2019; Malone et al., 2024), weakening the trees' natural defense mechanisms. Carbon starvation during drought might also have decreased the allocation of nonstructural carbohydrates (NSC) to defensive metabolites in the tree's resin (Huang et al., 2020). These interacting stresses created ideal conditions for bark beetle outbreaks and explain the mortality patterns observed in our study.

Another layer of complexity lies in the interaction between bark beetle infestations and topography. Previous studies have shown that bark beetle infestations are often more severe on south- and east-facing slopes, at lower elevations, and on steeper terrain (Akkuzu et al., 2009; Blomqvist et al., 2018; Jakoby et al., 2019). Blomqvist et al., 2018 also found more severe bark beetle infestations on shallow soils with low water storage capabilities. While such topographic patterns were not dominant in our mortality models, it does not necessarily mean such relationships were absent. Rather, they may have been masked by the overriding biotic effect of infestation.

Canopy mortality in broadleaf trees also showed high impact of two variables in the group that was supposed to indicate the spread of bark beetle infestation. These variables were the $dist_{19}$ and $\Delta area$, while $dist_{20}$ had little explanatory power. This suggests that while the loss of large-crowned individuals strongly increased the mortality area, new deaths were not spatially contagious (Fig. 9). Proximity to dead canopies in 2019 ($dist_{19}$) must also be interpreted with caution, as it partly reflects the persistence of already-dead trees rather than true neighbourhood effects in both forest types (Fig. 9). Taken together, these patterns suggest that in conifers, canopy mortality is shaped by contagious bark beetle outbreaks, whereas in broadleaves it reflects the loss of structurally dominant individuals under stress.

Our findings strongly support hypothesis (3): conifer canopy mortality was closely linked to the spatial and temporal dynamics of bark beetle spread. At the same time, the contrasting patterns in broadleaf forests emphasise that identical predictor variables can reflect very different underlying processes depending on forest type.



410 **Figure 9: Example of dead canopy area within a 50 m radius around a dead canopy core in (a) coniferous and (b) broadleaf forest. Blue areas indicate canopy mortality detected in 2019, and red areas indicate mortality in 2020. The figure highlights contrasting mortality patterns between the two forest types: in broadleaf forests, individual dead trees tend to cover larger areas, so additional mortality in 2020 substantially expands the affected area, comparable in magnitude to the clustered expansion observed in coniferous stands. The figure also illustrates how proximity to dead canopies from 2019 may contribute to high correlation in the GAM model, as trees already dead in 2019 generally remain dead in 2020.**

5 Conclusions

This study shows that drought-driven canopy mortality in Luxembourg is strongly shaped by forest structure and bark beetle dynamics, whereas topography and soil type had comparatively limited impact. By leveraging an extremely rich high-resolution mortality dataset, we were able to capture fine-scale patterns of mortality across the landscape, underscoring the value of detailed large-scale datasets for understanding forest responses to extreme drought. With new data collecting platforms developing (e.g., deadtrees.org) there is a growing need to develop analytical methodologies capable of analysing these high-resolution mortality datasets. Addressing current limitations, such as potential noise in micro-topographic variables and under-representation of soil characteristics or young and understory vegetation, through long-term monitoring and improved analytical approaches will further enhance our ability to predict and guide management of forest vulnerability under changing climate conditions.

Data availability

Model data will be made publicly available upon publication.

Author contribution

SS, FEF, and NKR conceptualised the study and developed the methodology. SS curated, analysed, and visualised the data. LH contributed to the statistical approach and supported model code development. SS prepared the original draft, and all authors contributed to and edited the manuscript.

Competing interests

The authors declare that they have no conflict of interest.

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References

Adams, H. D., Zeppel, M. J. B., Anderegg, W. R. L., Hartmann, H., Landhäusser, S. M., Tissue, D. T., Huxman, T. E., Hudson, P. J., Franz, T. E., Allen, C. D., Anderegg, L. D. L., Barron-Gafford, G. A., Beerling, D. J., Breshears, D. D., Brodribb, T. J., Bugmann, H., Cobb, R. C., Collins, A. D., Dickman, L. T., Duan, H., Ewers, B. E., Galiano, L., Galvez, D. A., Garcia-Forner, N., Gaylord, M. L., Germino, M. J., Gessler, A., Hacke, U. G., Hakamada, R., Hector, A., Jenkins, M. W., Kane, J. M., Kolb, T. E., Law, D. J., Lewis, J. D., Limousin, J.-M., Love, D. M., Macalady, A. K., Martínez-Vilalta, J., Mencuccini, M., Mitchell, P. J., Muss, J. D., O'Brien, M. J., O'Grady, A. P., Pangle, R. E., Pinkard, E. A., Piper, F. I., Plaut, J. A., Pockman, W. T., Quirk, J., Reinhardt, K., Ripullone, F., Ryan, M. G., Sala, A., Sevanto, S., Sperry, J. S., Vargas, R., Vennetier, M., Way, D. A., Xu, C., Yepez, E. A., and McDowell, N. G.: A multi-species synthesis of physiological mechanisms in drought-induced tree mortality, Nat Ecol Evol, 1, 1285–1291, https://doi.org/10.1038/s41559-017-0248-x, 2017.

Akkuzu, E., Eroğlu, H., Sonmez, T., Yolasığmaz, H., and Sariyildiz, T.: Effects of forest roads on foliage discoloration of oriental spruce by Ips typographus (L.), African Journal of Agricultural Research, 4, 468–473, 2009.

Allen, C. D. and Breshears, D. D.: Drought-induced shift of a forest–woodland ecotone: Rapid landscape response to climate variation, Proceedings of the National Academy of Sciences, 95, 14839–14842, https://doi.org/10.1073/pnas.95.25.14839, 1998.

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. H. (Ted), Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S. W., Semerci, A., and Cobb, N.: A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests, Forest Ecology and Management, 259, 660–684, https://doi.org/10.1016/j.foreco.2009.09.001, 2010.

Altman, J., Fibich, P., Trotsiuk, V., and Altmanova, N.: Global pattern of forest disturbances and its shift under climate change, Science of The Total Environment, 915, 170117, https://doi.org/10.1016/j.scitotenv.2024.170117, 2024.

Anderegg, W. R. L., Kane, J. M., and Anderegg, L. D. L.: Consequences of widespread tree mortality triggered by drought and temperature stress, Nature Clim Change, 3, 30–36, https://doi.org/10.1038/nclimate1635, 2013.

Anderegg, W. R. L., Martinez-Vilalta, J., Cailleret, M., Camarero, J. J., Ewers, B. E., Galbraith, D., Gessler, A., Grote, R., Huang, C., Levick, S. R., Powell, T. L., Rowland, L., Sánchez-Salguero, R., and Trotsiuk, V.: When a Tree Dies in the Forest: Scaling Climate-Driven Tree Mortality to Ecosystem Water and Carbon Fluxes, Ecosystems, 19, 1133–1147, https://doi.org/10.1007/s10021-016-9982-1, 2016.

Anderegg, W. R. L., Trugman, A. T., Badgley, G., Anderson, C. M., Bartuska, A., Ciais, P., Cullenward, D., Field, C. B., Freeman, J., Goetz, S. J., Hicke, J. A., Huntzinger, D., Jackson, R. B., Nickerson, J., Pacala, S., and Randerson, J. T.: Climate-driven risks to the climate mitigation potential of forests, Science, 368, eaaz7005, https://doi.org/10.1126/science.aaz7005, 2020.

Arend, M., Link, R. M., Patthey, R., Hoch, G., Schuldt, B., and Kahmen, A.: Rapid hydraulic collapse as cause of drought-induced mortality in conifers, Proceedings of the National Academy of Sciences, 118, e2025251118, https://doi.org/10.1073/pnas.2025251118, 2021.

ASTA, M. de l’Agriculture, de la Viticulture et du Développement rural Administration des services techniques de l’agriculture, Luxembourg: 50 ans cartographie des sols Administration des services techniques de l’agriculture, 2020.

Belmonte, A., Ts. Sankey, T., Biederman, J., Bradford, J. B., and Kolb, T.: Soil moisture response to seasonal drought conditions and post-thinning forest structure, Ecohydrology, 15, e2406, https://doi.org/10.1002/eco.2406, 2022.

Bennett, A. C., McDowell, N. G., Allen, C. D., and Anderson-Teixeira, K. J.: Larger trees suffer most during drought in forests worldwide, Nature Plants, 1, 1–5, https://doi.org/10.1038/nplants.2015.139, 2015.

Beven, K. J. and Kirkby, M. J.: A physically based, variable contributing area model of basin hydrology / Un modèle à base physique de zone d’appel variable de l’hydrologie du bassin versant, Hydrological Sciences Bulletin, 24, 43–69, https://doi.org/10.1080/02626667909491834, 1979.

Blomqvist, M., Kosunen, M., Starr, M., Kantola, T., Holopainen, M., and Lyytikäinen-Saarenmaa, P.: Modelling the predisposition of Norway spruce to Ips typographus L. infestation by means of environmental factors in southern Finland, Eur J Forest Res, 137, 675–691, https://doi.org/10.1007/s10342-018-1133-0, 2018.

Breshears, D. D., Cobb, N. S., Rich, P. M., Price, K. P., Allen, C. D., Balice, R. G., Romme, W. H., Kastens, J. H., Floyd, M. L., Belnap, J., Anderson, J. J., Myers, O. B., and Meyer, C. W.: Regional vegetation die-off in response to global-change-type drought, Proc Natl Acad Sci U S A, 102, 15144–15148, https://doi.org/10.1073/pnas.0505734102, 2005.

Breshears, D. D., Carroll, C. J. W., Redmond, M. D., Wion, A. P., Allen, C. D., Cobb, N. S., Meneses, N., Field, J. P., Wilson, L. A., Law, D. J., McCabe, L. M., and Newell-Bauer, O.: A Dirty Dozen Ways to Die: Metrics and Modifiers of Mortality Driven by Drought and Warming for a Tree Species, Front. For. Glob. Change, 1, https://doi.org/10.3389/ffgc.2018.00004, 2018.

Brouwers, N., Matusick, G., Ruthrof, K., Lyons, T., and Hardy, G.: Landscape-scale assessment of tree crown dieback following extreme drought and heat in a Mediterranean eucalypt forest ecosystem, Landscape Ecol, 28, 69–80, https://doi.org/10.1007/s10980-012-9815-3, 2013.

Brun, P., Psomas, A., Ginzler, C., Thuiller, W., Zappa, M., and Zimmermann, N. E.: Large-scale early-wilting response of Central European forests to the 2018 extreme drought, Global Change Biology, 26, 7021–7035, https://doi.org/10.1111/gcb.15360, 2020.

Buras, A., Schunk, C., Zeiträg, C., Herrmann, C., Kaiser, L., Lemme, H., Straub, C., Taeger, S., Gößwein, S., Klemmt, H.-J., and Menzel, A.: Are Scots pine forest edges particularly prone to drought-induced mortality?, Environ. Res. Lett., 13, 025001, https://doi.org/10.1088/1748-9326/aaa0b4, 2018.

Cailleret, M., Nourtier, M., Amm, A., Durand-Gillmann, M., and Davi, H.: Drought-induced decline and mortality of silver fir differ among three sites in Southern France, Annals of Forest Science, 71, 643–657, https://doi.org/10.1007/s13595-013-0265-0, 2014.

Cervantes-Martínez, R., Cerano-Paredes, J., Sánchez-Martínez, G., Villanueva-Díaz, J., Esquivel-Arriaga, G., Cambrón-Sandoval, V. H., Méndez-González, J., and Castruita-Esparza, L. U.: Brotes históricos de descortezadores en México, Guatemala y Honduras (1895-2015) y su relación con las sequías, Rev Cha Se Cie For y del Amb, 25, 269–290, https://doi.org/10.5154/r.rchscfa.2019.01.006, 2019.

Choat, B., Jansen, S., Brodribb, T. J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S. J., Feild, T. S., Gleason, S. M., Hacke, U. G., Jacobsen, A. L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P. J., Nardini, A., Pittermann, J., Pratt, R. B., Sperry, J. S., Westoby, M., Wright, I. J., and Zanne, A. E.: Global convergence in the vulnerability of forests to drought, Nature, 491, 752–755, https://doi.org/10.1038/nature11688, 2012.

Clifford, M. J. and Booth, R. K.: Late-Holocene drought and fire drove a widespread change in forest community composition in eastern North America, The Holocene, 25, 1102–1110, https://doi.org/10.1177/0959683615580182, 2015.

Conrad, O., Bechtel, B., Bock, M., Dietrich, H., Fischer, E., Gerlitz, L., Wehberg, J., Wichmann, V., and Böhner, J.: System for Automated Geoscientific Analyses (SAGA) v. 2.1.4, Geoscientific Model Development, 8, 1991–2007, https://doi.org/10.5194/gmd-8-1991-2015, 2015.

Dorman, M., Svoray, T., Perevolotsky, A., Moshe, Y., and Sarris, D.: What determines tree mortality in dry environments? a multi-perspective approach, Ecological Applications, 25, 1054–1071, https://doi.org/10.1890/14-0698.1, 2015.

Dutta, A. and Dutta, H.: The Biotic Implications of Forest Fragmentation, International Research Journal of Environmental Sciences, 5, 58–62, 2016.

Feleha, D. D., Tymińska-Czabańska, L., and Netzel, P.: Forest Fragmentation and Forest Mortality—An In-Depth Systematic Review, Forests, 16, 565, https://doi.org/10.3390/f16040565, 2025.

Fleischer, P. 1, Ferenčík, J. 2, Hlaváč, P. 1, Kozánek, M. 3 1 T. U. in Z., and Scientica, s r o: Elevated bark temperature in unremoved stumps after disturbances facilitates multi-voltinism in Ips typographus population in a mountainous forest, 15–22, https://doi.org/10.1515/forj-2016-0002, 2016.

Floyd, M. L., Clifford, M., Cobb, N. S., Hanna, D., Delph, R., Ford, P., and Turner, D.: Relationship of stand characteristics to drought-induced mortality in three Southwestern piñon–juniper woodlands, Ecological Applications, 19, 1223–1230, https://doi.org/10.1890/08-1265.1, 2009.

Frei, E. R., Gossner, M. M., Vitasse, Y., Queloz, V., Dubach, V., Gessler, A., Ginzler, C., Hagedorn, F., Meusburger, K., Moor, M., Samblás Vives, E., Rigling, A., Uitentuis, I., von Arx, G., and Wohlgemuth, T.: European beech dieback after premature leaf senescence during the 2018 drought in northern Switzerland, Plant Biology, 24, 1132–1145, https://doi.org/10.1111/plb.13467, 2022.

Gilles, A., Lisein, J., Cansell, J., Latte, N., Piedallu, C., and Claessens, H.: Evolution of the bark beetle crisis in spruce (Picea abies) forests: A spatial and temporal remote sensing analysis in Belgium and North- eastern Franc, https://doi.org/10.21203/rs.3.rs-3051830/v1, 2023.

Guarín, A. and Taylor, A. H.: Drought triggered tree mortality in mixed conifer forests in Yosemite National Park, California, USA, Forest Ecology and Management, 218, 229–244, https://doi.org/10.1016/j.foreco.2005.07.014, 2005.

Guillaume, A. S., Leempoel, K., Rochat, E., Rogivue, A., Kasser, M., Gugerli, F., Parisod, C., and Joost, S.: Multiscale Very High Resolution Topographic Models in Alpine Ecology: Pros and Cons of Airborne LiDAR and Drone-Based Stereo-Photogrammetry Technologies, Remote Sensing, 13, 1588, https://doi.org/10.3390/rs13081588, 2021.

Hajek, P., Link, R. M., Nock, C. A., Bauhus, J., Gebauer, T., Gessler, A., Kovach, K., Messier, C., Paquette, A., Saurer, M., Scherer-Lorenzen, M., Rose, L., and Schuldt, B.: Mutually inclusive mechanisms of drought-induced tree mortality, Global Change Biology, 28, 3365–3378, https://doi.org/10.1111/gcb.16146, 2022.

Hammond, W. M., Williams, A. P., Abatzoglou, J. T., Adams, H. D., Klein, T., López, R., Sáenz-Romero, C., Hartmann, H., Breshears, D. D., and Allen, C. D.: Global field observations of tree die-off reveal hotter-drought fingerprint for Earth's forests, Nat Commun, 13, 1761, https://doi.org/10.1038/s41467-022-29289-2, 2022.

Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A., Chini, L., Justice, C. O., and Townshend, J. R. G.: High-Resolution Global Maps of 21st-Century Forest Cover Change, Science, https://doi.org/10.1126/science.1244693, 2013.

Hartig, F.: DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models, 2022.

Hartmann, H., Moura, C. F., Anderegg, W. R. L., Ruehr, N. K., Salmon, Y., Allen, C. D., Arndt, S. K., Breshears, D. D., Davi, H., Galbraith, D., Ruthrof, K. X., Wunder, J., Adams, H. D., Bloemen, J., Cailleret, M., Cobb, R., Gessler, A., Grams, T. E. E., Jansen, S., Kautz, M., Lloret, F., and O'Brien, M.: Research frontiers for improving our understanding of drought-induced tree and forest mortality, New Phytologist, 218, 15–28, https://doi.org/10.1111/nph.15048, 2018.

Hartmann, H., Bastos, A., Das, A. J., Esquivel-Muelbert, A., Hammond, W. M., Martínez-Vilalta, J., McDowell, N. G., Powers, J. S., Pugh, T. A. M., Ruthrof, K. X., and Allen, C. D.: Climate Change Risks to Global Forest Health: Emergence of Unexpected Events of Elevated Tree Mortality Worldwide, Annu Rev Plant Biol, 73, 673–702, https://doi.org/10.1146/annurev-arplant-102820-012804, 2022.

Hastie, T. and Tibshirani, R.: Generalized Additive Models, Statistical Science, 1, 297–310, 1986.

Hlásny, T., König, L., Krokene, P., Lindner, M., Montagné-Huck, C., Müller, J., Qin, H., Raffa, K., Schelhaas, M.-J., Svoboda, M., Viiri, H., and Seidl, R.: Bark Beetle Outbreaks in Europe: State of Knowledge and Ways Forward for Management, Current Forestry Reports, 7, 1–28, https://doi.org/10.1007/s40725-021-00142-x, 2021.

Huang, J., Kautz, M., Trowbridge, A. M., Hammerbacher, A., Raffa, K. F., Adams, H. D., Goodsman, D. W., Xu, C., Meddens, A. J. H., Kandasamy, D., Gershenzon, J., Seidl, R., and Hartmann, H.: Tree defence and bark beetles in a drying world: carbon partitioning, functioning and modelling, New Phytologist, 225, 26–36, https://doi.org/10.1111/nph.16173, 2020.

Hülsmann, L., Bugmann, H. K. M., Commarmot, B., Meyer, P., Zimmermann, S., and Brang, P.: Does one model fit all? Patterns of beech mortality in natural forests of three European regions, Ecological Applications, 26, 2465–2479, https://doi.org/10.1002/eap.1388, 2016.

Jakoby, O., Lischke, H., and Wermelinger, B.: Climate change alters elevational phenology patterns of the European spruce bark beetle (Ips typographus), Global Change Biology, 25, 4048–4063, https://doi.org/10.1111/gcb.14766, 2019.

James, G., Witten, D., Hastie, T., and Tibshirani, R.: An Introduction to Statistical Learning: With Applications in R, 2013.

Kärvemo, S., Huo, L., Öhrn, P., Lindberg, E., and Persson, H. J.: Different triggers, different stories: Bark-beetle infestation patterns after storm and drought-induced outbreaks, Forest Ecology and Management, 545, 121255, https://doi.org/10.1016/j.foreco.2023.121255, 2023.

Kattenborn, T., Mosig, C., Vajna-Jehle, J., Cheng, Y., Hartmann, H., Montero, D., Juntilla, S., Horion, S., Schwenke, M. B., and Mahecha, M.: deadtrees.earth: tree mortality monitoring from local to global scales with AI and remote sensing, Copernicus Meetings, https://doi.org/10.5194/egusphere-egu25-19718, 2025.

Knutzen, F., Averbeck, P., Barrasso, C., Bouwer, L. M., Gardiner, B., Grünzweig, J. M., Hänel, S., Haustein, K., Johannessen, M. R., Kollet, S., Müller, M. M., Pietikäinen, J.-P., Pietras-Couffignal, K., Pinto, J. G., Rechid, D., Rousi, E., Russo, A., Suarez-Gutierrez, L., Veit, S., Wendler, J., Xoplaki, E., and Gliksman, D.: Impacts on and damage to European forests from the 2018–2022 heat and drought events, Natural Hazards and Earth System Sciences, 25, 77–117, https://doi.org/10.5194/nhess-25-77-2025, 2025.

Kolb, T., Keefover-Ring, K., Burr, S. J., Hofstetter, R., Gaylord, M., and Raffa, K. F.: Drought-Mediated Changes in Tree Physiological Processes Weaken Tree Defenses to Bark Beetle Attack, J Chem Ecol, 45, 888–900, https://doi.org/10.1007/s10886-019-01105-0, 2019.

König, L. A., Mohren, F., Schelhaas, M.-J., Astigarraga, J., Cienciala, E., Flury, R., Fridman, J., Govaere, L., Lehtonen, A., Muelbert, A. E., Pugh, T. A. M., Rohner, B., Ruiz-Benito, P., Suvanto, S., Talarczyk, A., Zavala, M. A., Vega, J. M., Staritsky, I., Hengeveld, G., and Nabuurs, G.-J.: Combining national forest inventories reveals distinct role of climate on tree recruitment in European forests, Ecological Modelling, 505, 111112, https://doi.org/10.1016/j.ecolmodel.2025.111112, 2025.

Korzeniowska, K.: Mapping Land Use 2018 in Luxembourg: an approach based on aerial images, LiDAR and ancillary GIS data, 2020.

Lannuzel, G., Balmot, J., Dubos, N., Thibault, M., and Fogliani, B.: High-resolution topographic variables accurately predict the distribution of rare plant species for conservation area selection in a narrow-endemism hotspot in New Caledonia, Biodivers Conserv, 30, 963–990, https://doi.org/10.1007/s10531-021-02126-6, 2021.

Lindman, L., Ranius, T., and Schroeder, M.: Regional climate affects habitat preferences and thermal sums required for development of the Eurasian spruce bark beetle, *Ips typographus*, Forest Ecology and Management, 544, 121216, https://doi.org/10.1016/j.foreco.2023.121216, 2023.

Lugo, A. E. and Gucinski, H.: Function, effects, and management of forest roads, Forest Ecology and Management, 133, 249–262, https://doi.org/10.1016/S0378-1127(99)00237-6, 2000.

Luo, Y. and Chen, H. Y. H.: Observations from old forests underestimate climate change effects on tree mortality, Nat Commun, 4, 1655, https://doi.org/10.1038/ncomms2681, 2013.

Malone, S., Thompson, R. A., Chow, P. S., De Oliveira Jr., C. R., Landhäusser, S. M., Six, D. L., McCulloh, K. A., Adams, H. D., and Trowbridge, A. M.: Water, not carbon, drives drought-constraints on stem terpene defense against simulated bark beetle attack in Pinus edulis (4), https://doi.org/10.5061/DRYAD.TMPG4F57N, 2024.

Mann, D., Gohr, C., Blumröder, J. S., and Ibisch, P. L.: Does fragmentation contribute to the forest crisis in Germany?, Front. For. Glob. Change, 6, https://doi.org/10.3389/ffgc.2023.1099460, 2023.

McDowell, N. G. and Allen, C. D.: Darcy's law predicts widespread forest mortality under climate warming, Nature Clim Change, 5, 669–672, https://doi.org/10.1038/nclimate2641, 2015.

McDowell, N. G., Fisher, R. A., Xu, C., Domec, J. C., Hölttä, T., Mackay, D. S., Sperry, J. S., Boutz, A., Dickman, L., Gehres, N., Limousin, J. M., Macalady, A., Martínez-Vilalta, J., Mencuccini, M., Plaut, J. A., Ogée, J., Pangle, R. E., Rasse, D. P., Ryan, M. G., Sevanto, S., Waring, R. H., Williams, A. P., Yepez, E. A., and Pockman, W. T.: Evaluating theories of drought-induced vegetation mortality using a multimodel–experiment framework, New Phytologist, 200, 304–321, https://doi.org/10.1111/nph.12465, 2013.

McDowell, N. G., Sapes, G., Pivovaroff, A., Adams, H. D., Allen, C. D., Anderegg, W. R. L., Arend, M., Breshears, D. D., Brodribb, T., Choat, B., Cochard, H., De Cáceres, M., De Kauwe, M. G., Grossiord, C., Hammond, W. M., Hartmann, H., Hoch, G., Kahmen, A., Klein, T., Mackay, D. S., Mantova, M., Martínez-Vilalta, J., Medlyn, B. E., Mencuccini, M., Nardini, A., Oliveira, R. S., Sala, A., Tissue, D. T., Torres-Ruiz, J. M., Trowbridge, A. M., Trugman, A. T., Wiley, E., and Xu, C.: Mechanisms of woody-plant mortality under rising drought, CO2 and vapour pressure deficit, Nature Reviews Earth & Environment, 3, https://doi.org/10.1038/s43017-022-00272-1, 2022.

McFadden, D.: Conditional logit analysis of qualitative choice behavior, 1974.

Meddens, A. J. H., Hicke, J. A., Macalady, A. K., Buotte, P. C., Cowles, T. R., and Allen, C. D.: Patterns and causes of observed piñon pine mortality in the southwestern United States, New Phytologist, 206, 91–97, https://doi.org/10.1111/nph.13193, 2015.

Mosig, C., Vajna-Jehle, J., Mahecha, M. D., Cheng, Y., Hartmann, H., Montero, D., Junttila, S., Horion, S., Adu-Bredu, S., Al-Halbouni, D., Allen, M., Altman, J., Angiolini, C., Astrup, R., Barrasso, C., Bartholomeus, H., Brede, B., Buras, A., Carrieri, E., Chirici, G., Cloutier, M., Cushman, K. C., Dalling, J. W., Dempewolf, J., Denter, M., Ecke, S., Eichel, J., Eltner, A., Fabi, M., Fassnacht, F., Feirreira, M. P., Frey, J., Frick, A., Ganz, S., Garbarino, M., Garćıa, M., Gassilloud, M., Ghasemi, M., Giannetti, F., Gonzalez, R., Gosper, C., Greinwald, K., Grieve, S., Gutierrez, J. A., Göritz, A., Hajek, P., Hedding, D., Hempel, J., Hernández, M., Heurich, M., Honkavaara, E., Jucker, T., Kalwij, J. M., Khatri-Chhetri, P., Klemmt, H.-J., Koivumäki, N., Korznikov, K., Kruse, S., Krüger, R., Laliberté, E., Langan, L., Latifi, H., Lehmann, J., Li, L., Lines, E., Lopatin, J., Lucieer, A., Ludwig, M., Ludwig, A., Lyytikäinen-Saarenmaa, P., Ma, Q., Marino, G., Maroschek, M., Meloni, F., Menzel, A., Meyer, H., Miraki, M., Moreno-Fernández, D., Muller-Landau, H. C., Mälicke, M., Möhring, J., Müllerova, J., Neumeier, P., Näsi, R., Oppgenoorth, L., Palmer, M., Paul, T., Potts, A., Prober, S., Puliti, S., Pérez-Priego, O., Reudenbach, C., Rossi, C., Ruehr, N. K., Ruiz-Benito, P., Runge, C. M., Scherer-Lorenzen, M., Schiefer, F., Schladebach, J., et al.: deadtrees.earth - An Open-Access and Interactive Database for Centimeter-Scale Aerial Imagery to Uncover Global Tree Mortality Dynamics, https://doi.org/10.1101/2024.10.18.619094, 20 October 2024.

Paz-Kagan, T., Brodrick, P. G., Vaughn, N. R., Das, A. J., Stephenson, N. L., Nydick, K. R., and Asner, G. P.: What mediates tree mortality during drought in the southern Sierra Nevada?, Ecological Applications, 27, 2443–2457, https://doi.org/10.1002/eap.1620, 2017.

Pellegrino, V., Godard, V., and Fleury, J.: Investigation of the use of topographic data derived from Pléiades imagery for high-resolution hillslope-scale morphometry, Geomorphology, 454, 109162, https://doi.org/10.1016/j.geomorph.2024.109162, 2024.

Petritan, M. and Schwenke, M. B.: Forest Functioning under Climate Warming and Future Perspectives on Forest Disturbances, Forests, 14, 2302, https://doi.org/10.3390/f14122302, 2023.

Pirtskhalava-Karpova, N., Trubin, A., Karpov, A., and Jakuš, R.: Drought initialised bark beetle outbreak in Central Europe: Meteorological factors and infestation dynamic, Forest Ecology and Management, 554, 121666, https://doi.org/10.1016/j.foreco.2023.121666, 2024.

Potterf, M., Nikolov, C., Kočická, E., Ferenčík, J., Mezei, P., and Jakuš, R.: Landscape-level spread of beetle infestations from windthrown- and beetle-killed trees in the non-intervention zone of the Tatra National Park, Slovakia (Central Europe), Forest Ecology and Management, 432, 489–500, https://doi.org/10.1016/j.foreco.2018.09.050, 2019.

Príncipe, A., Nunes, A., Pinho, P., Aleixo, C., Neves, N., and Branquinho, C.: Local-scale factors matter for tree cover modelling in Mediterranean drylands, Science of The Total Environment, 831, 154877, https://doi.org/10.1016/j.scitotenv.2022.154877, 2022.

R Core Team: R: A Language and Environment for Statistical Computing, 2022.

Raffa, K. F., Aukema, B. H., Bentz, B. J., Carroll, A. L., Hicke, J. A., Turner, M. G., and Romme, W. H.: Cross-scale Drivers of Natural Disturbances Prone to Anthropogenic Amplification: The Dynamics of Bark Beetle Eruptions, BioScience, 58, 501–517, https://doi.org/10.1641/B580607, 2008.

Raffa, K. F., Andersson, M. N., and Schlyter, F.: Chapter One - Host Selection by Bark Beetles: Playing the Odds in a High-Stakes Game, in: Advances in Insect Physiology, vol. 50, edited by: Tittiger, C. and Blomquist, G. J., Academic Press, 1–74, https://doi.org/10.1016/bs.aiip.2016.02.001, 2016.

Rakovec, O., Samaniego, L., Hari, V., Markonis, Y., Moravec, V., Thober, S., Hanel, M., and Kumar, R.: The 2018–2020 Multi-Year Drought Sets a New Benchmark in Europe, Earth's Future, 10, https://doi.org/10.1029/2021EF002394, 2022.

Rita, A., Camarero, J. J., Nolè, A., Borghetti, M., Brunetti, M., Pergola, N., Serio, C., Vicente-Serrano, S. M., Tramutoli, V., and Ripullone, F.: The impact of drought spells on forests depends on site conditions: The case of 2017 summer heat wave in southern Europe, Global Change Biology, 26, 851–863, https://doi.org/10.1111/gcb.14825, 2020.

Robbins, Z. J., Xu, C., Aukema, B. H., Buotte, P. C., Chitra-Tarak, R., Fettig, C. J., Goulden, M. L., Goodsman, D. W., Hall, A. D., Koven, C. D., Kueppers, L. M., Madakumbura, G. D., Mortenson, L. A., Powell, J. A., and Scheller, R. M.: Warming increased bark beetle-induced tree mortality by 30% during an extreme drought in California, Global Change Biology, 28, 509–523, https://doi.org/10.1111/gcb.15927, 2022.

Rouault, G., Candau, J.-N., Lieutier, F., Nageleisen, L.-M., Martin, J.-C., and Warzée, N.: Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe, Ann. For. Sci., 63, 613–624, https://doi.org/10.1051/forest:2006044, 2006.

Schiefer, F., Schmidtlein, S., Hartmann, H., Schnabel, F., and Kattenborn, T.: Large-scale remote sensing reveals that tree mortality in Germany appears to be greater than previously expected, https://doi.org/10.1101/2024.11.10.622853, 11 November 2024.

Schwarz, S., Werner, C., Fassnacht, F. E., and Ruehr, N. K.: Forest canopy mortality during the 2018-2020 summer drought years in Central Europe: The application of a deep learning approach on aerial images across Luxembourg, Forestry: An International Journal of Forest Research, 97, 376–387, https://doi.org/10.1093/forestry/cpad049, 2024.

Senf, C. and Seidl, R.: Mapping the forest disturbance regimes of Europe, Nat Sustain, 4, 63–70, https://doi.org/10.1038/s41893-020-00609-y, 2021.

Šilhán, K., Pánek, T., and Škarpich, V.: Diversification of landslide areas as a means for reducing noise in dendrogeomorphic dating, Quaternary Geochronology, 72, 101362, https://doi.org/10.1016/j.quageo.2022.101362, 2022.

Socha, J., Hawryło, P., Tymińska-Czabańska, L., Reineking, B., Lindner, M., Netzel, P., Grabska-Szwagrzyk, E., Vallejos, R., and Reyer, C. P. O.: Higher site productivity and stand age enhance forest susceptibility to drought-induced mortality, Agricultural and Forest Meteorology, 341, 109680, https://doi.org/10.1016/j.agrformet.2023.109680, 2023.

Sørensen, R., Zinko, U., and Seibert, J.: On the calculation of the topographic wetness index: evaluation of different methods based on field observations, Hydrology and Earth System Sciences, 10, 101–112, https://doi.org/10.5194/hess-10-101-2006, 2006.

Stereńczak, K., Mielcarek, M., Modzelewska, A., Kraszewski, B., Fassnacht, F. E., and Hilszczański, J.: Intra-annual *Ips typographus* outbreak monitoring using a multi-temporal GIS analysis based on hyperspectral and ALS data in the Białowieża Forests, Forest Ecology and Management, 442, 105–116, https://doi.org/10.1016/j.foreco.2019.03.064, 2019.

Stovall, A. E. L., Shugart, H., and Yang, X.: Tree height explains mortality risk during an intense drought, Nat Commun, 10, 4385, https://doi.org/10.1038/s41467-019-12380-6, 2019.

Sturm, J., Santos, M. J., Schmid, B., and Damm, A.: Satellite data reveal differential responses of Swiss forests to unprecedented 2018 drought, Global Change Biology, 28, 2956–2978, https://doi.org/10.1111/gcb.16136, 2022.

Trugman, A. T., Detto, M., Bartlett, M. K., Medvigy, D., Anderegg, W. R. L., Schwalm, C., Schaffer, B., and Pacala, S. W.: Tree carbon allocation explains forest drought-kill and recovery patterns, Ecology Letters, 21, 1552–1560, https://doi.org/10.1111/ele.13136, 2018.

https://doi.org/10.5194/egusphere-2025-5021
Preprint. Discussion started: 23 October 2025

Trugman, A. T., Anderegg, L. D. L., Anderegg, W. R. L., Das, A. J., and Stephenson, N. L.: Why is Tree Drought Mortality so Hard to Predict?, Trends in Ecology & Evolution, 36, 520–532, https://doi.org/10.1016/j.tree.2021.02.001, 2021.

Webb, C. R., Blake, M., and Gilligan, C. A.: Phenology of the spruce bark beetle Ips typographus in the UK under past, current and future climate conditions, PLANTS, PEOPLE, PLANET, 7, 284–300, https://doi.org/10.1002/ppp3.10583, 2025.

Wood, S. N.: Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models, Journal of the Royal Statistical Society: Series B (Statistical Methodology), 73, 3–36, https://doi.org/10.1111/j.1467-9868.2010.00749.x, 2011.

Zhai, L., Coyle, D. R., Li, D., and Jonko, A.: Fire, insect and disease-caused tree mortalities increased in forests of greater structural diversity during drought, Journal of Ecology, 110, 673–685, https://doi.org/10.1111/1365-2745.13830, 2022.

Zhang, D.: Package 'rsq,' 2022.

Zhao, P., Olsson, P.-O., Øhrman Wellendorf, A., Müller, M., and Mansourian, A.: Exploring the spatial heterogeneity of bark beetle infestation risk factors with geographically weighted regression and random forest, Scandinavian Journal of Forest Research, 40, 188–204, https://doi.org/10.1080/02827581.2025.2503807, 2025.

Ziegler, Y., Grote, R., Alongi, F., Knüver, T., and Ruehr, N. K.: Capturing drought stress signals: the potential of dendrometers for monitoring tree water status, Tree Physiology, 44, tpae140, https://doi.org/10.1093/treephys/tpae140, 2024.