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Quantifying the probability of bark beetle induced damage in central German Norway spruce forests

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ABSTRACT

Norway spruce (*Picea abies*((L.)H.Karst)) is a tree species of great relevance to central and northern European forests and forest management, mainly due to its production potential and its natural dominance on certain higher altitude and latitude sites. However it is also prone to abiotic and biotic disturbances, frequently leading to economic damage and management challenges. Storms, bark beetles and droughts, in particular, contribute to such events. The European Spruce Bark Beetle (*Ips typographus*(L.)) has expanded its range, caused large scale disturbances in recent years and is predicted to further expand its range and damage potential due to climate change. Recent outbreak events are questioning the viability of spruce as a dominant forest tree species across central Europe.

In order to investigate the probability of bark beetle induced damage occurrence and its contributing factors in the predominantly secondary spruce stands in central Germany, we developed a model based on forest management and environmental data. The predictor variables comprise stand, soil and climate quantities as well as information on previous damage. We combined a large empiric data basis with the restrictive application of prior knowledge to ensure ecological plausibility, which enhances the potential of generalization. Our results indicate a limited mitigation potential of several proposed silvicultural counter measures in relation to the estimated impact of climate factors. The model will be used to evaluate and map the current and future risk of bark beetle induced damage in spruce stands, which can aid forest management in the prioritization of counter measures and tree species selection.

1. Introduction

Norway spruce (*Picea abies*((L.)H.Karst)) is an important tree species of central and northern European forests, but at the same time particularly susceptible to abiotic and biotic disturbance. Norway spruce owes its relevance mostly to its productive potential, which is based on fast growth and high timber quality, but also to its robustness against frost and browsing. Therefore, it has been widely planted outside its natural range. Despite its economic benefits it is prone to storm and insect damage, especially on those secondary sites where it does not occur naturally (Seidl et al., 2007), and has been found to be particularly susceptible to drought stress (Lévesque et al., 2013). In the last decades, disturbance regimes in Europe have intensified, driven by changes of climate and forest structure (Patacca et al., 2023; Seidl et al., 2011, 2014) and forest management needs to find ways to mitigate increasing instability.

Among biotic disturbance agents bark beetle species are particularly important in central and northern Europe and the European Spruce Bark Beetle (*Ips typographus*(L.)) dominates in terms of causing tree mortality (Seidl et al., 2016). Major outbreaks occur especially following storm damage or drought (Kärvemo et al., 2023; Marini et al., 2017). Storms may trigger outbreaks, as trees damaged in storms constitute a superb breeding habitat for bark beetles and allow them to raise population densities to epidemic levels, thus enabling them to colonize living and healthy trees (Christiansen and Bakke, 1988; Marini et al., 2013; Seidl and Rammer, 2017). Drought events can impair the defense mechanisms of vital living trees, again enabling bark beetles to overcome their defense mechanisms and to breed in living trees (Christiansen and Bakke, 1988; Lexer, 1995; Marini et al., 2012; Netherer et al., 2015, 2024; Rouault et al., 2006; Wermelinger and Jakoby, 2019).

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Bark beetle outbreaks have been increasing sharply (Patacca et al., 2023; Seidl et al., 2011, 2014) and this trend is likely to continue, both in other parts of the world (Jönsson et al., 2009, 2011; Weed et al., 2013) and in central Europe (Schelhaas et al., 2003; Seidl and Rammer, 2017; Seidl et al., 2014; Wermelinger, 2004). This is most likely related to ongoing climate change (Seidl et al., 2011), as rising temperatures accelerate the development of bark beetles (Wermelinger and Seifert, 1998, 1999), allowing for more generations to successfully develop per year (Baier et al., 2007; Jönsson et al., 2007, 2009), while increasing drought stress impairs defense mechanisms of host trees (Christiansen and Bakke, 1988; Lexer, 1995; Marini et al., 2012; Netherer et al., 2015, 2024; Rouault et al., 2006; Wermelinger and Jakoby, 2019). The years 2018 to 2020 exhibited one of the most severe drought events in recent European history, along with severe bark beetle calamities, temporarily deforesting vast areas of formerly spruce dominated landscapes, questioning the future suitability of Norway spruce as a dominant forest tree species on a wide range of sites. Several silvicultural approaches were proposed to reduce the management risk imposed by bark beetle induced disturbances, including reducing the target diameter or rotation period length, promoting admixed species, establishing mixed stands and, finally, replacing Norway spruce entirely by other tree species that are less prone to major calamities (Marini et al., 2012; Schelhaas et al., 2015; Seidl et al., 2008; Sonesson, 2004; Wermelinger, 2004). The future of Norway spruce in central Europe seems uncertain and one question arises: How effectively can proposed silvicultural strategies mitigate the risk imposed by bark beetles under a warming climate?

Modeling the risk of bark beetle induced damage may aid forest management by answering this question and estimating the current and future risk imposed by bark beetles. Existing modeling approaches can be divided into approaches based on bark beetle population ecology, those targeting host tree predisposition and those considering both perspectives simultaneously. Modeling approaches based on population ecology revolve around predicting bark beetle phenology (Baier et al., 2007), how many generations develop per year (Jönsson et al., 2007) or the population density (Gohli et al., 2024; Marini et al., 2013). However, when making deductions about damage potential, not only bark beetle population ecology is relevant, but also the predisposition of host trees toward successful bark beetle colonization. For that reason, modules integrating bark beetle inflicted damage in simulation studies frequently combine population ecology models with measures of predisposition (Seidl et al., 2007; Temperli et al., 2013). Approaches of evaluating the predisposition of spruce toward successful bark beetle colonization are frequently based on prior knowledge (Netherer and Nopp-Mayr, 2005; Nordkvist et al., 2023; Temperli et al., 2013). This ensures ecological plausibility of their predictor variables, however the magnitudes, patterns and relative weights of their effects often lack a solid empiric basis. Statistical models directly targeting bark beetle induced damage or disturbance offer an alternative to quantify predisposition. Depending on the research question, some focus on predictors either representing forest structure (Kärvemo et al., 2014, 2016), or climatic factors (Marini et al., 2017). Therefore, they rarely represent all groups of factors known to be relevant for predisposition or their relative impact. They vary in scale, with observation units sometimes as rough as forest districts (Stadelmann et al., 2013b) or counties (Gumpertz et al., 2000). Models on the stand level are preferable for some applications, as they can take into account smaller scale variation in forest structure and site properties. Also decision making concerning tree species selection usually takes place on the stand level. Overbeck and Schmidt (2012) have proposed a model on the stand scale, however, the highly relevant inter annual climate variability is not taken into account, due to its 10-year temporal resolution. The potential for generalization of many approaches is limited by either geographically or temporally restricted data sets.

The objective of this study is to present a model of the probability of bark beetle induced damage in central German Norway spruce stands and to evaluate contributing factors in terms of their effects and relative importance. Future applications of the model involve estimating the current and future risk in spruce stands imposed by bark beetles. To allow such predictions, the model needs to fulfill several requirements: (I) The predictor variables must be widely available at stand resolution; (II) The predictor variables must cover as many relevant factors as possible, including stand characteristics, previous damage, soil and climate parameters; (III) The model effects must be ecologically plausible; (IV) Future conditions must be covered in the data as far as possible.

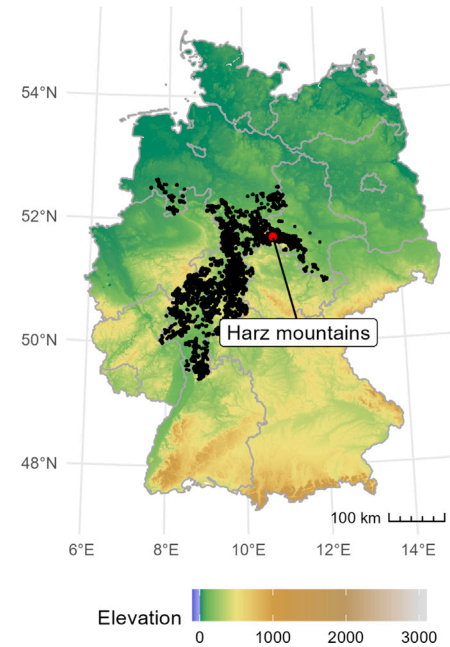

Fig. 1. Study area: Gray lines indicate German federal state borders. Black points indicate forest stands included in the data base.

2. Material & methods

2.1. Study area

The study area comprises the uplands of the German federal states of Lower Saxony, Saxony Anhalt and Hesse. It covers a wide range of site conditions and landscapes with altitudes ranging from 38 m to 1141 m and an area of about 33 000 km^2 (Fig. 1). The climate is diverse with annual average temperatures ranging from approximately 4 °C to 11 °C and annual precipitation sums between 520 mm and 1800 mm. Within this area, spruce occurs naturally only on the highest ranges of the Harz mountains, rendering most of the spruce stands secondary.

2.2. Data set and processing

The core data set is based on management data provided by the public forest administrations of the three federal states involved and combines timber harvest records with stand level information from forest management planning. The timber harvest records include information on stand, year and extracted wood volume as well as information on whether or not the harvest event was related to damages induced by insects or storm. Stand information from public forest management planning used in this study includes stand age, stand area, partial area covered per tree species, stand volume per tree species and the geographic location of forest management units. This data was preprocessed and merged using a PostgreSQL 15.2 database with a PostGIS3.3.2 extension. Further analysis was conducted in R version 4.4.1 (R Core Team, 2024).

Only publicly owned forests, featuring any non-zero proportion of spruce in the upper canopy layer, which are managed by the respective state forestry administration, are considered. We excluded stands with an age of less than 30 years. Uneven-aged stands were excluded from the analysis, because they are not represented sufficiently in our data. Harvest events that could not be assigned to a stand or harvest type were filtered. After pre-processing and filtering, the data base contained 48 666 logging records from 1999 to 2019. In the federal state of Lower Saxony the data set starts in 1999, in the federal state of Saxony Anhalt in 2001, and in the federal state of Hesse in 2009. The first year of each data set was not included in modeling, as one year preceding the focal year was necessary for deriving information on previous damage. The logging records stem from 27 154 stands totaling up to 152 675 ha.

Within the study area it is common practice to conduct sanitary cuttings whenever a notable amount of bark beetle induced damage occurs. For that reason, harvest records alone cannot be considered to be an unbiased sample in terms of bark beetle infestation, as the probability of an observation being part of the data set increases with the occurrence of bark beetle damage. Therefore, we filled in observations for each stand represented in our data set in years without harvest based on the assumption that any notable occurrence of bark beetle infection would have resulted in a harvest event. Appendix 1 features a more detailed description of our approach. This resulted in a total of 369 559 observations.

2.3. Response and predictor variables

We derived our response variable by classifying stands as infested or not infested with an annual resolution based on the relative proportion of harvested wood marked as harvested due to insect damage, with a threshold of 1 %. It is important to note that in the majority of harvest events this value was either 0 %, or close or equal to 100 %, and varying the threshold has a negligible effect on the model results.

Predictor variables contain information on forest structure, soil, previous damage, weather, and climate (Table 1). The quadratic mean diameter of a stand (QMD) is a variable that represents stand development over time. It can generally be derived based on forest management planning data. However, available information on the QMD is based on rough estimates and for some stands it is unavailable. Also extrapolation of the QMD would have been necessary, due to the temporal distance between the surveys of forest management data and observation years. In order to achieve consistent values for all stands, the QMD was estimated using a hierarchical model chain, based on a site index model (Schmidt, 2020) and a height–diameter model (Schmidt, 2009) for spruce. Both models are climate and site sensitive and were parameterized on data from the German national forest inventory and state forestry enterprise inventories. The prediction is done in two essential steps: First, the site index model is used to estimate the HQ, i.e. the stand height corresponding to the QMD, for a given age and environmental conditions. This HQ is then used in an inverted version of the height–diameter model to estimate the QMD. An alternative to represent stand development over time would be stand age. Integrating both QMD and age simultaneously is unfeasible, as they are highly correlated and essentially both represent the stand development over time. We assessed model prototypes including each of the two, but effect shapes, sensitivity and model performance did not differ notably. Unlike stand age the QMD is also sensitive to differences in site conditions and management. Assuming this site dependence to be relevant, we decided to use the QMD as a predictor variable instead of age.

The proportion of spruce at the stand level (variable sp_stand) was calculated based on stand information from forest management planning data by dividing the partial stand area of spruce by the total stand area. The proportion of spruce within a 500 m buffer around the stand centroid (sp_buffer) was calculated based on a map of dominant tree species in Germany, which is based on satellite imagery and maps the dominant species of the leading stand layer at a resolution of 10 m (Blickensdörfer et al., 2022). We also tested buffers of 1000 m, 1500 m and 2000 m radius, but the 500 m buffer performed best in terms of the deviance explained by the model. The available water capacity (AWC) was taken from three sources, according to the federal state (for Lower Saxony Overbeck et al., 2011, Hesse Ahrends et al., 2023 and Saxony-Anhalt Ahrends et al., 2016; Buresch et al., 2023). A previous damage indicator (prev_dmg) was deduced based on whether or not there was a harvest record noting storm or insect damage for the focal stand in the previous year. Where insect damage occurred, prev_dmg assumes the value 'bark beetle', otherwise if storm damage occurred the indicator assumes the value 'storm'. If neither was noted, it indicates 'no damage'.

Table 1
Metric predictor variables.

Predictor variable	Min	5% quantile	Mean	95% quantile	Max
QMD [cm]	17.3	21.8	36.6	54.1	70.7
sp_stand [%]	0.05	2.22	58.8	100	100
sp_buffer [%]	0	7.55	47.6	96.5	100
AWC [mm]	45	98	145	220	279
tsum [degree days (dd)]	1484	1982	2294	2621	3212
tsum_dif_py [Δdd]	−142	−27.9	136	379	441
psum [mm]	116	222	389	603	1080
psum_dif_py [Δmm]	−288	−136	22.8	203	541

Four weather and climate related predictor variables with annual resolution were calculated based on summation of daily average temperatures and precipitation within the vegetation period. Each climate sum was calculated based on daily weather station observations (Deutscher Wetterdienst, 2024) and subsequently regionalized to a 50 m × 50 m raster in case of the temperature sum (tsum) and a 100 m × 100 m raster in case of the precipitation sum (psum) based on spatial coordinates and elevation (Copernicus, 2020). The vegetation period of spruce used for tsum and psum was calculated annually using the 'vegperiod' R-package (Nuske, 2017), determining the beginning of the vegetation period for Norway spruce according to Menzel (1997) and the end of the vegetation period according to Nuske (2017). For the year preceding each data point we calculated detrended temperature (tsum_dif_py) and precipitation (psum_dif_py) sums by subtracting the stand specific 30 year moving averages of the respective climate sum, where the 30 year reference period finishes in the year preceding the observation. Considering the previous year's weather conditions serves two purposes: (I) It allows the model to take into account possible lag effects, where the temperature and precipitation in a particular year has an effect on the risk of bark beetle induced damage in the following year, and (II) to better fit data with a potential delay between bark beetle infection and harvest. Detrending the climate sums in our case enables the use of climate sums in subsequent years, as yearly weather parameters are usually correlated due to the underlying climate trend.

We tested two different approaches to include topography. At first we integrated a bark beetle specific implementation of a topographic exposition index (Topex) (cf. Overbeck and Schmidt, 2012; Scott and Mitchell, 2005). Assuming topography is linked to the risk of bark beetle infection through its effect on temperature, we also tried correcting the tsum and tsum_dif_py based on aspect and slope following the approach presented by Schick et al. (2023). After applying the temperature correction the effect of the Topex diminished, while switching direction in a way that north facing slopes would be at higher risk, which contradicts common knowledge and existing literature (Annila, 1969; Netherer and Nopp-Mayr, 2005). Accordingly we assume most of the effect of topography is covered by the applied temperature correction and dropped the Topex as a predictor variable.

2.4. Model development

We fitted generalized additive mixed models (GAMMs) to model the probability of bark beetle infection at the stand level, with an annual resolution, on the basis of a Bernoulli distributed response variable. An additive modeling approach allows us to cover potentially occurring non-linearity of effects and enables the utilization of a spatial smooth in order to handle spatial autocorrelation of the residuals. This occurs frequently in large-scale inventory data, due to unobserved site properties (Pya and Schmidt, 2016). Applying a mixed modeling approach with a random intercept on forest districts takes into account unknown confounding factors varying at the forest district level, such as different management schemes. By applying both a spatial smooth and a random effect on the forest district level, we follow the same approach as Brezger and Lang (2006) and Pya and Schmidt (2016), separating the overall spatial trend into a spatially structured and a spatially unstructured effect (serving as proxies for unobserved factors and reducing model bias). All other predictor variables were selected to feature known causal relationships with the response variable, hence we will call them causal variables.

$$
\begin{aligned}
y_{ij} &\sim \text{Bernoulli}\left(\pi_{ij}\right) \\
\pi_{ij} &= \text{E}\left(y_{ij} \mid \mathbf{x}_{ij}\right) \\
g\left(\pi_{ij}\right) &= \ln\left(\frac{\pi_{ij}}{1-\pi_{ij}}\right) \\
&= \beta_0 + f_1\left(x_{1,ij}\right) + \cdots + f_k\left(x_{k,ij}\right) + f_{k+1}\left(\text{easting}_{ij}, \text{northing}_{ij}\right) \\
&\quad + \mathbf{Z}_j \mathbf{b}_j
\end{aligned}
\tag{1}
$$

In Eq. (1), π_{ij} represents the conditional expectation of the Bernoulli distributed response variable y_{ij} on predictor variable vector $\mathbf{x}_{ij}$ for observation i within forest district j, $g()$ is the logistic link-function, β_0 is a global intercept, $f_k()$ are smooth functions representing the effects of k causal predictor variables x_k as well as the spatial effect, $f_{k+1}\left(\text{easting}_{ij}, \text{northing}_{ij}\right)$, and a random intercept term, $Z_j b_j$, for forest district identity.

We started off, by fitting an unconstrained GAMM (model variant A), using the R-package ‘mgcv’ (Wood, 2022), in order to establish general effect sizes and shapes. We then fitted a version, that is constrained in terms of function complexity (model variant B), by manually reducing the number of basis functions that are used to construct the spline functions, that represent each predictor variables effect. This reduces overfitting and helps isolating and visualizing meaningful signals in the data, that were masked by high levels of wiggliness in some effects of model variant A. Finally, we fitted a shape constrained GAMM (model variant C (Eq. (2))) using the R-package ‘scam’ (Pya, 2021). Defining shape constraints helps to prevent overfitting, improve the ecologic plausibility of the model effects and thus improve generalizability (Pya and Schmidt, 2016). In our case, shape constraints included fixing effect functions of individual predictor variables to be strictly monotonously increasing, decreasing or convex. These shape constraints were applied individually to effects, where general trends observed in model variant B were in line with the assumed underlying causal link over most of the variable’s range, but the effect was implausibly changing direction in other parts. This ensures that predictions and simulations based on the model do not result in patterns, that contradict prior knowledge on causal links.

$$
\begin{aligned}
g\left(\pi_{ij}\right) = \beta_0 &+ f_{1_{mi}}\left(\texttt{QMD}_{ij}\right) + f_2\left(\texttt{sp\_stand}_{ij}\right) + f_{3_{mi}}\left(\texttt{sp\_buffer}_{ij}\right) \\
&+ f_{4_{md}}\left(\texttt{AWC}_{ij}\right) + \texttt{prev\_dmg}_{ij}^{\top}\boldsymbol{\gamma} + f_5\left(\texttt{tsum}_{ij}\right) \\
&+ f_{6_{mi}}\left(\texttt{tsum\_dif\_py}_{ij}\right) + f_{7_{mdcx}}\left(\texttt{psum}_{ij}\right) \\
&+ f_{8_{cx}}\left(\texttt{psum\_dif\_py}_{ij}\right) + f_9\left(\text{easting}_{ij}, \text{northing}_{ij}\right) + \mathbf{Z}_j \mathbf{b}_j
\end{aligned}
\tag{2}
$$

Here, $f_{k_{mi}}$ represents a monotonously increasing function, $f_{k_{md}}$ a monotonously decreasing function, $f_{k_{cx}}$ a convex function, $f_{k_{mdcx}}$ a monotonously decreasing function that is convex and γ the effect vector of the categorical variable `prev_dmg`.

2.5. Sensitivity analysis

The relative importance of the effects of the causal variables was investigated by conducting a sensitivity analysis. Each of them was in turn varied while holding all other variables constant at a typical value (*i.e. ceteris paribus*). For most of the causal variables this typical value was represented by their respective empirical arithmetic mean value, or in case of `prev_dmg` the mode value ‘no damage’. The forest district and spatial smooth model terms were each set to the value corresponding to the mean of all predicted values for the respective model terms. This allowed ranking the causal variables according to their impact on model predictions in the average case of conditions represented by the data set.

To illustrate the model behavior when deviating from the aforementioned average case, as well as the proportion of sensitivity, that can be attributed to extreme values, we also varied each of the other causal variables in combination with the `QMD`. In this approach we varied the `QMD` across its range in the data set in 100 equidistant steps, while each of the other causal variables was varied in 3 or 5 steps depending on data coverage. The `QMD` was chosen as the interaction variable in the comparison of the other variables, because it represents the natural development each spruce stand undergoes in the course of its lifetime. Therefore, it is subject to a steady development over time, while other variables are either rather stable (e.g. `sp_stand`, `sp_buffer`, `AWC`) or exhibit a high inter-annual variability, such as the climate variables.

3. Results

The effect of the `QMD` shows an almost linear increase up to a `QMD` of about 45 cm, where the curve levels off. Past this point both the unconstrained models variant A and variant B feature a negative effect, while variant C features a plateau due to the application of a monotony constraint. The effect of `sp_stand` displays a positive relationship, gradually leveling off with increasing percentages of spruce. The three model variants differ only concerning the notably wigglier curve for the unconstrained variant A. Variable `sp_buffer` displays a positive effect up to around 60 %. Past this point in variant A the effect becomes extremely wiggly and in B it turns into a negative effect, while in variant C it levels off due to the application of a monotony constraint. The `AWC` has an overall negative effect, where model variants A and B display a notable amount of wiggliness and rather wide confidence bands, while in model variant C the effect of the `AWC` is linear with slim confidence bands. The categorical variable `prev_dmg` expresses a positive effect of previous storm damage and an even stronger positive effect of previous bark beetle infections.

The effect of `tsum` is positive, however above a `tsum` of around 2250 degree days (dd) the slope of this effect decreases notably. In variant B the effect essentially levels off to a plateau, while in variants A and C the slope remains positive. In addition the effect has a notably steeper slope but also wider confidence bands at values of `tsum` below 1750 dd in model variant A, than in the other two variants. Variable `tsum_dif_py` features a positive effect in the models with the strongest effect beyond a difference of 250 dd above the 30 year floating average. Variable `psum` has a negative effect, however it is hardly discernible in model variant A, due to an extreme amount of wiggliness. In variant B the effect has an overall negative effect but switching direction twice midway, whereas variant C is much smoother due to an applied monotony constraint, where the slope of the effect decreases with increasing values of `psum`. The effect of `psum_dif_py` is U-shaped with both very low and very high values resulting in higher predicted values and a pronounced dip in the center. Variant A has a

Table 2
Variable ranking based on the range of predicted probability of bark beetle induced damage, due to the variation of each causal variable across (I) the entire range of the variable and (II) the central 90 % from the 5 %-quantile to the 95 %-quantile, ceteris paribus.

Variable	Full range		Central 90 % range	
	Prediction range [%]	Rank	Prediction range [%]	Rank
prev_dmg	10.0	1	10.0	1
tsum_dif_py	7.03	2	6.07	2
psum	3.22	3	1.43	5
psum_dif_py	3.11	4	0.23	9
tsum	3.00	5	1.24	6
QMD	1.83	6	1.61	4
sp_stand	1.79	7	1.75	3
AWC	0.72	8	0.38	7
sp_buffer	0.58	9	0.36	8

much stronger effect, especially for extremely negative values, than the two constrained variants. In the effects of all metric causal variables the unconstrained model variant A features notably higher amounts of wiggliness. This is more pronounced in the effects of variables sp_buffer and AWC, which have a relatively small partial effect range and also feature rather wide confidence bands. However, the highest degrees of wiggliness are present in the effects of variables tsum_dif_py, psum and psum_dif_py.

3.1. Model sensitivity

First, the relative importance of the causal variables in the model was analyzed, based on the range of predictions resulting from varying the predictor variable (Prediction range), ceteris paribus. Not all metric predictor variables are equally well covered in our data (see Table 1). Therefore we decided to conduct the variable ranking twice: (I) based on the entire range of each of the predictor variables and (II) based on the central 90 % of the data, ranging from the 5 %-Quantile to the 95 %-Quantile. The results of these two rankings vary markedly (Table 2). The tsum_dif_py loses most of its prediction range and drops 5 ranks, demonstrating that most of its effect occurs at the extreme ends of its range. Also tsum and psum lose in prediction range and drop in rank, while QMD, sp_stand, AWC and sp_buffer gain ranks, indicating their effect is better covered by data across their entire value range. Especially for QMD and sp_stand the prediction range remains stable with changes of 0.22 % and 0.04 %, respectively.

In addition, the combined effect of varying the QMD in combination with each of the other variables illustrates the effects of deviating from average conditions and the proportion of their effect that is based on extreme values (Fig. 3). When deviating from the average case by variation of the other variables, the QMD-curves are compressed when approaching predicted values of 0. The same compression effect occurs when predicted values approach 1. This results in synergistic interactions at the lower end of predicted values and antagonistic interactions at the higher end of predicted values, which is an inherent property of logistic models without explicit interaction terms, due to the transformation through the link function.

4. Discussion

Beside the development of a model for predicting the probability of bark beetle induced damage in central German Norway spruce stands, another objective of this study was to evaluate its contributing factors in terms of their effect and relative importance. This evaluation sheds light on the potential impact of different mitigation strategies at hand. One proposed intermediate-term approach to reduce the risk imposed by bark beetles is reducing the target diameter or rotation period length (Hlásny et al., 2021; Schelhaas et al., 2015). The model effect of the QMD supports this approach, as the risk increases with stand development over time. As a consequence, harvesting trees at an earlier stage leads to a reduced time in which stands are exposed to higher levels of risk. Also, diversifying stand ages across the landscape is likely to reduce the overall risk, as not all stands would be in their most susceptible stage at the same time.

Reducing the percentage of spruce both at the stand level and within a buffer of 500 m around the stand also reduce the risk imposed by bark beetles in the model. Concerning species diversity, this supports Hlásny et al. (2021) and Wermelinger (2004), who suggest a transformation of pure homogeneous spruce stands toward stands with a higher diversity. They do not only call for species diversity, but also for structural diversity, but there was no information on this available in our data set. Considering the shape and amplitude of the effect curves of the percentage of spruce both on stand level as well as within the buffer of 500 m indicate a very limited mitigation potential of admixing or promoting smaller shares of other species. Only a substantial reduction of the share of spruce can notably reduce the probability of bark beetle induced damage, because the mixture effect becomes stronger the smaller the share of spruce.

Reducing the rotation period length and promoting admixed species may help to reduce the probability of bark beetle induced damage, however the results of the sensitivity analysis indicate, that climatic factors have a much higher impact, than the considered stand properties. Therefore, in order to handle the risk imposed by bark beetles on the large scale, the most promising approach is widely converting spruce forests on climatically unfavorable sites to other tree species, an approach that is frequently suggested (Marini et al., 2012; Schelhaas et al., 2015; Seidl et al., 2008; Sonesson, 2004). Planting and regenerating new spruce forests should be limited to climatically favorable sites, namely those with low temperature and high precipitation sums, which are mostly restricted to high elevation sites in central Europe. Especially north to east facing slopes appear more favorable in this regard, as they exhibit lower temperatures than other expositions at the same elevation and they are in most cases sheltered from winter storms, which mostly come from western to south-western direction. Even on those sites single extreme years with high temperatures, drought or extremely low or high summer precipitation increase the risk imposed by bark beetles decisively. This holds true even under recent conditions and as climate change is expected to raise temperatures and increase the frequency of extreme weather events like droughts (Intergovernmental Panel on Climate Change, 2023), an increase of the already high risk of bark beetle induced damages is expected in central Europe (Seidl et al., 2014). Considering our findings, ongoing climate change, and the significant delay between adaptive management and a reduction of bark beetle induced disturbance (Seidl et al., 2009), the need for forest conversion must be considered urgent.

4.1. Model effects and constraining their shapes

The QMD is closely linked to stand age, as both represent stand development over time. The bark is simultaneously the initial point of attack, the breeding habitat of bark beetles and features some of the main defense mechanisms against bark beetles (Paine et al., 1997; Wermelinger, 2004). Therefore, changes in bark structure in the course of stand development are likely the causal foundation to this relationship. We found an increasing risk of bark beetle induced damage with rising QMDs up to values of about 45 cm, which is in line with Lexer (1995), Netherer and Nopp-Mayr (2005) and Overbeck and Schmidt (2012). Past this point our results contradicts their findings, suggesting a negative effect, toward the end of stand development in model variants A and B contradicts previous findings. Considering the fact that this falling off toward the end is only covered by rather few extreme values and features relatively wide confidence bands (see Table 1 and Fig. 2), it is possibly coincidental or based on unobserved confounding factors. For example, high QMD values can be associated with protected areas or

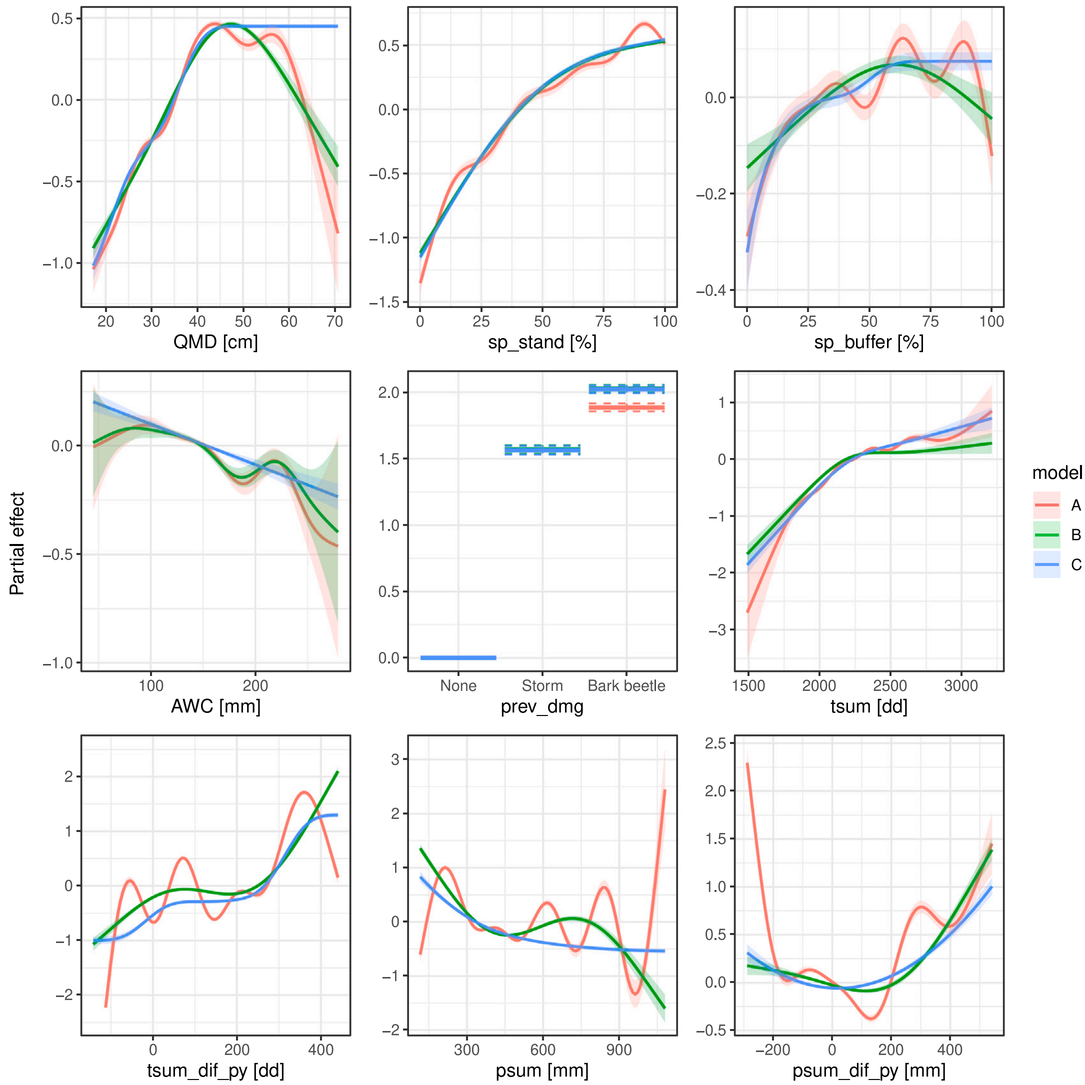

Fig. 2. Term plots for causal variables and model variants: (A) is an unrestricted reference version, while (B) is restricted in terms of the number of basis functions and (C) includes restrictions on the number of basis functions and shape constraints. Note that partial effects on the probability of bark beetle induced damage are on the scale of the linear predictor. Hence, the term plots presented here are intended for the interpretation of function shapes, while their magnitude on the scale of the response variable is addressed in Section 3.1.

inaccessible terrain and thus, with certain management restrictions or other factors potentially related to the observed pattern. In this case the negative effect toward the end of stand development lacks a causal link between the QMD and the risk of bark beetle infection and could lead to wrong conclusions, when assuming long rotation periods in predictive application or simulations based on the model. Therefore, we decided to apply a monotony constraint to this effect in model variant C.

The increasing risk with an increasing sp_stand is in line with the findings of other studies (Lexer, 1995; Netherer and Nopp-Mayr, 2005; Overbeck and Schmidt, 2012). Our results also support existing evidence that tree species diversity increases forest resistance to insect pests and disturbances in general, particularly for specialized insect pests (Jactel and Brockerhoff, 2007; Jactel et al., 2017, 2021). This is plausible, because the proportion of spruce represents a higher density and availability of the suitable host trees for bark beetles specialized on Norway spruce. Admixed species in spruce forests may also distract bark beetles by producing non-host volatiles potentially interfering with the beetle's pheromone system (Byers et al., 1998; Zhang et al., 1999). Other studies have identified the volume of spruce trees as a predictor variable (Kärvemo et al., 2014, 2016; Nordkvist et al., 2023). However, the volume of spruce is influenced both by the share of spruce and the stand development over time. Thus, it does not allow for a differentiation between the effects of tree species mixture and stand development, which is why we opted for integrating sp_spruce and the QMD separately, instead of spruce volume.

Much like the effect of sp_stand, sp_buffer expresses a positive effect on the risk of bark beetle induced timber in particular within the range from 0 to 60%. The higher availability of primary hosts in the closer surroundings can enable population densities of bark beetles to rise to levels enabling an infestation of vital spruce trees in focal stands. In model variants A and B, the effect switched to a negative direction at high values of sp_buffer. One possible explanation is that a higher availability of potential hosts in close proximity to the focal stand can increase the probability of bark beetles infesting a neighboring stand, instead of the focal stand, especially at low population densities of beetles. However, it is generally assumed that landscapes dominated widely by uniform stands of one species are at a higher risk of catastrophic outbreak events (Marini et al., 2022; Wermelinger and Jakoby, 2019). This is the main reason we decided to include a predictor representing the share of spruce trees in the forest surrounding the focal stand. Also, once a landscape-wide outbreak occurs, higher shares of spruce result in a greater proportion

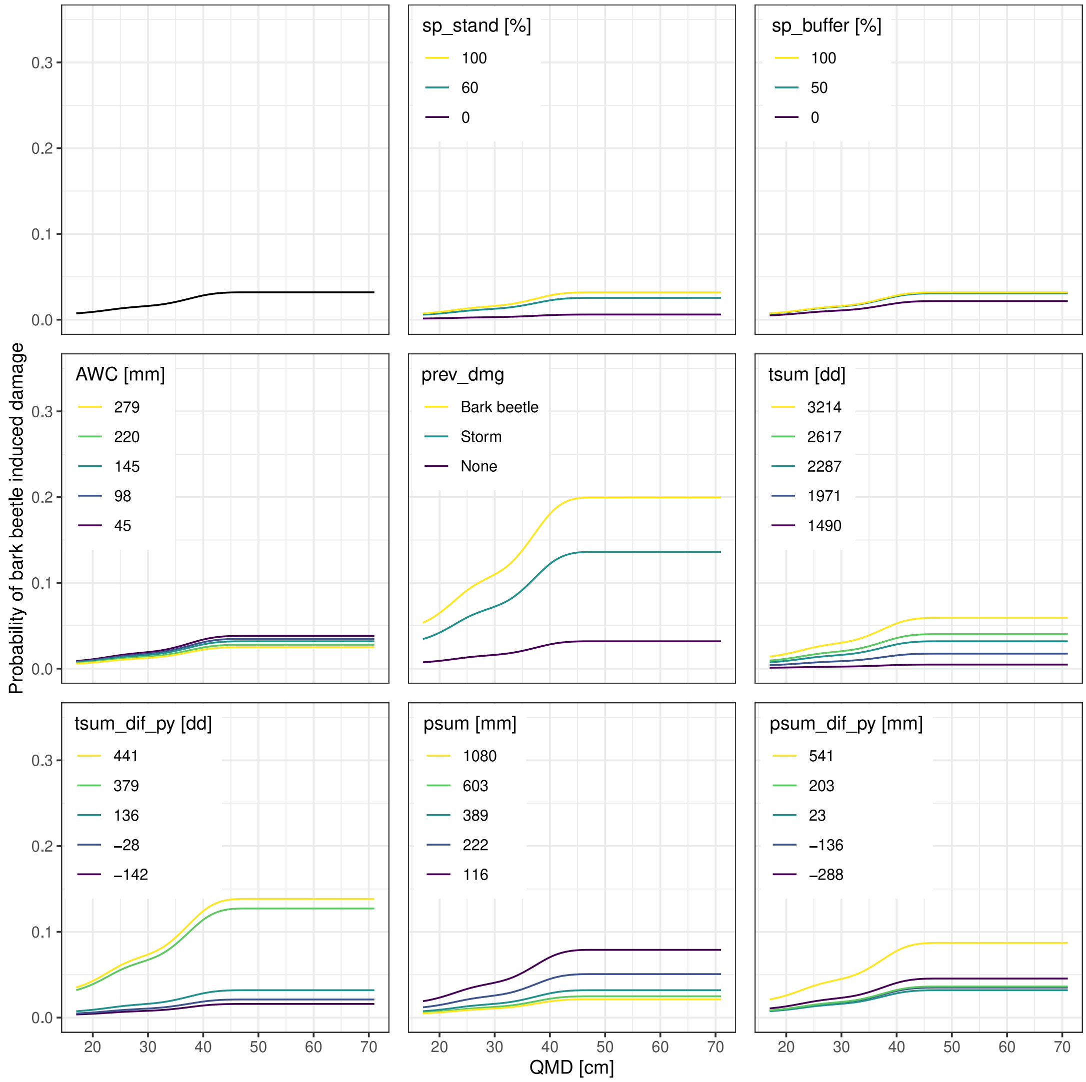

Fig. 3. Bivariate sensitivity plots for model variant (C): The QMD is varied across its range in 100 equidistant steps. Other variables are varied in combination with the QMD and in steps of min, 5 %-quantile, mean, 95 %-quantile and max. Variables sp_stand and sp_buffer were varied between minimum, mean and maximum as the minimum approximately coincided with the 5 %-quantile and the maximum with the 95 %-quantile after rounding. prev_dmg is varied over its 3 levels.

of stands at risk within the forest landscape. Therefore, we decided to apply a monotony constraint in variant C, which overrides the negative effect at higher values of sp_buffer, resulting in a similar shape to the effect of sp_stand.

The effect of prev_dmg is in line with common knowledge that bark beetle induced damage is closely related to preceding storm damage (Christiansen and Bakke, 1988; Marini et al., 2013, 2017; Stadelmann et al., 2013a). Preceding damage by bark beetles may be considered an indication of elevated population densities of beetles. Therefore, the effect of previous beetle damage is plausible as well as in line with previous findings (Kärvemo et al., 2014; Stadelmann et al., 2013b). It is important to note that the prev_dmg is a rather simple indicator of factors related to population density. Previous damage is only considered within the focal stand itself and not within the immediate surroundings. However, bark beetles may well spread across stand borders, if neighboring stands feature spruce of suitable dimensions. The restriction of the data set on publicly owned and managed forest poses a major limitation in this regard, as continuous information on previous damage across ownership types is missing. The model is highly sensitive even to this simplified representation of previous damage. This stresses the relevance of preceding storm damage as well as population density for bark beetle calamities, but also the importance of short term management approaches, that aim at reducing brood material or population densities of bark beetles, such as salvage logging or sanitary cuttings. These measures are common practice in managed Norway spruce forests, however the efficiency of such measures greatly depends on timing and diligence during their application (Wermelinger, 2004). Therefore, the risk of bark beetle damage is also related to the diligence of local forest managers, the availability of machinery and workforce, the quality of forest infrastructure and other factors, on which no suitable data is available. These are some of the factors we intend to capture in part by the integration of a random intercept at the forest district level.

The remaining five predictors are all related to a key factor for the risk of bark beetle infection: Drought stress weakening the defense capacities of spruce trees against bark beetles (Christiansen and Bakke, 1988; Lexer, 1995; Marini et al., 2012; Netherer et al., 2015, 2024; Rouault et al., 2006; Wermelinger and Jakoby, 2019). Temperature is relevant for drought stress, because the vapor pressure deficit depends on temperature and is itself one of the major drivers for evapotranspiration and, thus, plant water demand (Allen et al., 2015). Precipitation on the other hand is the main source of water for plants on most terrestrial sites. This explains the positive effects of tsum and tsum_dif_py, as well as the negative effect of psum. The effect of tsum match those of

Overbeck and Schmidt (2012) and both the effects of tsum and psum are in line with the results of Marini et al. (2017). However, they do not find a similar effect of temperature in the previous year and their indicator of rain in the previous year has a purely negative effect as opposed to our U-shaped effect. Monotony constraints were applied for tsum_dif_py and psum, as their effects were extremely wiggly in the unconstraint model variant A. In model variant B, the effect featured mid-range changes of direction, that are implausible in the light of the assumed underlying causal links. Other studies have also found lag effects of precipitation (Faccoli, 2009) and temperature on bark beetle induced damage (Marini et al., 2012). Drought stress may prevail in years after a drought event and elevated temperatures may lead to a population build up of bark beetles taking effect in the following year. One rather unexpected finding is that not only strongly negative deviations of precipitation in the vegetation period increase the risk of bark beetle infection in the following year, but also strongly positive deviations. This effect is only present at positive precipitation deviations above 200 mm with higher impact at values around 400 mm,which are covered only by a limited amount of data representing extremely wet conditions in the vegetation period. Especially at higher temperatures, an oversupply of water can cause oxygen limitation, potentially leading to fine root damage (Drew, 1997), which may increase drought stress in following years. As the overall effect of psum_dif_py was clearly U-shaped with increased risk at both extremes, we decided to apply a convexity-constraint in order to capture this overall shape while reducing the amount of wiggliness present in the unconstraint variant A. Including the AWC as a predictor is in line with Netherer and Nopp-Mayr (2005), who state that any soil property influencing water supply should have an impact on the risk of bark beetle attacks, due to the relevance of drought stress for predisposition. The negative effect plausibly reflects higher capacity of the soil to hold plant available water, reducing drought stress and, thus, the risk of bark beetle infection. Some studies use indicators of the current drought status of the soil instead of the AWC. However, these are generally closely related and correlated to precipitation and temperature, so we decided to include climate information and the AWC, in order to capture the effects of climate and soil separately.

The temperature sums are not only relevant through their influence on drought stress, but also have a direct impact on the individual development and population dynamics of bark beetles, as the beetles are highly temperature dependent (Annila, 1969; Baier et al., 2007; Wermelinger and Seifert, 1998, 1999). This means the effects of temperature sums presented in this paper encompass a mix of two major causal links working in the same direction, where higher temperatures increase the risk of bark beetle induced damage. This further justifies the applied monotony constraint for tsum_dif_py.

Previous work has considered topography to be a relevant factor, usually relating its impact to higher temperatures due increased solar irradiation on sun-exposed slopes (Annila, 1969; Christiansen and Bakke, 1988; Netherer and Nopp-Mayr, 2005; Overbeck and Schmidt, 2012). Based on the assumed underlying causal link via temperature we decided to include topography into the model indirectly by the correction of temperature sums accordingly. This results in the model being sensitive to topography without adding another predictor variable.

4.2. Model limitations

Utilizing management data opens up an extensive pool of empiric information, but also inherits challenges and imperfections. Forest harvest information cannot be considered an unbiased sample with respect to bark beetle infection. This issue was solved by filling in years with no harvest as described in Section 2.2 and Appendix A. Also harvest records can be faulty or in some cases they cannot be assigned to a forest stand, in which case they had to be excluded. Differences in booking behavior are in partly covered by the random effect on forest district level. This help estimating unbiased predictor effects, however, the model will have to be marginalized when making predictions, meaning that differences in the random intercept will not be taken into account in predictions.

Another challenge is the potential temporal delay between the infection of a stand with bark beetles and subsequent sanitation cutting. Especially during greater bark beetle calamities it is possible that infested stands cannot be harvested timely, so harvest events cannot be reliably related to the time of infection and, thus, to the factors favoring the infection. Especially bark beetle infections, which occur later in the season are occasionally harvested in the following year. This is one of the reasons why it was important to consider climate variables from the previous year in our case, in addition to potential causal lag effects, such as drought stress, prevailing beyond the time of drought. That means that the model does not allow for discriminating between causal lag effects and artifacts due to a delayed harvest. As a consequence it seems advisable to aggregate the predicted risk over a series of subsequent years in model application, rather than interpreting the results for individual years, despite its annual resolution.

4.3. Conclusion

We modeled the probability of bark beetle induced damage in central German Norway spruce forests using generalized additive mixed models based on extensive management and environmental data. Causal predictor variables cover the most important influential factors, including stand characteristics, previous damage, soil and climate parameters. The wide range and diversity within values of the predictor variables, combined with the restrictive application of prior knowledge through shape constraints, ensures the ecologic plausibility of the effects across a broad range of environmental conditions, which improves the generalizability of the model.

Our results suggest, that the probability of bark beetle induced damage is highly site dependent, especially regarding climatic factors. Reducing target diameters or rotation period length as well as promoting mixed species stands may help reducing this probability, however climatic factors have a higher impact. Therefore, the share of spruce on unfavorable sites should be reduced to amounts, that are acceptable to lose at once. This holds true even under current conditions, however shape and strength of the effects of climate variables hint toward a sharp increase of the risk, imposed by bark beetles in the course of climate change, which is in line with previous study results.

Future model applications will estimate the current risk in order to guide the prioritization of countermeasures and predict the future risk, to aid in the identification of favorable and unfavorable sites for growing spruce in the context of tree species selection.

CRediT authorship contribution statement

Luca Ehrminger: Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation, Conceptualization. **Thorsten Zeppenfeld:** Writing – review & editing, Data curation. **Jan Schick:** Writing – review & editing, Data curation. **Holger Sennhenn-Reulen:** Writing – review & editing, Supervision. **Samuel Schleich:** Writing – review & editing, Data curation. **Anika Hittenbeck:** Writing – review & editing, Data curation. **Matthias Albert:** Writing – review & editing, Supervision. **Matthias Schmidt:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

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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.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.foreco.2026.123688.

Data availability

The authors do not have permission to share data.

References

Ahrends, B., Hafner, S., Evers, J., Steinicke, C., Schmidt, W., Meesenburg, H., 2016. Regionalisierung bodenphysikalischer Parameter für Waldstandorte in Sachsen-Anhalt - Unsicherheitsbetrachtung an Standorten verschiedener Umweltmessnetze. Beitr. Aus der NW-FVA 14, 1–13. http://dx.doi.org/10.17875/gup2016-975.

Ahrends, B., Heitkamp, F., Buresch, M., Evers, J., Hentschel, S., Bialozyt, R., Meesenburg, H., 2023. Neue Herausforderungen an das Waldmanagement: Möglichkeiten und Grenzen des "Digital Soil Mapping" bei der Bereitstellung flächenhafter Datensätze für die Forstplanung am Beispiel von Hessen. Allg. Forst- U. J.-Ztg 192, 193–218. http://dx.doi.org/10.23765/afjz0002085.

Allen, C.D., Breshears, D.D., McDowell, N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the anthropocene. Ecosphere 6 (8), 1–55. http://dx.doi.org/10.1890/ES15-00203.1.

Annila, E., 1969. Influence of temperature upon the development and voltinism of ips typographus L.(Coleoptera, Scolytidae). Ann. Zool. Fennici. 6 (2), 161–208.

Baier, P., Pennerstorfer, J., Schopf, A., 2007. PHENIPS - A comprehensive phenology model of ips typographus (L.) (Col., Scolytinae) as a tool for hazard rating of bark beetle infestation. Forest Ecol. Manag. 249 (3), 171–186. http://dx.doi.org/10.1016/j.foreco.2007.05.020.

Blickensdörfer, L., Oehmichen, K., Pflugmacher, D., Kleinschmit, B., Hostert, P., 2022. Dominant tree species for Germany (2017/2018). http://dx.doi.org/10.3220/DATA20221214084846, [dataset].

Brezger, A., Lang, S., 2006. Generalized structured additive regression based on Bayesian P-splines. Comput. Statist. Data Anal. 50 (4), 967–991. http://dx.doi.org/10.1016/j.csda.2004.10.011.

Buresch, M., Evers, J., Meesenburg, H., Nagel, R.-V., Paar, U., Spellmann, H., Sutmöller, J., 2023. Grundlagen der klimaangepassten Baumartenempfehlung. Beitr. Aus der NW-FVA 21, 47–64. http://dx.doi.org/10.17875/gup2023-2394.

Byers, J.A., Zhang, Q.-H., Schlyter, F., Birgersson, G., 1998. Volatiles from nonhost birch trees inhibit pheromone response in spruce bark beetles. Sci. Nat. 85, 557–561.

Christiansen, E., Bakke, A., 1988. The spruce bark beetle of Eurasia. In: Dynamics of Forest Insect Populations: Patterns, Causes, Implications. Springer, pp. 479–503.

Copernicus, 2020. Copernicus DEM - GLO-90l. http://dx.doi.org/10.5270/ESA-c5d3d65.

Deutscher Wetterdienst, 2024. Daily station observations (temperature, precipitation, sunshine duration, etc.) for Germany, version v24.3. URL https://opendata.dwd.de/climate_environment/CDC/observations_germany/climate/daily/kl/.

Drew, M.C., 1997. Oxygen deficiency and root metabolism: Injury and acclimation under hypoxia and anoxia. Annu. Rev. Plant Biol. 48 (1), 223–250. http://dx.doi.org/10.1146/annurev.arplant.48.1.223.

Faccoli, M., 2009. Effect of weather on ips typographus (coleoptera curculionidae) phenology, voltinism, and associated spruce mortality in the southeastern alps. Environ. Èntomol. 38 (2), 307–316. http://dx.doi.org/10.1603/022.038.0202.

Gohli, J., Krokene, P., Flo Heggem, E.S., Økland, B., 2024. Climatic and management-related drivers of endemic European spruce bark beetle populations in boreal forests. J. Appl. Ecol. http://dx.doi.org/10.1111/1365-2664.14606.

Gumpertz, M.L., Wu, C.T., Pye, J.M., 2000. Logistic regression for southern pine beetle outbreaks with spatial and temporal autocorrelation. For. Sci. 46 (1), 95–107. http://dx.doi.org/10.1093/forestscience/46.1.95.

Hlásny, T., König, L., Krokene, P., Lindner, M., Montagné-Huck, C., Müller, J., Qin, H., Raffa, K.F., Schelhaas, M.-J., Svoboda, M., et al., 2021. Bark beetle outbreaks in europe: State of knowledge and ways forward for management. Curr. For. Rep. 7 (3), 138–165. http://dx.doi.org/10.1007/s40725-021-00142-x.

Intergovernmental Panel on Climate Change, 2023. In: Team, C.W., Lee, H., Romero, J. (Eds.), Climate change 2023: Synthesis report. Contribution of working groups I, II and III to the sixth assessment report of the Intergovernmental Panel on Climate Change. Tech. Rep., Intergovernmental Panel on Climate Change (IPCC), http://dx.doi.org/10.59327/IPCC/AR6-9789291691647.001.

Jactel, H., Bauhus, J., Boberg, J., Bonal, D., Castagneyrol, B., Gardiner, B., Gonzalez-Olabarria, J.R., Koricheva, J., Meurisse, N., Brockerhoff, E.G., 2017. Tree diversity drives forest stand resistance to natural disturbances. Curr. For. Rep. 3 (3), 223–243. http://dx.doi.org/10.1007/s40725-017-0064-1.

Jactel, H., Brockerhoff, E.G., 2007. Tree diversity reduces herbivory by forest insects. Ecol. Lett. 10 (9), 835–848. http://dx.doi.org/10.1111/j.1461-0248.2007.01073.x.

Jactel, H., Moreira, X., Castagneyrol, B., 2021. Tree diversity and forest resistance to insect pests: Patterns, mechanisms, and prospects. Annu. Rev. Entomol. 66 (1), 277–296. http://dx.doi.org/10.1146/annurev-ento-041720-075234.

Jönsson, A.M., Appelberg, G., Harding, S., Bärring, L., 2009. Spatio-temporal impact of climate change on the activity and voltinism of the spruce bark beetle, ips typographus. Global Change Biol. 15 (2), 486–499. http://dx.doi.org/10.1111/j.1365-2486.2008.01742.x.

Jönsson, A.M., Harding, S., Bärring, L., Ravn, H.P., 2007. Impact of climate change on the population dynamics of ips typographus in southern Sweden. Agricult. Forest. Meterol. 146 (1–2), 70–81. http://dx.doi.org/10.1016/j.agrformet.2007.05.006.

Jönsson, A.M., Harding, S., Krokene, P., Lange, H., Lindelöw, Å., Økland, B., Ravn, H.P., Schroeder, L.M., 2011. Modelling the potential impact of global warming on ips typographus voltinism and reproductive diapause. Clim. Change 109, 695–718. http://dx.doi.org/10.1007/s10584-011-0038-4.

Kärvemo, S., Huo, L., Öhrn, P., Lindberg, E., Persson, H., 2023. Different triggers, different stories: Bark-beetle infestation patterns after storm and drought-induced outbreaks. Forest Ecol. Manag. 545, 1–11. http://dx.doi.org/10.1016/j.foreco.2023.121255.

Kärvemo, S., Johansson, V., Schroeder, M., Ranius, T., 2016. Local colonization-extinction dynamics of a tree-killing bark beetle during a large-scale outbreak. Ecosphere 7 (3), e01257. http://dx.doi.org/10.1002/ecs2.1257.

Kärvemo, S., Rogell, B., Schroeder, M., 2014. Dynamics of spruce bark beetle infestation spots: Importance of local population size and landscape characteristics after a storm disturbance. Forest Ecol. Manag. 334, 232–240. http://dx.doi.org/10.1016/j.foreco.2014.09.011.

Lévesque, M., Saurer, M., Siegwolf, R., Eilmann, B., Brang, P., Bugmann, H., Rigling, A., 2013. Drought response of five conifer species under contrasting water availability suggests high vulnerability of Norway spruce and European larch. Global Change Biol. 19 (10), 3184–3199. http://dx.doi.org/10.1111/gcb.12268.

Lexer, M., 1995. Beziehungen zwischen Standorts-und Bestandesmerkmalen von Fichtenbeständen (Picea abies (L.) Karst.) und der Anfälligkeit für Borkenkäferschäden unter besonderer Berücksichtigung der Wasserversorgung (Doctoral dissertation). Universität für Bodenkultur, Wien.

Marini, L., Ayres, M.P., Battisti, A., Faccoli, M., 2012. Climate affects severity and altitudinal distribution of outbreaks in an eruptive bark beetle. Clim. Change 115 (2), 327–341. http://dx.doi.org/10.1007/s10584-012-0463-z.

Marini, L., Ayres, M.P., Jactel, H., 2022. Impact of stand and landscape management on forest pest damage. Annu. Rev. Entomol. 67 (1), 181–199. http://dx.doi.org/10.1146/annurev-ento-062321-065511.

Marini, L., Lindelöw, Å., Jönsson, A.M., Wulff, S., Schroeder, L.M., 2013. Population dynamics of the spruce bark beetle: A long-term study. Oikos 122 (12), 1768–1776. http://dx.doi.org/10.1111/j.1600-0706.2013.00431.x.

Marini, L., Økland, B., Jönsson, A.M., Bentz, B., Carroll, A., Forster, B., Grégoire, J.C., Hurling, R., Nageleisen, L.M., Netherer, S., Ravn, H.P., Weed, A., Schroeder, M., 2017. Climate drivers of bark beetle outbreak dynamics in Norway spruce forests. Ecography 40 (12), 1426–1435. http://dx.doi.org/10.1111/ecog.02769.

Menzel, A., 1997. Phänologie von Waldbäumen unter sich ändernden Klimabedingungen: Auswertung der Beobachtungen in den internationalen phänologischen Gärten und Möglichkeiten der Modellierung von Phänodaten. Forstl. Forsch.ber. München.

Netherer, S., Lehmanski, L., Bachlehner, A., Rosner, S., Savi, T., Schmidt, A., Huang, J., Paiva, M.R., Mateus, E., Hartmann, H., et al., 2024. Drought increases Norway spruce susceptibility to the Eurasian spruce bark beetle and its associated fungi. New Phytol. 242 (3), 1000–1017. http://dx.doi.org/10.1111/nph.19635.

Netherer, S., Matthews, B., Katzensteiner, K., Blackwell, E., Henschke, P., Hietz, P., Pennerstorfer, J., Rosner, S., Kikuta, S., Schume, H., Schopf, A., 2015. Do water-limiting conditions predispose Norway spruce to bark beetle attack? New Phytol. 205 (3), 1128–1141. http://dx.doi.org/10.1111/nph.13166.

Netherer, S., Nopp-Mayr, U., 2005. Predisposition assessment systems (PAS) as supportive tools in forest management - Rating of site and stand-related hazards of bark beetle infestation in the high Tatra mountains as an example for system application and verification. Forest Ecol. Manag. 207 (1-2 SPEC. ISS.), 99–107. http://dx.doi.org/10.1016/j.foreco.2004.10.020.

Nordkvist, M., Eggers, J., Fustel, T.L.-A., Klapwijk, M.J., 2023. Development and implementation of a spruce bark beetle susceptibility index: A framework to compare bark beetle susceptibility on stand level. Trees, For. People 11, 100364. http://dx.doi.org/10.1016/j.tfp.2022.100364.

Nuske, R., 2017. vegperiod: Determine thermal vegetation periods. http://dx.doi.org/10.5281/zenodo.1466541, R-package version 0.4.0.

Overbeck, M., Schmidt, M., 2012. Modelling infestation risk of Norway spruce by ips typographus (L.) in the lower Saxon Harz Mountains (Germany). Forest Ecol. Manag. 266, 115–125. http://dx.doi.org/10.1016/j.foreco.2011.11.011.

Overbeck, M., Schmidt, M., Fischer, C., Evers, J., Schultze, A., Hövelmann, T., Spellmann, H., 2011. Ein statistisches Modell zur Regionalisierung der nutzbaren Feldkapazität von Waldstandorten in Niedersachsen. Forstarchiv 82 (3), 92–100. http://dx.doi.org/10.2376/0300-4112-82-92.

Paine, T., Raffa, K., Harrington, T., 1997. Interactions among scolytid bark beetles, their associated fungi, and live host conifers. Annu. Rev. Entomol. 42 (1), 179–206. http://dx.doi.org/10.1146/annurev.ento.42.1.179.

Patacca, M., Lindner, M., Lucas-Borja, M.E., Cordonnier, T., Fidej, G., Gardiner, B., Hauf, Y., Jasinevičius, G., Labonne, S., Linkevičius, E., et al., 2023. Significant increase in natural disturbance impacts on European forests since 1950. Global Change Biol. 29 (5), 1359–1376. http://dx.doi.org/10.1111/gcb.16531.

Pya, N., 2021. scam: Shape constrained additive models. http://dx.doi.org/10.32614/CRAN.package.scam, R-package version 1.2-12. URL https://CRAN.R-project.org/package=scam.

Pya, N., Schmidt, M., 2016. Incorporating shape constraints in generalized additive modelling of the height-diameter relationship for Norway spruce. For. Ecosyst. 3, 1–14. http://dx.doi.org/10.1186/s40663-016-0061-z.

R Core Team, 2024. R: A language and environment for statistical computing. [Software version 4.4.0]. R Foundation for Statistical Computing. Vienna, Austria. URL https://www.R-project.org/.

Rouault, G., Candau, J.-N., Lieutier, F., Nageleisen, L.-M., Martin, J.-C., Warzée, N., 2006. Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. Ann. For. Sci. 63 (6), 613–624. http://dx.doi.org/10.1051/forest:2006044.

Schelhaas, M.-J., Nabuurs, G.-J., Hengeveld, G., Reyer, C., Hanewinkel, M., Zimmermann, N.E., Cullmann, D., 2015. Alternative forest management strategies to account for climate change-induced productivity and species suitability changes in Europe. Reg. Environ. Chang. 15 (8), 1581–1594. http://dx.doi.org/10.1007/s10113-015-0788-z.

Schelhaas, M.-J., Nabuurs, G.-J., Schuck, A., 2003. Natural disturbances in the European forests in the 19th and 20th centuries. Global Change Biol. 9 (11), 1620–1633. http://dx.doi.org/10.1046/j.1365-2486.2003.00684.x.

Schick, J., Albert, M., Schmidt, M., 2023. A new approach for modeling stand height development of German forests under climate change. Front. For. Glob. Chang. 6, 1201636. http://dx.doi.org/10.3389/ffgc.2023.1201636.

Schmidt, M., 2009. Ein longitudinales Höhen-Durchmesser Modell für Fichte in Deutschland. In: Tagungsband der Jahrestagung der Sektion Ertragskunde des DVFFA. pp. 69–82, URL https://sektionertragskunde.nw-fva.de/band2009/Tag2009_08.pdf.

Schmidt, M., 2020. Standortsensitive und kalibrierbare Bonitätsfächer: Wachstumspotenziale wichtiger Baumarten unter Klimawandel. Allg. Forst- Und Jagdztg. 190 (5/6), 136–160. http://dx.doi.org/10.23765/afjz0002043.

Scott, R.E., Mitchell, S.J., 2005. Empirical modelling of windthrow risk in partially harvested stands using tree, neighbourhood, and stand attributes. Forest Ecol. Manag. 218 (1–3), 193–209. http://dx.doi.org/10.1016/j.foreco.2005.07.012.

Seidl, R., Baier, P., Rammer, W., Schopf, A., Lexer, M.J., 2007. Modelling tree mortality by bark beetle infestation in Norway spruce forests. Ecol. Model. 206 (3–4), 383–399. http://dx.doi.org/10.1016/j.ecolmodel.2007.04.002.

Seidl, R., Müller, J., Hothorn, T., Bässler, C., Heurich, M., Kautz, M., 2016. Small beetle, large-scale drivers: How regional and landscape factors affect outbreaks of the European spruce bark beetle. J. Appl. Ecol. 53 (2), 530–540. http://dx.doi.org/10.1111/1365-2664.12540.

Seidl, R., Rammer, W., 2017. Climate change amplifies the interactions between wind and bark beetle disturbances in forest landscapes. Landsc. Ecol. 32 (7), 1485–1498. http://dx.doi.org/10.1007/s10980-016-0396-4.

Seidl, R., Rammer, W., Jäger, D., Lexer, M.J., 2008. Impact of bark beetle (Ips typographus L.) disturbance on timber production and carbon sequestration in different management strategies under climate change. Forest Ecol. Manag. 256 (3), 209–220. http://dx.doi.org/10.1016/j.foreco.2008.04.002.

Seidl, R., Schelhaas, M.-J., Lexer, M.J., 2011. Unraveling the drivers of intensifying forest disturbance regimes in europe. Global Change Biol. 17 (9), 2842–2852. http://dx.doi.org/10.1111/j.1365-2486.2011.02452.x.

Seidl, R., Schelhaas, M.-J., Lindner, M., Lexer, M.J., 2009. Modelling bark beetle disturbances in a large scale forest scenario model to assess climate change impacts and evaluate adaptive management strategies. Reg. Environ. Chang. 9 (2), 101–119. http://dx.doi.org/10.1007/s10113-008-0068-2.

Seidl, R., Schelhaas, M.-J., Rammer, W., Verkerk, P.J., 2014. Increasing forest disturbances in europe and their impact on carbon storage. Nat. Clim. Chang. 4 (9), 806–810. http://dx.doi.org/10.1038/nclimate2318.

Sonesson, J., 2004. Climate change and forestry in Sweden - a literature review. J. R. Swed. Acad. For. Agric. 143 (18), 1–42.

Stadelmann, G., Bugmann, H., Meier, F., Wermelinger, B., Bigler, C., 2013a. Effects of salvage logging and sanitation felling on bark beetle (Ips typographus L.) infestations. Forest Ecol. Manag. 305, 273–281. http://dx.doi.org/10.1016/j.foreco.2013.06.003.

Stadelmann, G., Bugmann, H., Wermelinger, B., Meier, F., Bigler, C., 2013b. A predictive framework to assess spatio - temporal variability of infestations by the european spruce bark beetle. Ecography 36 (11), 1208–1217. http://dx.doi.org/10.1111/j.1600-0587.2013.00177.x.

Temperli, C., Bugmann, H., Elkin, C., 2013. Cross-scale interactions among bark beetles, climate change, and wind disturbances: A landscape modeling approach. Ecol. Monograph. 83 (3), 383–402. http://dx.doi.org/10.1890/12-1503.1.

Weed, A.S., Ayres, M.P., Hicke, J.A., 2013. Consequences of climate change for biotic disturbances in north American forests. Ecol. Monograph. 83 (4), 441–470. http://dx.doi.org/10.1890/13-0160.1.

Wermelinger, B., 2004. Ecology and management of the spruce bark beetle ips typographus - A review of recent research. Forest Ecol. Manag. 202 (1–3), 67–82. http://dx.doi.org/10.1016/j.foreco.2004.07.018.

Wermelinger, B., Jakoby, O., 2019. Borkenkäfer. In: Wohlgemuth, T., Jentsch, A., Seidl, R. (Eds.), Störungsökologie. utb GmbH, pp. 236–255.

Wermelinger, B., Seifert, M., 1998. Analysis of the temperature dependent development of the spruce bark beetle ips typographus (L)(Col., Scolytidae). J. Appl. Entomol. 122 (1–5), 185–191. http://dx.doi.org/10.1111/j.1439-0418.1998.tb01482.x.

Wermelinger, B., Seifert, M., 1999. Temperature-dependent reproduction of the spruce bark beetle ips typographus, and analysis of the potential population growth. Ecol. Entomol. 24 (1), 103–110. http://dx.doi.org/10.1046/j.1365-2311.1999.00175.x.

Wood, S., 2022. mgcv: Mixed GAM computation vehicle with automatic smoothness estimation. http://dx.doi.org/10.32614/CRAN.package.scam, R-package version 1.8-40.

Zhang, Q.-H., Schlyter, F., Anderson, P., 1999. Green leaf volatiles interrupt pheromone response of spruce bark beetle, ips typographus. J. Chem. Ecol. 25, 2847–2861. http://dx.doi.org/10.1023/A:1020816011131.