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The Last Trees Standing: Climate modulates tree survival factors during a prolonged bark beetle outbreak in Europe

Nataliya Korolyova [a,*,#], Arne Buechling [a,*,#], Renata Ďuračiová [b], Khodabakhsh Zabihi [a], Marek Turčáni [a], Miroslav Svoboda [a], Jaromír Bláha [a], Kelly Swarts [c], Miroslav Poláček [a], Jaromir Hradecký [a], Jaroslav Červenka [d], Pavel Němčák [d], Fredrik Schlyter [a,e], Rastislav Jakuš [a,f]

[a] *Fac. of Forestry and Wood Sciences, Czech Univ. of Life Sciences, Kamýcká 129, 165 00 Praha-Suchdol, Czech Rep*
[b] *Dep. of Theoretical Geodesy and Geoinformatics, Fac. of Civil Engineering, Slovak Univ. of Technology in Bratislava, Radlinského 11, 810 05 Bratislava, Slovak Republic*
[c] *Dep. of Structural and Computational Biology, Univ. of Vienna, Campus-Vienna-Biocenter 5, 1030 Wien, Austria*
[d] *Dep. of Nature Protection, Šumava National Park administration, Sušická 339,341 92 Kašperské Hory, Czech Rep*
[e] *Dep. of Plant Protection Biology, Swedish Univ. of Agricultural Sciences, Box 102, 23053 Alnarp, Sweden*
[f] *Inst. of Forest Ecology, Slovak Acad. of Sciences, Ľ. Štúra 2, 960 53 Zvolen, Slovak Republic*

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ABSTRACT

Plant traits are an expression of strategic tradeoffs in plant performance that determine variation in allocation of finite resources to alternate physiological functions. Climate factors interact with plant traits to mediate tree survival. This study investigated survival dynamics in Norway spruce (*Picea abies*) in relation to tree-level morphological traits during a prolonged multi-year outbreak of the bark beetle, *Ips typographus*, in Central Europe. We acquired datasets describing the trait attributes of individual spruce using remote sensing and field surveys. We used nonlinear regression in a hypothesis-driven framework to quantify survival probability as a function of tree size, crown morphology, intraspecific competition and a growing season water balance. Extant spruce trees that persisted through the outbreak were spatially clustered, suggesting that survival was a non-random process. Larger diameter trees were more susceptible to bark beetles, reflecting either life history tradeoffs or a dynamic interaction between defense capacity and insect aggregation behavior. Competition had a strong negative effect on survival, presumably through resource limitation. Trees with more extensive crowns were buffered against bark beetles, ostensibly by a more robust photosynthetic capability and greater carbon reserves. The outbreak spanned a warming trend and conditions of anomalous aridity. Sustained water limitation during this period amplified the consequences of other factors, rendering even smaller trees vulnerable to colonization by insects. Our results are in agreement with prior research indicating that climate change has the potential to intensify bark beetle activity. However, forest outcomes will depend on complex cross-scale interactions between global climate trends and tree-level trait factors, as well as feedback effects associated with landscape patterns of stand structural diversity.

Introduction

Substantial recent increases in insect related disturbances of forest ecosystems have been documented in Europe and for the northern hemisphere generally (Bytnerowicz et al., 2007; Kautz et al., 2017; Millar and Stephenson, 2015). These trends are largely driven by outbreaks of bark beetles, including, in European forests, the Eurasian bark beetle *Ips typographus* L. (Müller et al., 2008; Schebeck et al., 2017). In Central Europe, insect disturbances have contributed to a doubling of the proportion of forests affected by tree mortality since 1984 (Senf and Seidl, 2018). Highlighting this trend, aggregate harvest levels of *Picea abies* (L.) Karst. (Norway spruce) have increased twofold since 2018, rising from 31 $Mm^3\ year^{-1}$ to 70 $Mm^3\ year^{-1}$ in 2020 (Czech Statistical Office, 2021; German Federal Statistical Office, 2021; Swiss Federal Statistical Office, 2021; The Federal Forest Research Center, 2021). In the Czech Republic, the scale of recent bark beetle outbreaks is

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* Corresponding authors.
E-mail addresses: korolyova@fld.czu.cz (N. Korolyova), buechling@fld.czu.cz (A. Buechling).
\# The first two authors contributed equally to the paper

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unprecedented (Hlásny et al., 2021). Forest timber stocks damaged by *I. typographus* have increased sevenfold in recent years, rising from ~3.5 Mm^3 in 2016 to 25 Mm^3 in 2020 (Knížek, 2021). Simulation models further predict substantial increases of up to ~200% in the extent of future insect disturbance in European forests (Sommerfeld et al., 2021). Concerns related to the economic and ecological consequences of extreme levels of insect disturbance have fueled numerous empirical studies. Despite a rich literature, continuing uncertainties relative to the nature of underlying mechanisms constrain inference and an ability to robustly forecast responses to global change (Biedermann et al., 2019; Carmona et al., 2011; Meddens et al., 2015).

In general terms, relationships between trees and bark beetles are characterized by an interplay between (1) the defensive traits of a host species, (2) external processes, including variation in climate, habitat and resources, and (3) stochastic events. The life cycle of bark beetles is dependent on the phloem of trees, where oviposition and larval development takes place (Raffa et al., 2008). Gallery construction, insect feeding and the vectoring of symbiotic fungi disrupt vascular function leading to tree mortality (Meddens et al., 2015). Bark beetle activity is generally constrained to endemic levels by co-evolved plant defenses, but exponential insect population growth may occur when critical drivers exceed particular thresholds (Raffa et al., 2013). For example, anomalous climate, such as high temperature and water deficit, may impair physiological functions and the dependent defensive facility of trees (Matthews et al., 2018; Netherer et al., 2019). Temperature extremes may concurrently promote bark beetle population expansion, via effects on dormancy, developmental rates, voltinism and synchronous emergence and dispersal (Bentz et al., 2019, 2010; Wermelinger, 2004). Prior studies have identified a myriad of factors that further interact with this system, including host tree characteristics (Jakuš et al., 2011; Sproull et al., 2015) and site factors, such as elevation (Jakoby et al., 2019), aspect (Mezei et al., 2014), soil fertility (Grodzki et al., 2014), and forest stand structure (Hilszczański et al., 2006).

Continuing disagreement in the literature regarding the strength and direction of various mortality drivers mentioned above (Meddens et al., 2015) reflects the challenge of understanding the dynamics of complex systems in terms of the biology of individual plants. We argue that a robust analytical framework grounded in demographic theory is required to develop a unifying mechanistic understanding of a host species' survival potential (Biedermann et al., 2019). A basic premise is that plant performance is constrained by limited internal resources (energy and nutrients), resulting in performance tradeoffs among plant functions, including growth, reproduction, carbon storage and defense (Herms and Mattson, 1992; Pacala et al., 1996). Plant resistance to herbivory consists of spatially and temporally sequenced mechanical and chemical-based processes, including the exudation of stored resins and the disturbance-induced production of allelochemicals (Raffa et al., 2008; Roth et al., 2018). In combination, these activities repel and kill both colonizing insects and fungal symbionts (Franceschi et al., 2005; Keeling and Bohlmann, 2006). The metabolic production of carbon-rich defense compounds requires a substantial energy investment in the form of non-structural carbohydrates (Bazzaz et al., 2011; Guérard et al., 2007; Loehle, 1988; Roth et al., 2018; Waring and Pitman, 1985). Thus, defense capability and tree survival will vary as a function of carbon supply, hypothesized to depend in part on net photosynthesis and surplus non-structural carbon storage, as well as the translocation potential of carbon reserves (Wiley, 2020).

In this study, we investigated patterns and processes determining tree survival in a bark beetle disturbance system. We present a flexible analytical framework that accounts for and partitions the effects of multiple structuring drivers, including tree level characteristics and environmental factors. Our approach accommodates nonlinearities and interactions across scales. Factors directly affecting survival and resistance at an individual tree level have largely been neglected in prior studies that have focused on correlates of outbreak patterns at broad spatial scales (Biedermann et al., 2019). Multi-dimensional, cross-scale analyses that integrate both individual tree attributes and climatic stress factors have not been sufficiently explored (but see Koontz et al., 2021). Our study system is defined by a prolonged *I. typographus* outbreak that has caused widespread *P. abies* mortality in forests across multiple countries in Central Europe (Seidl et al., 2016). Data were acquired using both remote sensing analyses and field surveys. Regression models were formulated to quantify survival probability based on a theoretical underpinning that carbon- and water-limited trees have a compromised facility to resist herbivory. We posited that physiological thresholds underlying survival are shaped by tree-level trait characters (tree size and relative crown height) and environmental drivers (resource competition and water stress). Empirical findings have demonstrated that bark beetles preferentially target larger trees during outbreaks. At the same time, mechanical constraints on water transport from roots to leaves increase with tree height, potentially limiting photosynthesis and defense functions in larger individuals. We therefore assumed that survivorship declines with increasing tree size. In contrast, we expected that defense capability is more robust in trees with larger crowns, as total leaf area regulates photosynthetic capacity. We postulated that high competition in dense forests for finite resources depresses physiological performance in individual trees and lowers ensuing survival probability. Finally, we hypothesized that reductions in soil water limit photosynthesis and exacerbate other stress factors (e.g. height-induced water constraints and resource competition), thus weakening tree defenses.

Methods

Study area

We investigated tree survival dynamics in the Bohemian Forest region, one of the largest contiguous forested landscapes in Central Europe. A severe outbreak of *I. typographus* began in the mid 1990s and is ongoing (Knížek and Liška, 2020). Our analyses were restricted to a mountainous region spanning the borders of Germany, Austria, and the Czech Republic. The current areal extent of disturbed forest is ~12400 ha (Fig. 1). Elevations range from ~950 to 1400 m. The climate is continental with 4 distinct seasons, a notably absent dry period, and moisture approximately evenly distributed throughout the year. Total annual precipitation ranges from ~740 to 1455 mm $year^{-1}$ and mean annual temperatures range from 4.6 to 7.4°C. The study region experienced a clear warming trend and intervals of anomalously dry conditions since ~1980 (Appendix S1, Fig. S1.1), consistent with conditions in Europe generally (Moravec et al., 2021). Forest composition is dominated by *P. abies* with scattered occurrences of *Sorbus aucuparia* L. (European mountain ash) and *Fagus sylvatica* L. (European beech). Forest structure is shaped by highly variable mixed-severity natural disturbances (Svoboda et al., 2012), consisting of windstorms and outbreaks of bark beetles (Emborg et al., 2000). At local site scales, gap forming wind disturbances re-occur with an average frequency of ~40 years (Janda et al., 2017). High-severity landscape-scale wind or insect events that cause extensive tree mortality (>50% of canopy trees) are also prevalent. A previously published 500-year disturbance reconstruction quantified a mean rotation period of ~170 years, where rotation was defined as the average interval between high-severity events at a given location (Čada et al., 2016).

A substantial proportion of the extant Bohemian forest developed following a period of high natural disturbance activity in the early 1800s. Most stands are considered to be relatively unmodified by anthropogenic land use, as logging rates were limited in the 19th century and increasingly curtailed by conservation measures in the 20th century (Brůna et al., 2013; Čada et al., 2016; Svoboda et al., 2012). A majority of the region is now protected by two reserves, the Bavarian Forest National Park in Germany and Šumava National Park in Czechia. However, ongoing wind and insect disturbances are partly managed near political borders to mitigate beetle spread to commercial forests.

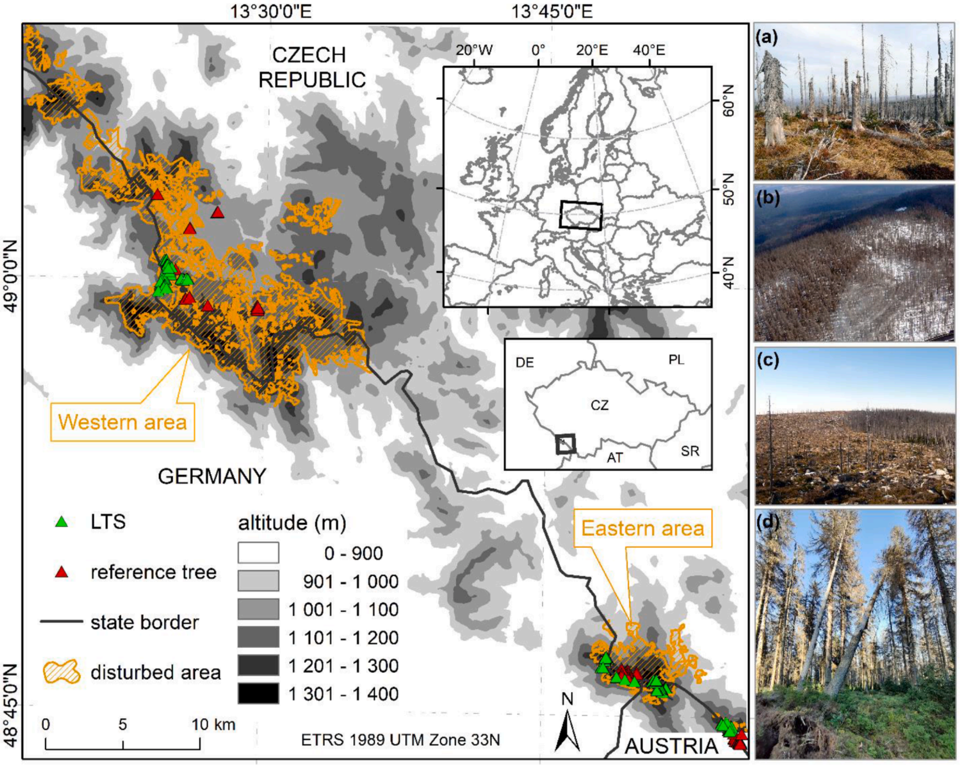

Fig. 1. Bohemian Forest study region showing the extent of severely bark beetle-disturbed spruce forest and the location of all trees used in the regression analyses, including surviving trees (N=184), termed *last trees standing* (LTS), and reference trees (N=414). Reference trees were living trees sampled from the general population of spruce in the study area (see Methods).The study region is comprised of two spatially disjunct areas (western and eastern). Tree data from the two disturbance areas were pooled in analyses. Photos (a) and (c) show landscapes in Šumava National Park (Czech Republic) near sampled LTS. Photo (b) was taken from a helicopter overflight of the same area. Photo (d), captured in July of 2021, shows reference trees that were killed by beetles but that were alive at the time of sampling in 2020. Map was generated in ArcGIS (Environmental Systems Research Institute, 2021).

Typical management actions include salvage logging or stem debarking.

Detection of surviving trees

Data quantifying tree survival were acquired from a combination of remote sensing analyses and field surveys. A preliminary field reconnaissance confirmed the presence of scattered surviving trees, hereafter referred to as “last trees standing” (LTS), in the study region. However, logistical constraints, including access to disturbed forests that spanned international boundaries, precluded comprehensive field data collection. We therefore elected to survey LTS occurrences using remote sensing techniques. Analyses were conducted in Google Earth Pro (GE), a geographical information system that is increasingly being used in the academic community for environmental research (Liang et al., 2018; Yu and Gong, 2012). GE datasets are mosaics of satellite images or aerial photography. We used aerial photos with a spatial resolution of 15 cm. The bark beetle outbreak initially began following a series of windstorms that occurred in the 1980s (Čada et al., 2016). However, images of sufficient resolution and quality were only available for the years 2000 to 2019. LTS occurrences were identified through manual inspection (Röder et al., 2018) of the time series of snow-free images that covered the geographical extent of heavily disturbed forest (12400 ha). Thus, each image that captured a disturbance area was visually and systematically examined for surviving trees. Extant living trees with intact crowns that persisted in post-outbreak images were classified as LTS.

We conducted a field survey in the fall of 2020 to evaluate LTS detection accuracy. We randomly selected 20% (37 trees) of all detected LTS occurrences (184 trees) for field verification. Tree attributes including overall height, diameter at breast height (dbh) and crown length were measured.

Quantifying tree size, crown height and the competitive environment of LTS

Additional image analyses were performed to determine selected attributes of all detected LTS, including diameter at breast height (dbh) and crown dimensions, as well as pre-disturbance stand densities. Metabolic theory (Enquist and Niklas, 2001) and empirical analyses (Forrester et al., 2017) have established general relationships among various aspects of plant form, including crown dimensions and stem diameter (Grote, 2003; Jucker et al., 2017; Lehnebach et al., 2018; Verma et al., 2014). We therefore developed and used an allometric model to estimate dbh for all LTS based on associated crown projection area. The allometry model was generated using a power function fit with field measurements (N=2175 trees) of crown dimensions from an international network of permanent forest monitoring plots (https://www.remoteforests.org/project.php, downloaded November 2019) that overlaps with our study area. The fitting dataset also incorporated crown measurements for a limited number of trees located within the Bohemian Forest study area (N=99). Model performance was evaluated using two test datasets: (1) 222 independent tree records from the Remote database, and (2) field measurements for 37 LTS that were surveyed in 2020 for assessing image detection accuracy (described previously). We then used the final parameterized allometric model to estimate dbh values for all image-detected LTS based on associated crown dimensions derived from aerial photography (see details in Appendix S2).

We also used post-disturbance images to quantify a measure of relative crown height, termed self-shading. The height or length of a crown, from the apex to the lowest living branch, determines the proportion of a stem shaded by canopy leaves. We therefore computed an index of self-shading, defined as the ratio of crown length to overall tree height, from measurements of corresponding shadow projections in GE. Self-shading levels were determined from images that were temporally proximate to a given disturbance event. We validated our self-shading estimates with field data (see Appendix S3).

Finally, we quantified a simple proxy of resource competition based on forest stand density levels prior to beetle outbreak. We inspected pre-disturbance imagery to obtain a count of neighboring trees within a 30 m radius of a target tree.

Reference trees

We used data describing the attributes of living trees susceptible to bark beetles to serve as reference data in regression models. The direct sampling of beetle-killed trees using post-disturbance imagery or field surveys was impeded by post-disturbance landscape processes, including natural wind-throw and degradation of standing dead trees, as well as the removal of dead wood by land managers to reduce beetle proliferation. Additionally, though beetle-killed trees were present in pre-disturbance imagery, canopy overlap from adjacent trees in intact stands prevented reliable measurement of their crown dimensions (i.e. crown width and shadow projections were obscured). Therefore, following methods in Six et al. (2018), we used information describing individual, living trees in the general population of spruce in the study region to represent the attributes of trees vulnerable to bark beetle colonization. Due to the extremely high rates of beetle-driven tree mortality (see Fig. 1), we assumed that a survey of the general population would be strongly dominated by susceptible trees and would not significantly bias modelling outcomes. We acquired and combined three independent datasets quantifying the attributes of reference trees to maximize total sample size and the corresponding spatial distribution of data across climate gradients. Data sources included:

1 The Remote Forest inventory network, which was described previously (see allometric models in previous section). From the Remote database, we used records for 300 spruce trees located in the Bohemian forest study region that were surveyed in 2002. These datasets provided field measurements of dbh and crown dimensions for trees located within 25 m circular plots.
2 A limited field survey performed in 2020. We measured the size and canopy dimensions for a total of 99 spruce trees within intact forest patches (N=7 stands) that were proximate to beetle activity. Target stands for sampling were identified using GE imagery and surveyed using variable length transects. Transects were established on the southern edge of a given forest patch and followed a random bearing that bisected the patch interior. Trees within 5 m of a transect were sampled for dbh, height and canopy dimensions. We excluded juvenile spruce (dbh < 15 cm) to conform with well-documented host selection preferences by *I. typographus* during outbreaks (Seidl and Rammer, 2017; Sommerfeld et al., 2021). We also only sampled intact trees without apparent structural damage, such as crown breakage. We observed active logging of beetle-killed trees within the survey area.
3 A parallel, independent field survey conducted in 2020 for the purposes of investigating genomic markers of tree resistance to bark beetles. The size and crown dimensions of 15 spruce trees were measured within circular (radius=26 m) survey plots (N=3).

In the summer of 2021, we revisited a subsample (~20%) of the reference trees that had been surveyed in the previous year (from datasets 2 and 3), to informally assess the efficacy of using data from the general population to represent beetle-susceptible trees. Of those trees that had not already been salvage logged, a vast majority (~99%) had been colonized and killed by bark beetles (Fig. 1 photo d).

Exploratory analyses

We assumed that tree survival is a non-random process governed by interactions between biotic and environmental factors. We consequently expected to detect evidence for a spatial structure within the distribution of LTS. The Optimized Hot Spot Analysis (Getis and Ord, 2010) function in ArcGIS was used to test for statistically significant clusters of LTS.

We then used a Random Forest classifier to assess relationships between tree survival and environmental factors at a broad spatial scale. Training data for the classifier incorporated LTS and the distribution of beetle-killed trees across the entire disturbed portion of the study region (derived from regression modelling as described in Appendix S4). We hypothesized that moisture or thermal limitations could stress tree physiology and consequently influence survival potential. We therefore developed several topographical and spectral-based explanatory variables (N=13) as proxies for climatic stress. Specifically, we quantified terrain characteristics, such as shape and orientation, that could influence site water supply. For each tree, we estimated levels of incident solar radiation, expected to impact evapotranspiration rates. We used a Tasseled Cap transformation of Landsat 5 spectral data (Appendix 4) to generate reflectance-based indicators of soil and vegetation properties, including a wetness index (Kauth and Thomas, 1976). From the same Landsat dataset, we computed a Normalized Difference Vegetation Index (NDVI) as an additional proxy for relative plant vigor. Low values of NDVI are potentially associated with limited water supply and elevated levels of physiological stress.

LTS and beetle-killed trees were attributed with corresponding values of the explanatory variables. A Random Forest classifier was then fit with the resulting training datasets to investigate patterns underlying tree survival at the scale of the entire study region (see Appendix S5).

Survival modelling

We used a form of nonlinear logistic regression to investigate the shape and magnitude of factors influencing spruce survival. One objective in this study was to present a robust nonparametric modeling framework that extends more traditional linear methods. Models were based on maximum-likelihood estimation techniques (Hilborn and Mangel, 1997). We used model selection based on Akaike information criterion (AIC) to determine the strength of support for a given model, rather than parametric-based significance tests. This approach facilitates an understanding of the shape of survival responses to different ecological variables. We posited that survival capacity is strongly dependent on host tree carbon balance, which may be affected by tree size, crown morphology, stand density prior to outbreak (resource competition), and long-term water supply at a site. As in previously published analyses (Canham and Murphy, 2017; Uriarte et al., 2004a, 2004b), our model was multiplicative in form:

$$s = s_m^* \times \text{ size } \times \delta \times L \times \text{ CWB} \tag{1}$$

where s is predicted tree survival probability, s_m^* is maximum potential survival probability, size is diameter at breast height (dbh), δ is stand density, L is a measure of tree self-shading based on relative crown length, and CWB is a climatic water balance (precipitation - potential evapotranspiration; see Appendix S1). A multiplicative model structure inherently accounts for interactions between variables (Buechling et al., 2017; Rollinson et al., 2016). We detected no evidence for collinearity among predictors, based on values of variance inflation factors (<1.25 for all covariates) from an equivalent general linear model. Additionally, all covariates were dimensionless scalars that ranged from 0 to 1 to reduce parameter trade-offs during model fitting (Canham and Murphy, 2017). These scalars reduce estimated maximum potential tree survival, s_m^*. Potential survival represents expected survival under optimal levels of all the other factors. Unique values of this term (N=3) were estimated, using likelihood analyses, for different countries (Austria, Germany and Czechia) to account for any possible geographical variation in expected survival due to contrasting edaphic conditions or other unknown factors (Canham and Murphy, 2017).

We assumed that mortality rates would increase, both, with increasing tree size (dbh) and in denser forest stands (δ) where competition for resources is higher. We estimated the shapes of both variables using exponential functions, capable of fitting either monotonically increasing or decreasing survival responses:

$$\text{size } or\ \delta = e^{\left(-a \times X^b\right)} \tag{2}$$

where a and b are shape parameters estimated by likelihood analyses and X is a vector of observations of either dbh (cm) or stand density (trees ha^{-1}).

We assumed that higher levels of self-shading (L) would enhance survival potential. We estimated the survival response to variation in self-shading using a logistic function, which saturates at high levels of self-shading:

$$L = L_a + \frac{1 - L_a}{\left(1 + \left(\frac{S}{L_b}\right)^{L_c}\right)} \tag{3}$$

where L_a, L_b, and L_c are estimated parameters and S is a vector of observed self-shading levels, defined as the ratio of crown length to tree height (%).

The effect of variation in a long-term, growing season climatic water balance (CWB) was estimated using a Gaussian function:

$$\mathrm{CWB} = e^{-0.5 \times \left(\frac{C - C_a}{C_b}\right)^2} \tag{4}$$

where C_a and C_b are estimated parameters and C is observed water balance (mm year^{-1}). The Gaussian is a flexible function that can fit responses that are monotonically increasing (when C_a is large), decreasing (when C_a is small), or unimodal (when values of C_a occur within the range of observed CWB).

We fit regression models with datasets describing our sample of LTS (N=184) and the reference, general population of spruce (N=414). Models were fit in a maximum likelihood framework (Canham and Uriarte, 2006). Simulated annealing (Goffe et al., 1994), a global optimization algorithm, was used to determine maximum likelihood estimates of model parameters. The likelihood function for probability of survival assumed the following form:

$$\text{log likelihood} = \sum_{i=1}^{n} \begin{cases} \log(p_i) & \text{if tree } i \text{ survived} \\ \log(1 - p_i) & \text{if tree } i \text{ died} \end{cases} \tag{5}$$

where p_i is the probability that an individual tree survived and $(1 - p_i)$ is the probability that a given tree died. Computations of log likelihood using Eqn. 5 assume independence among observations. However, in contrast with traditional parametric approaches, parameter estimation and model comparisons using AIC are robust to autocorrelated data structures (Buechling et al., 2017; Hubbell, 2001; Uriarte et al., 2004a).

We constructed a series of nested models based on different permutations of terms in Eqn. 1. Competing models were evaluated using AIC with a bias correction for model complexity and small sample size (Johnson and Omland, 2004). Prediction uncertainty was quantified using likelihood-based support intervals, which are comparable to 95% confidence intervals (Edwards, 1992; Uriarte et al., 2004b). We adopted a pseudo-R^2 approach to assess model goodness of fit (Canham and Murphy, 2017; Uriarte et al., 2004a). For each sample tree, we calculated a probability of survival given the best model form, and then binned those predictions into equivalent 5% survival classes (0-5%, 5-10%, etc). The mean predicted probability of survival within each class was then compared with the observed proportion of individuals that had actually survived in that class, thereby providing an estimate of overall explained variance. We tested for bias using the slope of the regression of observed vs. predicted survival across the binned classes. Unbiased predictions have slopes approaching 1.0. Analyses were performed in R (R Development Core team, 2021). Regression models were fit using the 'likelihood' package (Version 1.7; Murphy, 2015).

Results

LTS Detection

Image analyses resulted in the detection of 184 occurrences of LTS in 3 countries (Table 1). Field surveys conducted to verify LTS detection accuracy found no commission errors. All 37 field-surveyed LTS (random test samples) were correctly identified in prior image analyses. Omission error was not evaluated. Subsequent windthrow and sanitation logging of most neighboring beetle-killed trees also precluded an evaluation of the accuracy of image-based stand density estimation.

We used allometric models to estimate dbh for image-detected trees. Mean prediction errors associated with model-derived estimates of tree dbh were on average less than 10 cm according to comparisons with two independent test datasets (Appendix S2). Predictions for a large independent test dataset (N=222 trees) were unbiased. The model slightly underestimated, on average, dbh for 30 ground-truthed LTS (bias=1.1, Fig. S2.1).

Based on field measurements of LTS crown dimensions (N=37), GE-derived estimates of tree self-shading had a mean absolute error of 15% (Appendix S3). Estimates of tree self-shading were essentially unbiased (slope of observed vs. predicted ~ 1.03).

Reconstructed pre-outbreak stand densities for LTS ranged from a minimum of 30 to a maximum of 365 trees/ha, reflecting comparatively open stand conditions. Estimated levels of tree self-shading were higher for LTS than general population trees, with overall means of 76% and 55%, respectively (Table 1). All detected LTS occurrences were distributed within a relatively narrow elevation band (~1100 to 1370 m) and were significantly clustered according to Optimized Hot Spot Analysis (Fig. 2).

Random Forest analysis

Random Forest classification was used as an exploratory learning tool to discriminate among environmental conditions promoting or diminishing tree survival at the scale of the study region. Predictive performance was high, with average error or mis-classification rates of 6.3% for LTS and 5.7% for beetle-killed trees. The intensity of solar radiation at a site and the spectral-derived vegetation index (NDVI) were the most important factors distinguishing survival (Appendix S5: Fig. S5.1). Topographical variables, including aspect, slope and terrain shape were relatively unimportant after accounting for insolation and NDVI. Results were used to inform the selection of explanatory variables in regression models, including a climate term that integrated variation in insolation.

Survival models

The best-supported regression model incorporated the effects of tree size, stand density, self-shading and site water balance (Table 2). Tree survival varied nonlinearly in response to model covariates. Predicted survival probabilities were unbiased and explained ~78% of the variation in the observation dataset, based on a pseudo-R^2 statistic (Fig. 3). A total of 166 of the 184 LTS (90.2%) were predicted to have survival

Table 1
Biotic and environmental attributes of trees used in regression models.

Tree type	Sample size	Stem diameter (cm)	Stand density (trees ha^{-1})	Self-shading (%)	Climatic water balance (mm)
Reference	414	49 (31, 69)	363 (184, 608)	55 (27, 87)	-131 (-179, -97)
LTS	184	41 (26, 57)	117 (72, 176)	76 (53, 95)	-148 (-194, -117)
All trees	598	47 (29, 66)	288 (95, 594)	61 (32, 91)	-136 (-185, -97)

Notes: Mean values are shown with 10th and 90th percentiles in parentheses. A mean climatic water balance was computed for each tree from the difference of precipitation and PET for growing season months (May-Sept) averaged over 30 years (1990-2019).

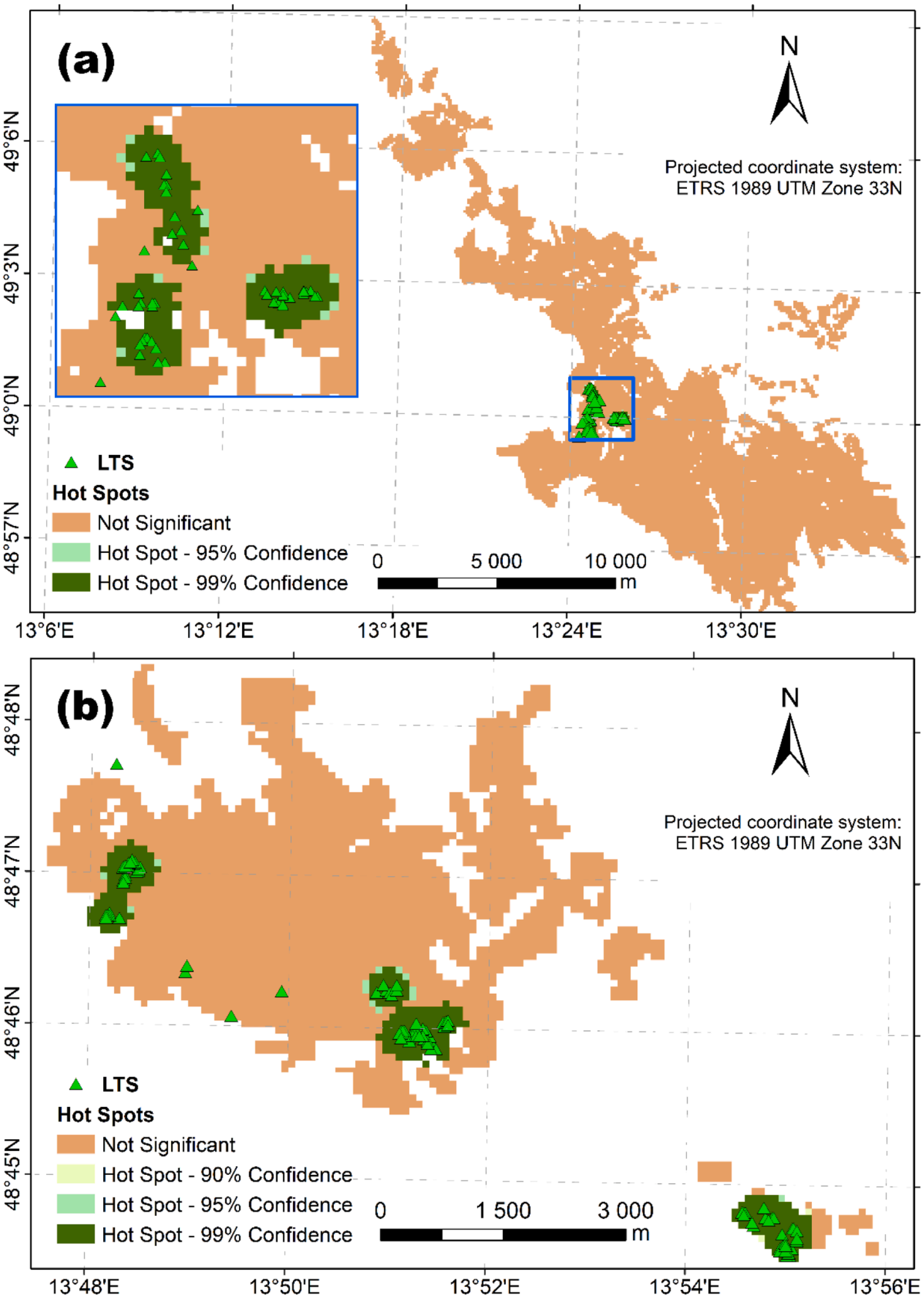

Fig. 2. Locations of statistically significant spatial clusters of surviving trees, termed *last trees standing* (LTS), identified using Optimized Hot Spot Analysis in the western (a) and eastern parts (b) of the study region. Locations of LTS are shown in green.

probabilities greater than 50%. Only 17 of 414 dead reference trees (4.1%) had estimated survival probabilities exceeding 50%.

As expected, larger trees were more susceptible to bark beetles (Fig. 4a). Survival probability was predicted to decrease rapidly in trees with diameters exceeding ~35 cm, dropping to near zero for trees with stems larger than ~75 cm. Small sample size for very large diameter trees resulted in some uncertainty (wide support intervals) in the predicted absolute magnitude of the decline in survival among large trees.

Stand density was used as a simple proxy for resource competition. Analyses indicated a steep decline in survival probability with increases in stand density above observed mean levels in the dataset, controlling for other factors (Fig. 4b). Comparatively dense stands that deviated from mean observed conditions by more than ~50% were associated with near complete spruce mortality.

Also as expected, higher levels of tree self-shading by canopy leaves promoted tree resistance to bark beetles (Fig. 4c). Survival probability increased monotonically with increasing self-shading levels, approaching 100% for trees with full crowns.

We quantified a 30-year average, spatially-explicit water balance variable that integrated temperature, precipitation, insolation, and terrain characteristics to investigate evidence for relationships between environmentally-driven physiological stress and survival, as suggested by Random Forest analyses. Regression results indicate that water balance levels substantially influenced survival probability. Survival potential declined steeply for individual trees when mean water availability was consistently depressed relative to average conditions

Table 2

Results for alternate models of survival probability.

*Model	Explanatory variables	†ΔAICc	§NP
1	Tree size	309.14	5
2	Model 1 & stand density	7.28	7
3	Model 2 & crown self-shading	2.64	10
4	Model 3 & water balance	0	12

Notes: *Models are hierarchical. Each successive model combines explanatory variables from the previous model and a new covariate term as shown. †Difference between AIC of the best model (ΔAIC = 0) and alternative models. AIC was corrected for model complexity (Johnson and Omland, 2004): AICc = – 2log(likelihood) + 2NP * [N / (N – NP – 1)] where N is the total sample size used to fit a model (N=598 trees for all models). §Number of parameters in each model.

across the study region, other factors constant (Fig 4d).

Limited water availability also modulated the effects of other factors. For example, survival potential in a 50 cm diameter spruce decreased from 78%, in mesic sites with high water balance levels (95th percentile level), to 43% in locations where available moisture was comparatively low (5th percentile) (Fig. 5a). Similarly, the negative effects of competition (stand density) were magnified (Fig. 5b) and the positive effects of self-shading were reduced (Fig. 5c) when long-term water supply was constrained. However, support intervals did substantially overlap for all but stand density effects.

Discussion

This study demonstrates that spruce survival during a severe, multiyear outbreak of I. typographus was a non-random process influenced by tree phenotype, forest structure, and climatic conditions. Model results reveal clear nonlinear relationships between tree survival and ecological drivers. Consistent with other studies, survival outcomes varied with the size of host trees and density-dependent levels of resource competition. Crown height was diagnostic of the physiological condition of trees and their capacity to resist herbivores. Although climate conditions in the study area are generally mesic, long-term anomalies in water availability (drier than average) intensified tree-level physiological stress factors and decreased survival probability.

Phenotypic traits of trees

Authors have argued that tree senescence, due to deteriorating metabolic function in older and larger trees, is relatively uncommon (Stephenson et al., 2011). Thus, mortality rates, in the absence of disturbance, have been shown to increase only modestly in larger and older trees (Canham and Murphy, 2017). Our findings revealed that, in response to bark beetle pressure, mortality substantially increased in larger trees when other factors, such as water supply, were constant (Fig. 4a). This observed size-dependent pattern in disturbance-driven mortality is largely consistent with prior bark beetle research (Buonanduci et al., 2020; Koontz et al., 2021), though the mechanistic underpinning remains equivocal (Meddens et al., 2015). Experiments have shown that non-structural carbohydrate pools scale with tree size (Carbone et al., 2013; Sala et al., 2010; Woodruff and Meinzer, 2011), suggesting that larger individuals are potentially equipped with an enhanced defensive capacity (Wiley, 2020). However, metabolic demands also increase with plant biomass, and the ability of individual trees to remobilize and utilize previously stored carbon to fuel defense functions is unclear (Sala et al., 2010; Wiley et al., 2019). Furthermore, studies have revealed ontogenetic constraints on the synthesis of defensive compounds, with concentrations of terpenes and phenolics decreasing in larger or older trees (Herms and Mattson, 1992; Netherer et al., 2021). A negative relationship between size and survival could

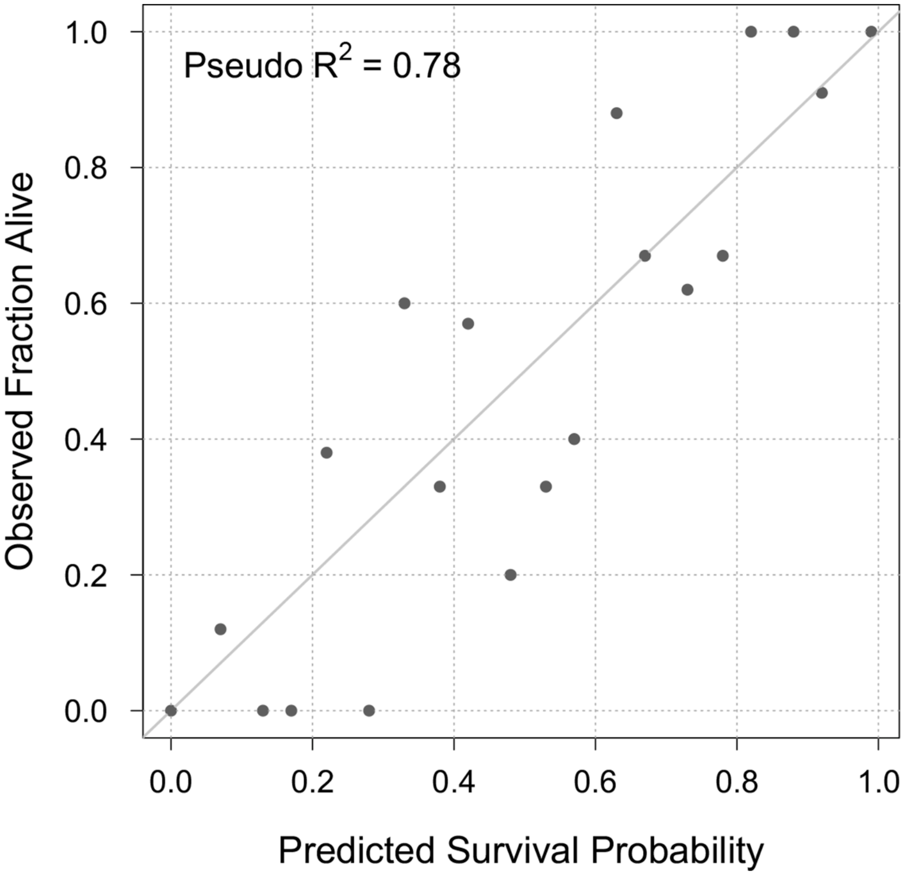

Fig. 3. Goodness of fit of the logistic regression model with four covariates: dbh, stand density, self-shading and water balance (Model 4 in Table 2). Predicted survival probabilities for all trees (N=598) were grouped into uniform class intervals (0-0.05, 0.05-0.1, etc). The observed fraction of trees that actually survived within a class were then plotted as a function of the corresponding mean predicted survival probability of that class. Predictions were unbiased, based on the slope of the regression of observed vs. predicted values across the binned classes (slope~1.0). A 1:1 diagonal line representing perfect agreement between observed and predicted is shown for reference.

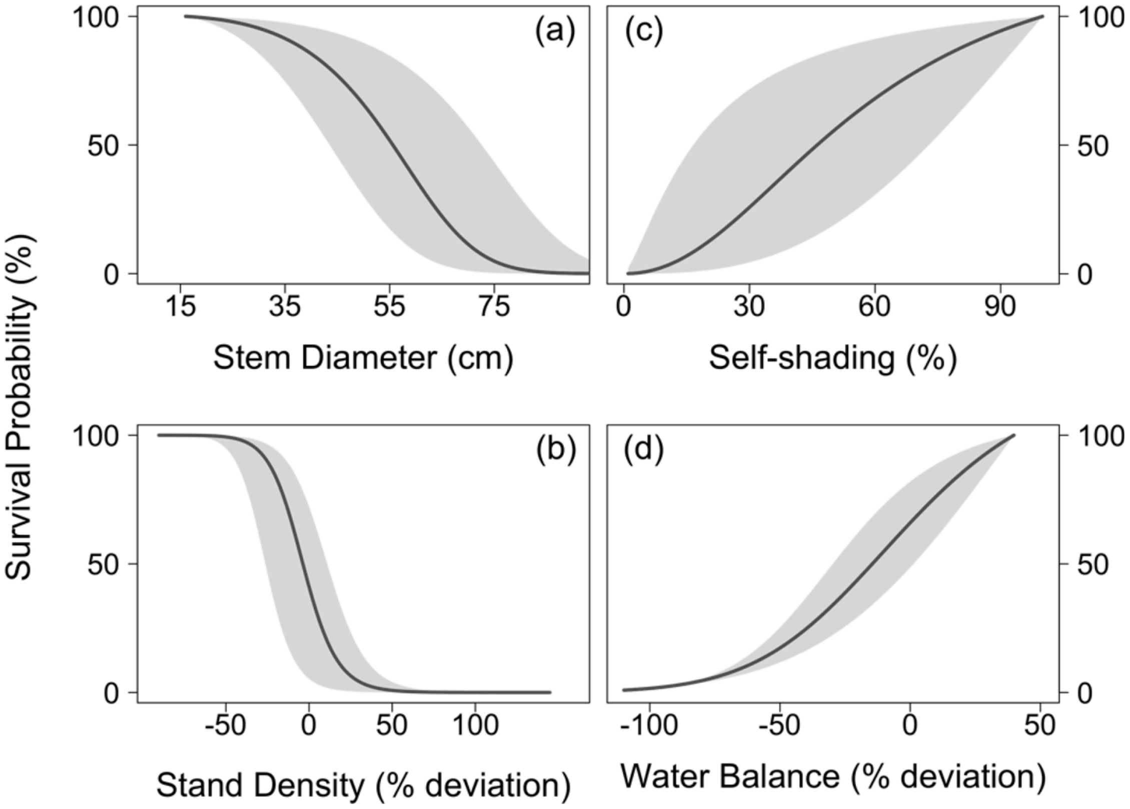

Fig. 4. Predicted survival probability as a function of biotic variables (stand density, stem diameter and tree self-shading) and long-term moisture conditions (climatic water balance). Variation in both stand density and mean climatic water balance (precipitation minus PET) are shown as percent deviations from corresponding mean values (scaled to zero). Stem diameter (dbh) was estimated from allometric analyses (Appendix S2). Tree self-shading was calculated as a ratio of crown length to overall tree height. All factors (a through d) were plotted within the range of the observational data. Shaded regions delineate 2-unit support intervals.

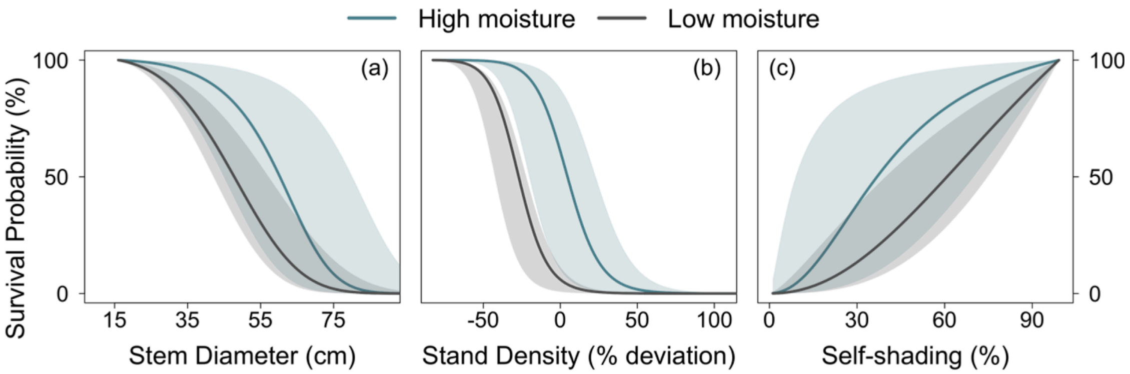

Fig. 5. Predicted survival probability as a function of stem diameter, relative stand density, and tree self-shading and for two contrasting levels of long-term moisture conditions. Site moisture status was determined from a climatic water balance and was alternately fixed at low (5th percentile) vs. high (95th percentile) levels, based on the observational dataset. Shaded regions delineate 2-unit support intervals.

also reflect trait differences among individual trees that promote rapid growth to overcome competition from neighbors vs. a greater allocation of carbon resources to defenses at the expense of growth (de la Mata et al., 2017; Loehle, 1988; Pacala et al., 1996). Though we did not quantify growth rates, larger diameters may reflect an elevated growth potential in some cases. The current prevailing theory concerning variation in size-dependent mortality is that host tree selection by bark beetles is idiosyncratic and dynamic, shifting over time due to complex interactions between insect population density and environmental conditions, such as prolonged climatic stress, that affect threshold levels of tree resistance (Buonanduci et al., 2020; Koontz et al., 2021; Stephenson et al., 2019).

Our results demonstrate a positive association between relative crown height, termed self-shading, and tree survival (Fig. 4c). A simple explanation is that long crowns obstruct visual stimuli, such as color or shape, that are used by insects to locate host trees (Goyer et al., 2004; Sanders, 1984). Alternately, larger crowns enhance the carbon balance of trees. The cumulative extent of leaf area governs net carbon uptake in a tree (Bazzaz, 1979; West et al., 1999) and consequently influences carbohydrate allocation to reserve pools and defense function (Wiley, 2020). Crown structure may further mediate photosynthesis by generating spatially varying microclimates. Experimental studies have identified vertical gradients in air temperature and humidity within the crowns of individual trees (Zweifel et al., 2002) and dependent variation in rates of photosynthesis (Bauerle et al., 2007). Carbon assimilation is governed by enzymatic activity, which is stimulated by temperature increases. However, photosynthetic responses to warming are nonlinear and peak at an optimum temperature level, beyond which assimilation rates decline (Smith and Dukes, 2013). Therefore, varying crown environments that cause some leaf temperatures to exceed metabolic optima may be expected to potentially reduce whole-tree net photosynthesis (Gunderson et al., 2010). Though speculative, the long-term warming trends observed in this study (Fig. S1.1) may have had divergent and negative consequences for some trees if warming rates were elevated in sparser crowns, and if associated temperature increases exceeded optimum conditions for leaf photosynthesis. However, a well-documented physiological acclimation capacity within plants may compensate for spatial (or temporal) within-crown temperature variation (Smith and Dukes, 2013).

Theoretically, canopy-regulated temperatures may also modulate bark beetle performance via effects on insect aggregation behavior. Although not yet clearly demonstrated, bark beetles purportedly respond to emission rates of organic compounds, primarily monoterpenes, from bark tissues (Hulcr et al., 2006). The relative emission rates of monoterpenes vs. insect-synthesized pheromones are hypothesized to synergistically affect beetle olfactory responses (Jakuš and Blaženec, 2003). For example, limited experimental evidence has found increased levels of attraction in *I. typographus* to spruce trees when terpene to pheromone ratios exceed particular levels (Erbilgin et al., 2007). As production and release rates of monoterpenes have been found to increase with temperature (Esposito et al., 2016; Hietz et al., 2005; Marešová et al., 2020), crown-mediated microclimate variation may affect host tree selection by insects. A cooling effect associated with xylem sap flow may further modulate these dynamics (Hietz et al., 2005). Experiments are needed to elucidate the sensitivity and scale of potential bark beetle responses to plant-emitted organic compounds, and whether variation in temperature-regulated emissions of volatiles is sufficient to affect beetle behavior.

Competition

In contrast to more complex, mechanistic-based indices of plant competition (Canham et al., 2004; Coates et al., 2009), we used a simple metric of stand density to serve as a proxy for crowding effects. Nevertheless, even this simple formulation was able to capture a strong competition signal (Fig 4b), revealing that variation in stand density was the most important factor determining survival potential in this study. Ecological theory and empirical analyses have demonstrated clear relationships between plant competition and demographic rates through the partitioning and depletion of site resources (Goldberg and Fleetwood, 1987). Constraints on resource availability presumably impair dependent plant functions, including photosynthesis and carbon allocation for defense (Bazzaz et al., 1987). Competition has been identified as an important driver of tree survival in some (Buonanduci et al., 2020) but not all published studies (e.g. Koontz et al., 2021). The role of competition is potentially confounded by climatic or edaphic factors (Meddens et al., 2015), but our results suggest that the negative effects of higher stand density were exacerbated by anomalous reductions in water supply (discussed below).

Water supply

Our results suggest that defensive mechanisms were substantially impaired for trees in comparatively more water limited environments (Fig. 4d), consistent with numerous empirical studies relating bark beetle impacts to climatic water deficits (Matthews et al., 2018; Netherer et al., 2019; Stephenson et al., 2019). Patterns identified in this study also support conceptual models of tree mortality that integrate the effects of both carbon limitation and water relations (McDowell et al., 2008). Physiological stress due to water deficit has long been recognized to predispose trees to herbivory via effects on their internal carbon and energy stores (e.g. Berryman, 1972; Christiansen et al., 1987). Water stress, resulting from extended periods of high atmospheric evaporative demand (i.e. vapor pressure deficit) relative to water supply from soils, may lead to mechanical damage in the network of water conducting xylem cells. According to cohesion theory, water is transported along a vertical gradient of decreasing pressure from roots to leaves. Leaf transpiration, tension via hydrogen bonding, and water adhesion to cell walls generate forces that facilitate the upward movement of water against gravity (Koch et al., 2004). High levels of tension due to water stress may lead to xylem cell cavitation, disrupting the continuity of a water column and disabling water flow in a conduit (Tyree and Sperry, 1989). Desiccation effects that cause extensive damage may trigger tree mortality directly through hydraulic failure (Tyree and Ewers, 1991). Plants respond to water stress by increasing stomatal regulation to limit water losses via transpiration. However, stomatal closure decreases carbon dioxide diffusion into leaves and associated rates of photosynthesis (Ryan and Yoder, 1997). A consequent depletion of nonstructural carbohydrates (NSC) may have downstream effects on secondary metabolic pathways (Herms and Mattson, 1992). Thus, the production of carbon-rich defensive compounds, such as terpenes and phenols (Franceschi et al., 2005; Korolyova et al., 2022), is potentially reduced, which may subsequently decrease resistance to herbivores (Huang et al., 2020).

Tree survival is also influenced by fundamental energetic tradeoffs among physiological functions. Both primary growth and secondary metabolism are energy and carbon demanding processes (Herms and Mattson, 1992). Growth activity is a strong sink for available photosynthates, but is also highly sensitive to water and nutrient limitation (Fatichi et al., 2016). Photosynthetic capacity, on the other hand, tends to be maintained during mild drought by stomatal regulation of leaf gas exchange (Cornic et al., 1992; Li et al., 2017), broad physiological optima (Hsiao, 1973), or potentially plastic responses to climate (Cunningham and Read, 2002). Growth inhibition during transitory periods of water deficit may lead to an accumulation of NSCs, which are then available for allocation to constitutive and induced defenses (Herms and Mattson, 1992). Consequently, mild drought has been associated with increased resistance to insect herbivory (Hartmann and Trumbore, 2016). However, cumulative stress through prolonged water limitation, a condition assessed in this study, may impair multiple processes, including photosynthesis, leading to a progressive depletion of NSCs (Erbilgin et al., 2021). A concurrent malfunction of phloem transport also impedes the mobilization of stored photosynthate, compounding the effects of diminished carbon assimilation (Wiley, 2020). Thus, persistent water stress will compromise defense function, consistent with our evidence of lower survival probability within environments that were drier relative to the long-term mean of the study region.

Interactions

In this study, water availability modulated the effects on survival of within-tree trait factors and between-tree competitive interactions. Although the mechanisms determining plant responses to water stress have long been understood (Hsiao, 1973; Tyree and Sperry, 1989), the integrity of defensive function under drought and the underlying linkages are less well established (Huang et al., 2020). We posit that relationships between water stress and other survival factors may be interpreted in terms of their aggregate effects on tree carbon balance.

Larger trees in drier environments were substantially more susceptible to beetle-driven mortality than equivalent diameter individuals in more mesic sites (Fig 5a). These results are in agreement with recent patterns of tree senescence under drought (Koontz et al., 2021; McDowell et al., 2020; Stovall et al., 2019). Water relations in trees are governed by functional tradeoffs between transport capacity and vulnerability to stress-induced disfunction (Tyree and Ewers, 1991). Friction and gravity limit vertical water conductance from roots to leaves (Ryan and Yoder, 1997). According to the Hagen–Poiseuille formula for fluid flow through cylindrical pipes, hydraulic resistance is directly proportional to path length, but scales inversely with the 4th power of conduit diameter (Prendin et al., 2018). Thus, resistance to flow increases with tree height and transport distance, inherently constraining hydraulic capacity. Consequently, effects related to low soil water or high atmospheric demand may be expected to interact with mechanical constraints imposed by tree height, amplifying the potential for embolism formation and xylem disfunction in taller trees (Koch et al., 2004). Loss of hydraulic conductance may lead to reductions in net carbon assimilation, with attendant effects on secondary metabolism.

Our analyses provide evidence that the beneficial effect of a larger crown, in terms of tree survival, was lower in relatively drier environments (Fig. 5c). Plastic physiological responses to water limitation are known to affect patterns of resource allocation that modify plant architecture (Fonti et al., 2010). A number of theoretical models have been developed to explain biomass partitioning strategies that induce structural modifications in trees, such as sapwood to leaf area ratios (Lehnebach et al., 2018; Mencuccini et al., 2019). Prior research suggests that photosynthate may be prioritized for fine root production under persistent stress in some species (Magnani et al., 2002; Meier and Leuschner, 2008). Deficient water supply may also lead to leaf shedding (Wiley, 2020). Consequent reductions in total leaf area may compensate for low water conductance, moderating transpiration losses and associated xylem vulnerability to cavitation under sustained moisture limitation (Poyatos et al., 2013). However, smaller crowns will limit net photosynthesis and dependent defense functions.

Our results are consistent with recent studies (e.g. Young et al., 2017) indicating that the negative effect of high levels of resource competition on tree performance is compounded by water limitation (Fig. 5b). Presumably, higher evapotranspiration levels in denser stands accelerate the depletion of available soil water, elevating the degree of water stress in individual trees (Clark et al., 2016; Gleason et al., 2017). Low soil water may also induce nutrient limitation in plants. Below-ground microbial communities facilitate the decomposition of organic matter and subsequent availability of minerals. Microbial function is mediated by climate (Crowther et al., 2019; Li et al., 2019). For example, low soil water may constrain the mineralization of organic nitrogen by inhibiting, either, the diffusion of soluble substrates or the mobility of soil biota (Agehara and Warncke, 2005; Schjønning et al., 2003). Thus, below-ground water limitations may exacerbate, albeit indirectly, the negative effects of competition on tree defense by decreasing nutrient availability. Severe nutrient deficiencies in trees may constrain photosynthesis (Hsiao, 1973) and the subsequent production of secondary metabolites that support defenses (Herms and Mattson, 1992).

Climate change consequences

Climate change is predicted to amplify insect-driven disturbance impacts (Seidl and Rammer, 2017). Warming temperatures increase bark beetle voltinism, enhance reproductive rates and promote range expansion (Jakoby et al., 2019). Concurrently, periods of anomalous drought, expected to become more frequent and persistent in Central Europe (Hari et al., 2020), degrade tree defense capability by limiting water conductance, photosynthesis, and the metabolic production of defensive chemicals. However, our results suggest that the trait characteristics of trees will modulate outcomes. For example, more prevalent future droughts may constrain average potential height growth due to hydraulic limitations (McDowell et al., 2020). Trees with a reduced stature may then be less susceptible to drought-induced xylem damage (Koch et al., 2004) and may be more likely to sustain metabolic and defense functions. On the other hand, literature evidence suggests that growth rates in Norway spruce have accelerated in response to recent environmental changes (Cienciala et al., 2018). If these trends continue, insect-driven tree mortality may increase due to negative relationships between tree size and survivorship.

The dynamics of future insect outbreaks will further be governed by complex feedbacks. For example, natural disturbances generate structural and compositional diversity (Turner, 2010). Model simulations have demonstrated that disturbance-driven heterogeneity in forest structure dampens the potential severity of subsequent insect herbivory (Sommerfeld et al., 2021). Thus, natural historical processes shape developmental pathways in forested landscapes, establishing a template of varying stand conditions that, in addition to climate, mediate ensuing bark beetle activity (Thom and Seidl, 2021). Prior research based on dendroecological evidence indicates that the duration and severity of recent bark beetle outbreaks in Central Europe are not unprecedented historically (Čada et al., 2016). Čada et al. (2016) also argue that antecedent patterns of disturbance during the 19th and 20th centuries have preconditioned forests in this region to sustain outbreak populations of herbivores. An interval of relatively benign disturbance activity has promoted the development of a sufficient density and distribution of large host trees that, in turn, have facilitated outbreak populations of bark beetles. Similarly, land use activities outside of forest reserves, such as timber harvest or post-disturbance logging, potentially homogenize landscapes and promote insect expansion. The long-term consequences of climate warming for disturbance-driven trajectories of change are therefore uncertain, but will be determined by complex interactions between climate, the metabolic and demographic responses of trees to environmental change, and the existing and emerging patterns of landscape form.

Geospatial patterns

Our results indicate that survival outcomes exhibited a spatial patterning at landscape scales. We argue that these distribution patterns are explained, in large part, by geographical variation in climate conditions and forest structure, factors we parameterized in our models. We also suggest that a portion of the unexplained variance in the survival models may be attributed to innate physiological mechanisms that are potentially underlain by genetic factors. The existence of high levels of genetic variation for quantitative traits within and among tree populations has been well documented in common garden experiments (Aitken et al., 2008). Thus, our evidence for a spatial clustering of survivors may reflect local differences in the genomic architecture of trees (Six et al., 2018). The role of genetic variation and local adaptation in tree defense was beyond the scope of this research, but merits further investigation.

Conclusions

Ecological theory suggests that variation among species and individuals in survival depends, in part, on resource allocation strategies that differentially support structural biomass vs. defense and storage functions (Loehle, 1988). Experimental studies have identified evidence for a conservative strategy in *P. abies* whereby carbon is prioritized for storage to promote survival during periods of stress, such as drought (Huang et al., 2019). Nevertheless, our results indicate that prolonged water limitation degrades defense capability in spruce, even within the generally mesic environments of Central Europe. Outcomes in this study support a growing body of evidence that the water relations of trees significantly mediate their ability to resist insect herbivory (Koontz et al., 2021). Although climate change is widely expected to increase future disturbance impacts, we show that tree resistance and survival responses are complex and will be influenced by local factors, such as plant size and stand structure.

Legal and societal pressure to control the dynamics of forests are growing as a consequence of more prevalent and severe disturbances. Since the severity of insect outbreaks varies as a function of stand structure, land management actions that lead to a homogenization of ecosystems in which all trees are equally susceptible may intensify potential impacts. On the other hand, natural disturbances that generate structural and functional heterogeneity, from the scale of individual trees to landscapes, will likely promote future ecological resilience and adaptation in the face of climate and environmental change (Kulakowski et al., 2017).

Data availability statement

Data are openly available from the Mendeley data repository at: <https://data.mendeley.com/drafts/nd799rkrtt> (doi: 10.17632/nd799rkrtt.2).

Author contribution

A.B., N.K., M.T., F.S. and R.J. conceptualized the study; A.B. and N.K. constructed models, performed statistical analyses, interpreted results and wrote the manuscript; R.D. performed spatial analysis of surviving tree distribution; N.K., A.B. and R.D. processed remote sensing data; K. Z., A.B. and N.K. filtered study region for non-spruce areas; N.K., R.J., J. B., M.S., M.P., K.S., J.H., J.Č. and P.N. collected field data. All authors contributed to manuscript revisions and approved the final version.

Declaration of Competing Interest

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

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2022.109025.

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