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Drought and stand susceptibility to attacks by the European spruce bark beetle: A remote sensing approach

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Abstract

1. Several time-series analyses have demonstrated that after extreme summer drought bark beetle damage increased. However, studies predicting stand susceptibility over large spatial extents are limited by technical constraints in obtaining detailed, spatially-explicit data on infestation spot occurrence.
2. Using a unique dataset of georeferenced bark beetle infestation data, we tested whether the spatial variation of local growing conditions of forest stands, topography, and landscape variables modified the local occurrence of *Ips typographus* infestations after a severe hot drought in Central Europe.
3. Bark beetle infestation occurrence depended on soil-related aridity intensity, elevation, slope, and soil conditions. We showed that elevation interacted with growing conditions and topography. At low elevations, spruce forests growing on flat areas and wetter soils were more sensitive to the infestations. On the contrary, forests on steep slopes and soils with low water availability were rarely attacked. At the landscape scale, bark beetle damage increased with host tree cover but decreased with compositional diversity.
4. Our findings are generally consistent with the growth-differentiation balance hypothesis that predicts that trees growing under chronic dry conditions tend to be more resistant against biotic disturbances.
5. Spruce stands at low elevations located in homogeneous landscapes dominated by spruce were those more exposed to bark beetles in the initial phase of a drought-induced outbreak.

KEYWORDS

aridity, dryness, *Ips typographus*, landscape diversity, topography, water limitation

INTRODUCTION

The European spruce bark beetle *Ips typographus* L. (Coleoptera: Curculionidae) is one of the most important insect pests of European forests. In the last decades, climate change has caused an increased

outbreak propensity of this species causing severe economic damages to spruce forests (Hlásny et al., 2021; Marini et al., 2017). Warmer climate leads to a faster development of the insect and to an increased number of generations per year (Annala, 1969; Netherer & Pennerstorfer, 2001; Seitner, 1923). Under a warmer and drier climate also tree defence

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decreases due to transpiration deficits, thus increasing the vulnerability of spruce trees to bark beetle infestations (Hlásny et al., 2021; Marini et al., 2012; Matthews et al., 2018). Although higher temperatures and drought events usually increase bark beetle damage at the regional scale, local infestations are often patchy. Many studies have tried to understand how tree or forest conditions could impact the risk of bark beetle outbreaks at the local scale (Baier, 1996; Baier et al., 2002; Berryman, 1982; Blomqvist et al., 2018; Overbeck & Schmidt, 2012). However, studies attempting to upscale these factors at the regional scale are still rare (Trubin et al., 2022). Recent evidence on resistance to bark beetle suggested that climate suitability (e.g., drought) and stand conditions are important factor at large scale and they should be included in risk assessment (Jaime et al., 2022). However, technical constraints in obtaining detailed, spatially explicit data on bark beetle infestations over a continuous large spatial extent still exist.

Across large geographical areas, the variability in elevation, slope, and aspect may increase microclimate heterogeneity due to multiple processes such as rain shading, radiation, and wind turbulences. The combination of local amount of rainfall and soil structure (e.g., water retention capacity, soil depth etc.) is also expected to shape the growing conditions of trees potentially modifying the short-term response of spruce to drought and bark beetles (Netherer et al., 2019). In this context, the growth-differentiation balance hypothesis (Hermes & Mattson, 1992) predicts that trees growing under moderate stress, that is, on soils with limited water and nutrient availability usually allocate more resources on defences than on growth, thus increasing their resistance against bark beetles (Ferrenberg et al., 2015; Huang et al., 2019, 2020). According to this hypothesis, steep and shallow soils may induce moderate chronic water deficiency conditions increasing the constitutive defences in slow-growing trees. On the contrary, in trees growing faster on fertile soils, extreme drought might lead to carbon depletion because of unbalanced carbohydrates demand and, thus, a systemic shortage of secondary metabolites and defence compounds may occur (Gely et al., 2020; Netherer et al., 2015). However, empirical data also support opposite patterns indicating a more complex trade-off between growth and defence depending on the environmental context and species involved (Baier et al., 2002; Kytö et al., 1996).

Besides the local factors described above, landscape processes can also affect infestation probability. As Norway spruce is the main host tree for *I. typographus*, infestation probability should be strongly influenced by spruce availability (Kärvemo et al., 2014; Netherer & Nopp-Mayr, 2005). In addition, variability in configuration and composition of the habitat mosaics can also affect local infestation occurrence (de Groot et al., 2019; Hlásny & Turčáni, 2013). Increased landscape heterogeneity should reduce pest damage as high tree species diversity can impair the pest capacity to locate the host (Kärvemo et al., 2016; Q.-H. Zhang & Schlyter, 2004) and/or increase the pressure from natural enemies (Jactel et al., 2021). We therefore expect that forest landscape composition can explain some of the within region spatial variability in the attacks (Jactel et al., 2017; Marini et al., 2022).

Here, we present a large-scale study to test whether the local condition of forest stands and landscape factors can explain the local occurrence of bark beetle infestations after a severe drought and heat wave that hit central European forests in summer 2017 and 2018 (Schuldt et al., 2020). We used a unique dataset of georeferenced spruce bark beetle infestation data obtained from a remote sensing campaign over a large area in France (103,920 km²). Longer time-series can reveal temporal trends of the infestation patterns (Marini et al., 2017; Stadelmann et al., 2013; Trubin et al., 2022) or highlight different key drivers of the infestation depending on the different phase (i.e., incipient, outbreak, or declining) (Lausch et al., 2011). Instead, here, we mainly focused on the spatial effects of local growing conditions and landscape-scale factors during the early phase of a drought-induced outbreak. In particular, our main objective was to test the interacting effect of both local-scale factors (spatial variability of temperature, precipitation, topography, and soil properties) and landscape-scale factors (e.g., compositional heterogeneity, host availability) on the spatial dynamics of bark beetle attacks during the initial phase of a large outbreak. Understanding how topography, local growing conditions, and landscape composition can modify the effects of local aridity on spruce susceptibility to bark beetle infestations may help predicting future forest vulnerability to climate change impacts over larger geographic areas and prioritizing surveillance efforts.

MATERIALS AND METHODS

Study area

The study area was located in the Bourgogne-Franche-Comté and Grand Est regions, in north-eastern France, extending for more than 100,000 km² (Figure 1). Spruce forests occur as large semi-natural and planted forests on hills and mountain areas as well as fragmented stands in the lowlands. The variation in elevation of spruce forests is generally low (mean = 513 m; SD = 238 m). During 2018, an outbreak of *I. typographus*, triggered by heat waves and dry conditions that occurred in 2017 and 2018, started to spread in the entire area (Département de la Santé des Forêts, 2020). No large windthrows occurred in the years before 2018 and therefore the observed attacks at the regional scale were very likely caused by the hot summer droughts in 2017 and 2018.

Infestation spot detection

Remote sensing detection was performed using free available Copernicus Sentinel 2 satellite images and particularly the L2A surface reflectance data products processed by Centre national d'études spatiales (CNES) for the Theia data centre (www.theia-land.fr). Sentinel 2 data consist in orthorectified multispectral satellite images available as tiles (100 km × 100 km; band resolution ranged from 10 to 20 m). Totally, 21 tiles were needed to cover the whole study area. Mapping of bark beetle spots was carried out by the processing steps listed below.

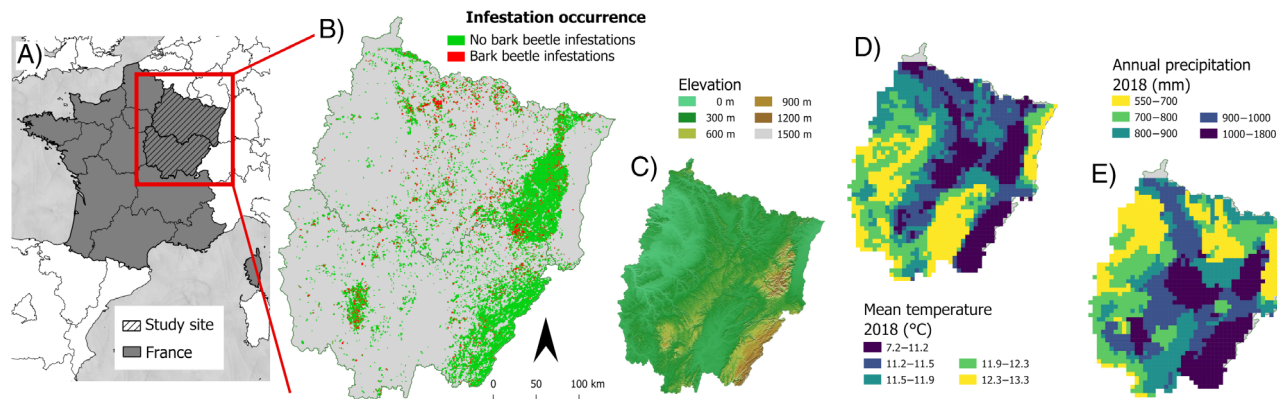


FIGURE 1 (A) Infestations of bark beetle have been continuously mapped for Bourgogne-Franche-Comté and Grand Est regions, in north-eastern France. (B) Spruce bark beetle infestation occurrence at 1 km cell size. Cells with spruce forest and without infestations are in green, cells with infestations are in red; (C) digital elevation model, (D) map of average annual temperature in 2018 and (E) map of annual cumulated precipitation in 2018

First, multispectral satellite images were collected from two time periods: February–March 2018 and February–April 2019 (see Appendix A for further details). For some tiles in 2018 more images were needed to reach a free-cloud coverage of our study area. Comparing spring 2019 with spring 2018 allowed us to depict the bark beetle infestations during the first year of the large-scale outbreak in 2018.

Second, ground observations within Grand Est province were carried out during winter 2018/2019 to detect new infestation spots. The resulting 75 sampled areas were georeferenced and polygonised using a GPS receiver.

Third, to analyse satellite data, four layers were created: a supervised classification and three inter-annual variation of spectral indices (namely the Normalized Red Index, Normalized Difference Vegetation Index, Normalized Burn Ratio) (Migas-Mazur et al., 2021). Ground observations were used for the initial supervised classification. After merging all four layers in a single layer, a final Support Vector Machine layer was produced and only detected *I. typographus* infestation spots having a surface greater than 0.1 ha were considered. Furthermore, to avoid false positive detections in no-spruce forests, spruce cover was retrieved from the forest type geodatabase BD Forêt (Institut National de l'Information Géographique et Forestière, 2018) and was used as a mask. As predominant tree species were not available for many forest polygons, the following forest-type classes were selected: 'spruce-fir forest' (the largely majority type), 'mixture of pine and spruce-fir', 'mixed forest of coniferous species without pine' and 'pure exotic coniferous forest (Douglas fir) without pine' (BD Forêt codes were FF2G61-61, FF2-00-00, FF2-90-90, FF2-91-91 respectively).

Fourth, to validate the satellite detection of bark beetle infestations we used high resolution aerial survey data. Aerial survey (conducted with airplane) was carried out in 14–15 April 2019 and 151 randomly sampled areas of 25 ha each were mapped with high-resolution images (5 cm of ground resolution). Within each sample, area damaged spruce forest was present. Two hundreds seventeen

polygons (8970 pixels including 899 in bark beetle damaged forests and 8071 in healthy forests) independently drawn by manual photointerpretation were used to assess the large-scale detection procedure by satellite by computing Overall Accuracy metric (Richards, 2013).

Ecological variables

To deal with continuous spatial variables, we superimposed a 1 km grid. Although using a grid-based approach to aggregate spatial data is a common method, choosing the correct cell size is often a critical point. When dealing with biological spatial data, considering the scale of ecological processes can inform the selection of the data resolution (Atkinson & Tate, 2000). For instance, previous studies on pest insects used the scale of insect dispersal to select the grid size (Potter et al., 2016). Analyses of temporal patterns suggest that infestation process mainly occurred with scale of few hundreds of meters (Kautz et al., 2011). However, forest fragmentation (Botterweg, 1982), outbreak phase (Økland et al., 2016), and wind strength (Byers, 2000) may increase dispersal distance up to several kilometres. Thus, a 1 km grid resolution (cell size = 1 km²) seems to be a good compromise to study bark beetle spatial patterns and it is also comparable with some explanatory variable at coarse spatial resolution.

For each 1 km² cell, we estimated several explanatory variables using the zonal statistic tool in QGIS (QGIS.org, 2022) (Table 1). Digital elevation model at 25 m of spatial resolution (EU-DEM v1.1 available at <https://land.copernicus.eu>) was used for computing topographic variables: elevation, slope, and annual insolation. Slope and insolation were calculated in SAGA (Conrad et al., 2015) and output maps were cropped using spruce cover to avoid including non-spruce areas in the computation. Then, within each cell we computed the average value of each variable of interest.

Besides insolation, cumulative thermal sum is an important factor to assess bark beetle activity and the number of generations during a year. We used 8.3°C as minimum temperature and 38.9°C as

TABLE 1 Descriptive statistics of the environmental parameters computed for 1 km grid resolution.

Variables	Mean	Unit	Min; max
Elevation	566	m	90; 1364
Slope	9	degree	0; 32
Available water content	0.11	volume fraction	0.07; 0.14
SPEI	−1.46	adimensional	−1.96; −0.12
Insolation (annual)	1635	kWh/m ²	1039; 2017
Thermal sum	1328	degree days	828; 1705
Soil depth	87	cm	20; 130
Host cover	29	adimensional	5; 100
Forest diversity (mixed forest proportion)	0.20	adimensional	0; 1

Abbreviation: SPEI, standardized precipitation-evapotranspiration index.

maximum temperature, considering the period from 1 April 2018 to 30 September 2018 (Baier et al., 2007).

Soil data were used to account for different soil conditions among stands. We used map of available water content (volume fraction), hereafter AWC, at 500 m resolution (Ballabio et al., 2016), and soil depth at 1 km resolution (Panagos, 2006).

To account for water deficiency stress, we computed April–September accumulated standardized precipitation–evapotranspiration index (SPEI) (Vicente-Serrano et al., 2010) in 2018. SPEI is a multiscale (it can be calculated for a specific period of time) and widely used index accounting for dryness (negative values) and wetness (positive values). Practically, negative values of SPEI indicate water deficiency, so SPEI decreases with aridity intensity. As SPEI is calculated as deviation from averaging climatic conditions, we used time series of water balance (monthly precipitation—monthly potential evapotranspiration [PET]) from 2011 to 2018 as input data. Temperature and precipitation data were retrieved from SAFRAN model (Durand et al., 2009) at 8 km resolution. Because temperature is mainly elevation-dependent, we down-scaled the mean temperature at cell size by applying a standard adiabatic correction (Sheridan et al., 2010). PET and SPEI were computed using functions *thornthwaite* and *spei* of SPEI package (Beguería & Vicente-Serrano, 2017).

To test the effect of landscape composition, we measured the proportion of spruce within each cell ('Host'). In addition, we computed the proportion of mixed forest on the total amount of host cover within each cell, hereafter called Forest Diversity. Computing of landscape metrics was performed in R using LANDSCAPEMETRICS package (Hesselbarth et al., 2019).

Finally, we used the occurrence of a bark beetle infestation (presence/absence data) in each cell as response variable (binary). In our study, the presence of bark beetle damage in that cell occurred when at least 0.1 ha of spruce were damaged by bark beetles. Spatial and no-spatial data were managed in R 4.0 (R Core Team, 2022) by using *sp* package (Bivand et al., 2013), *SF* package (Pebesma, 2018), *RASTER* package (Hijmans, 2020).

Statistical analyses

To avoid including cells with only marginal spruce forest along boundaries, only cells with at least 5% (i.e., 5 ha for 1 km side cells) of spruce cover were used in statistical analyses. Because a strong correlation was found between elevation and developmental thermal sum (Pearson correlation = −0.87), only elevation was included in the models, that is, most of the variation in developmental thermal sums was related to difference in average temperature across elevations.

A multi-model inference approach was used to evaluate alternative competing models involving climatic, topographic, and landscape variables (Burnham & Anderson, 2004). In particular, we used generalized linear models to estimate parameters with a binomial distribution (i.e., logistic models) using a maximum likelihood estimator. We ran residual autocorrelated logistic models, which are models with an additional distance-weighted function based on residuals to correct for spatial autocorrelation (Crase et al., 2012). We choose the greater neighbourhood distance for which Moran's *I* index was not significant (2 km for 1 km grid). Cells without neighbours within those distances were discarded. Then, we computed the spatial autocovariate of the residuals (RAC) by using the function *autocov_dist* in the *SPDEP* package (Bivand et al., 2013). Finally, we applied multi-model inference approach, by comparing all the possible nested models within the following global model:

$$\text{Infestation occurrence } (0, 1) \sim \text{Host} + \text{Forest diversity} + \text{Slope} + \text{AWC} + \text{Soil depth} + \text{SPEI} + \text{Insolation} + \text{SPEI} \times \text{Insolation} + \text{SPEI} \times \text{Slope} + \text{SPEI} \times \text{AWC} + \text{SPEI} \times \text{Soil depth} + \text{Elevation} + \text{Elevation} \times \text{Slope} + \text{Elevation} \times \text{Insolation} + \text{Elevation} \times \text{SPEI} + \text{Elevation} \times \text{AWC} + \text{Elevation} \times \text{Soil depth} + \text{RAC}.$$

We tested the interactions between large-scale factors, such as SPEI and elevation, and local scale factors, such as slope, AWC, soil depth, and insolation. To make estimates comparable, each included explanatory variable was standardized to mean 0 and SD 0.5 using the *ARM* package (Gelman & Su, 2020). *MuMIn* package (Barton, 2021) was used to perform multi model selection, and *MIXLM* package (Liland, 2021) to run models with maximum likelihood estimators. The goodness-of-fit of nested models was evaluated by second-order Akaike's criterion (AIC). The model having the minimum AIC value was considered the best-fitting model and the ranking was based on increasing difference of AIC from the best-fitting model. Usually, a cut-off value of $\Delta\text{AIC} = 7$ is used to define a top model set and lower-ranked models were treated as less meaningful (Burnham et al., 2011). Furthermore, model weight (w_i) represents the relative likelihood of a model *i* and can be interpreted as the probability that model *i* is the best model. Since there was more than one plausible model, averaging estimates of predictor slopes were computed following a full model averaging approach. Here, zero was substituted into those models where a parameter was absent, and the final parameter estimate was obtained by averaging over all models in the top model set (Nakagawa & Freckleton, 2011).

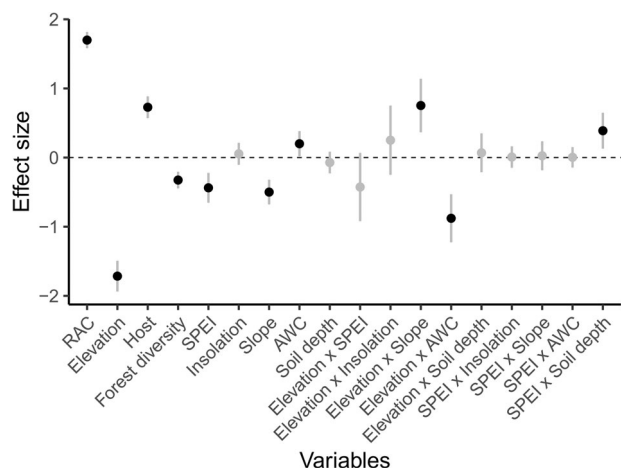


FIGURE 2 Model averaged estimates and interval of confidence (95%) from the multi model selection procedure testing the effect of the predictors on the probability of infestation (binary). Black dots indicate significant effects ($p < 0.05$); grey dots indicate non-significant effects ($p > 0.05$). AWC, available water content; RAC, residual spatial autocovariate; SPEI, standardized precipitation-evapotranspiration index

To evaluate potential collinearity issues among explanatory variables, we computed the variation inflation factors (VIFs) using *CAR* package (Fox & Weisberg, 2019) on models without interactions. Since in observational ecological studies in which signals are usually weak, even a low VIF value might lead to a biased parametrisation, we used a threshold of 2. We also present correlations between the predictors included in our global models (Appendix B, Table B.1). Residual diagnostic was checked using *DHARMA* package (Harting, 2021). Finally, AUC (Area Under the ROC Curve) was computed to assess the goodness of fit of the binomial model in R with *pROC* package (Robin et al., 2011). AUC value varies from 0.5 (i.e., null explaining power) to 1 (i.e., model perfectly predicts data). R squared and pseudo-R squared were computed with *RSQ* package (D. Zhang, 2021).

RESULTS

General results

Bark beetle damage could effectively be mapped over the entire area as confusion matrix revealed an overall accuracy of 95% (see Appendix A, Table A.2). A total of 1659 ha (approximately 4700 spots) of damaged forests by bark beetles have been detected during 2018 (0.5% of spruce forest area). The majority of the attacks (1185 ha) was located in the northern administrative region Grand-Est, whereas 473 ha were detected in the southern administrative region, Bourgogne-Franche-Comté.

Infestation occurrence

Multi model inference on autologistic models using presence/absence data ($N_{\text{cells}} = 10,244$, of which 1795 showed infestation occurrence)

identified 51 models with $\Delta\text{AIC} < 7$. Estimated effect sizes of the full averaging model are shown in Figure 2 (see Appendix B, Table B.1 for further details). No issues in the residuals were found and the global model achieved acceptable performance ($\text{AUC} = 0.82$).

Our model suggested that infestation occurrence of bark beetles was mainly driven by elevation (effect size = -1.71 , $p < 0.0001$), showing decreasing probability of outbreak with increasing elevation (Figure 3a,b). However, we also found significant interactions between elevation and slope and between elevation and AWC (elevation \times slope interaction $p < 0.001$; elevation \times AWC, $p < 0.0001$), that is, at low elevations bark beetle risk increased in flat areas, rather than on steep slopes, and also increased in soil with more water availability (Figure 3a,b). Moreover, we found a negative relation with SPEI index (effect size = -0.44 , $p < 0.0001$), meaning that bark beetle damage probability increased with aridity. SPEI also interacted with soil depth (effect size = 0.39 , $p = 0.003$) as we observed that bark beetle damaged increased more with aridity intensity in stands growing on shallow soils (Figure 3c). Furthermore, we found that landscape variables were important for predicting attacks. Host cover showed a positive correlation with infestation occurrence (effect size = 0.73 , $p < 0.0001$), while forest diversity (i.e., proportion of mixed forest on the total amount of host availability) showed a negative effect (effect size = -0.33 , $p < 0.0001$). Insolation did not act as a main driver for bark beetle occurrence. Finally, data showed a strong spatial structure, but RAC successfully accounted for spatial autocorrelation (global Moran's I of the residual autocovariate model was not significant, $p = 0.31$).

DISCUSSION

Although a large body of research has elucidated the drivers of temporal dynamics of bark beetle outbreaks at large spatial scale (Lausch et al., 2011; Marini et al., 2017; Seidl et al., 2016; Stadelmann et al., 2013), there are still only a few studies able to explain the within-region spatial variability in bark beetle attacks (Gilbert et al., 2005; Kärvelo et al., 2014). Many previous studies have already investigated local predisposing factors to bark beetle outbreak but usually over small spatial extents (Blomqvist et al., 2018; Lausch et al., 2011; Netherer & Nopp-Mayr, 2005; Overbeck & Schmidt, 2012; Pasztor et al., 2014). However, only few dealt with stand susceptibility after severe drought at regional scale (Netherer et al., 2019). Using remote-sensing techniques, this study contributes to understand the occurrence of bark beetle infestations at large spatial scale by upscaling the effects of forest landscape heterogeneity, topography, local growing conditions, and aridity intensity in explaining local bark beetle damage in absence of other major triggers, such as wind or snow storms. In particular, we showed that low elevation sites were more prone to be threatened by bark beetles, but also that bark beetle risk decreased in stands growing on steep slopes and on dry soils. We also found that the spatial distribution of the bark beetle was determined by landscape composition, with more damage in spruce monocultures and less in mixed forests.

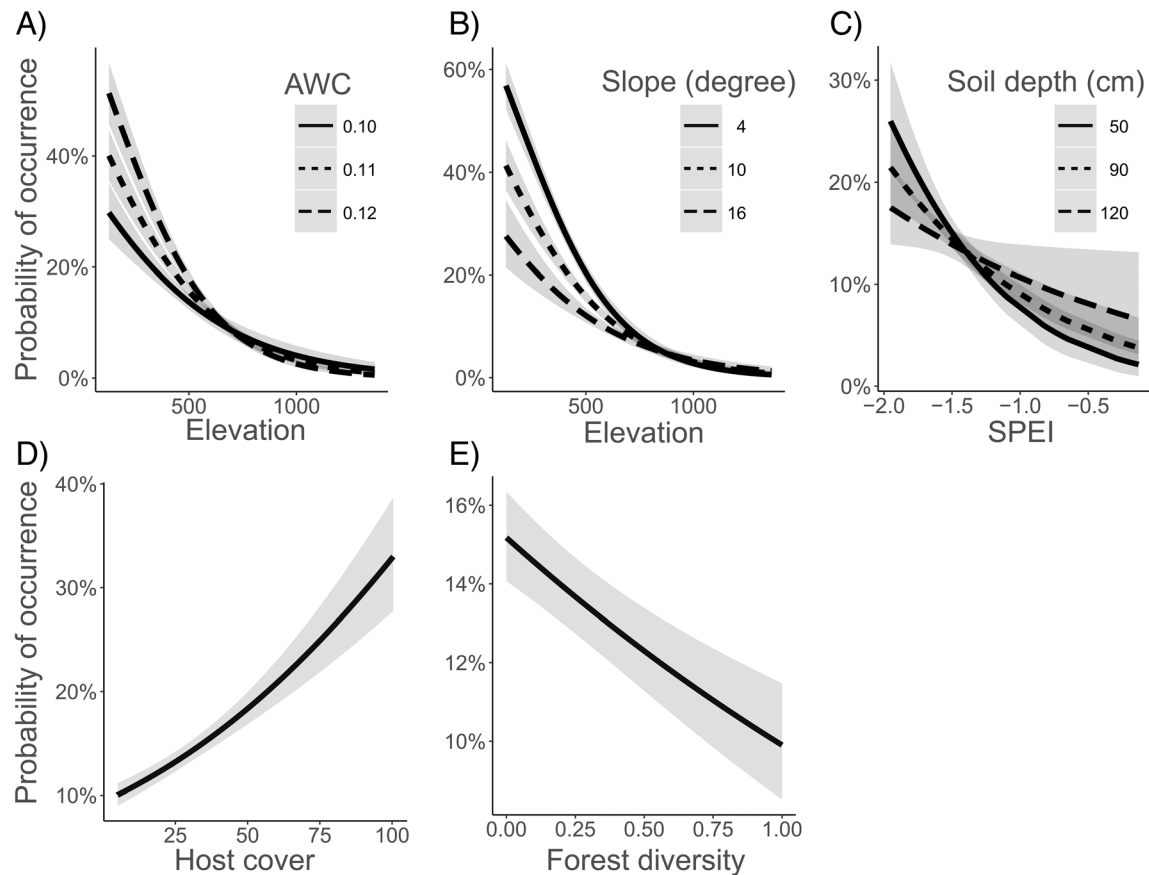


FIGURE 3 Significant interacting effects on the infestation occurrence (binary) of bark beetle. Probability of bark beetle occurrence decreased with elevation, however, interactions with available water content (AWC) (A) and slope (B) modified the elevation effect. Negative values of standardized precipitation-evapotranspiration index (SPEI) (i.e., increasing aridity intensity) increased bark beetle risk, especially in stands growing on shallow soils (C). Host cover increased the probability of infestations (D), however proportion of mixed forest had a negative effect (E).

Spatial variability in climate and topography

Consistently with previous studies on local predisposing factors (Faccoli & Bernardinelli, 2014; Lausch et al., 2011; Marini et al., 2012), we found that risk of bark beetle attack decreased with increasing elevation. Although within our study area two generations of *I. typographus* usually occur, a third generation may occasionally develop only below 500 m (Département de la Santé des Forêts, 2020). Temperature is a well-known factor of increasing bark beetle development and flight activity, thus more biotic pressure on spruce trees is expected under a warmer climate (Bentz et al., 2019; Jakoby et al., 2019; Jönsson et al., 2007). Consistently, we found a high correlation between elevation and thermal sum, which is a well-known parameter for predicting bark beetle development (Baier et al., 2007; Wermelinger & Seifert, 1998, 1999).

During severe drought events, elevation may also interact with local growing conditions. We found that increasing slope inclination and dryness of soil always reduced the infestation probability, especially at low elevations. Topography can change superficial soil properties by affecting transport and accumulation of solutes, and thus shaping growing vegetation (Tsui et al., 2004). In particular, steep

slopes can be considered a good proxy for low soil water and nutrient resources because soil erosion and matter transport hamper soil fertility (Scholten et al., 2017). Baier et al. (2002) suggested that when spruce trees grow under fertile conditions, they might exhibit low defence against bark beetles and others suggested that trees growing in N-rich soils may be prone to higher pest pressure due to thicker bark (Blomqvist et al., 2018; Dutilleul et al., 2000). On the other hand, dry soil conditions can induce a moderate chronic drought status making trees more resistant and thus less prone to bark beetles attacks (Netherer et al., 2019). This result is consistent with the growth-differentiation balance hypothesis that predicts a trade-off between costs of secondary metabolites relative to the demand for photosynthesis by growth (Herms & Mattson, 1992). Fast-growing trees are expected to be less resistant to bark beetle attacks because when more resources are allocated to growth, less are available for investment in physical and chemical defences (de la Mata et al., 2017). In previous experimental studies, the growth-differentiation balance hypothesis on host-bark beetle systems has been supported (Baier et al., 2002), but also questioned (Kytö et al., 1996). Besides the fundamental importance of these previous studies, here we want to stress the need for large-scale studies, which are able to test

ecological hypotheses over wide environmental ranges. On the contrary, we found that soil depth had an opposite effect, showing increasing bark beetle infestation probability in shallow soils. A previous study (Blomqvist et al., 2018) has already shown higher bark beetle infestation severity in trees growing on shallow soils in spite of fertile conditions, suggesting that different soil parameters may have different importance in explaining tree susceptibility. Our results, in agreement with previous observations, seem to suggest that growth-differentiation balance hypothesis works well with certain parameters (i.e., slope and overall water capacity), but bark beetle host tree susceptibility might increase under stronger limiting factors, potentially affecting resources availability (i.e., shallow soils and thin root depth) (Wild, 1953).

The key role of summer drought as an outbreak triggering factor is well-known (Wermelinger, 2004; Worrell, 1983). Consistently, the spatial variability in precipitation and evapotranspiration helped us predicting the local infestation occurrence of spruce bark beetle. We found a negative effect of SPEI on infestation occurrence of the European spruce bark beetle, that is, stands located in sites experiencing higher than average water deficiency during the summer 2018 had a higher mortality rate due to bark beetle infestations. Reduced water availability usually makes Norway spruce trees more susceptible to biotic disturbances (Netherer et al., 2021). However, besides the temporal effect of drought on bark beetles-host system, it is important to stress that here we aim to investigate the spatial variability of precipitation related to topography. Indeed, we observed that aridity intensity affected infestation occurrence of *I. typographus*, but this effect was modified by soil depth. Trees growing on shallow soils showed increasing bark beetle outbreak occurrence with increasing water deficiency, but no effect was observed on trees growing on deeper soils.

Finally, although solar radiation was found to be locally relevant in other studies (Blomqvist et al., 2018; Kautz et al., 2013; Mezei et al., 2019), we found no effect of this factor. This is probably due to the relatively flat terrain of our study area without high mountain ranges. Previous studies also found that solar radiation and aspect did not play an important role as predisposing factors of bark beetle infestations (Kaiser et al., 2013; Lausch et al., 2011), or even opposite pattern in which north-facing slopes showed higher damage (Jurc et al., 2006). These differences among studies might suggest that solar radiation might be more relevant under certain conditions, such as in mountain areas where strong gradients exist.

The role of the host availability and landscape heterogeneity

Besides local factors, landscape context has been revealed to be an important predictor for tree mortality during bark beetle outbreaks (Simard et al., 2012). We found that host availability within the cell was a strong predictor for bark beetle infestation occurrence. Our results are consistent with previous observational studies showing that higher percentage and/or volume of spruce forest at the

landscape scale increased the risk of attacks (Kärvelo et al., 2014, 2016; Netherer & Nopp-Mayr, 2005). At the landscape scale, the spatial structure of bark beetle populations is linked to host connectivity, thus increasing the risk of bark beetle damage in spruce-dominated landscape (Seidl et al., 2016). In addition, forest compositional diversity at the landscape scale could play a potential role in mitigating bark beetle damage due to reduced host availability and accessibility, enhanced natural enemy activity or barriers to dispersal (Hlásny & Turčáni, 2013; Jactel et al., 2021). In accordance with these predictions, we found that the proportion of mixed forest decreased the probability of infestation occurrence, although this effect is weaker than that of host (spruce) availability. Our results thus agreed with previous studies showing the beneficial effect of mixed forests rather than monocultures when dealing with bark beetles (de Groot et al., 2019; Kärvelo et al., 2014; Sommerfeld et al., 2021).

Potential limitations

Our models explained relatively low proportions of total variation (~23%). Indeed, several limitations in our approach might exist. First, we could not quantify other potential key drivers using remote sensing techniques, such as stand age and structure such as density of spruce or biomass data. Second, we could not distinguish between regular harvesting and sanitary cutting, thus all cuttings were identified and indifferently removed using inter-annual vegetation indices. However, the amount of sanitary logging was relatively low during 2018 since most of the clear cuts were carried out during 2019 and 2020 (Département de la Santé des Forêts, 2020, 2021). Third, our study was based on the spatial patterns of infestations during the first year after the drought event, whereas we cannot exclude that some of the observed effects may change with the progression of the outbreak or with drought persistence. Fourth, despite our selecting cell size (1 km²) seemed to be the best compromise to include both broad and fine resolution variables, we missed some small-scale processes such as edge effects.

CONCLUSIONS

Because of climate change, bark beetle outbreaks are expected to increase in the coming years with severe consequences for European forest landscapes (Hlásny et al., 2021). Although temporal dynamics of bark beetle populations have been thoroughly studied in Europe, investigations of spatial dynamics at large spatial extent are still scarce. Thanks to the availability of medium resolution satellite images, we are now able to better monitor forest disturbances across a wide geographical area and to upscale at the regional scale key risk factors to predict the first occurrence of *I. typographus* at medium spatial resolution (1 km). However, we still lack studies quantifying easily measurable physiological thresholds to predict tree susceptibility to bark beetle attacks (Baier et al., 2002; Blomqvist et al., 2018; Netherer et al., 2019). We thus suggest that remote sensing can be used in bark

beetle monitoring as a large-scale detection tool, integrating pheromone trap data which are still valuable as local warning system (Faccoli, 2009; Weslien et al., 1989). Finally, our study can provide useful practical outcomes for managing large outbreaks in spruce forests. In particular, it suggests that surveillance efforts after extreme drought events should be focused on stands growing at low elevations, on flat areas, and on wetter soils, whereas sites exhibiting chronic stress (i.e., drier soil and steep slopes) are less prone to bark beetle damage at least during the initial phase of the outbreak. In a long-term perspective, our study suggests to avoid planting spruce stands at lower elevation plains, since trees might experience more pest pressure due to a warmer climate. It also highlights the need to avoid large spruce monocultures. Considering the increasing risks of summer hot droughts in the next future due to climate change, forest managers should consider both the local stand and landscape susceptibility when implementing forestry planning.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Appendix A: Remote sensing information for bark beetle infestation detection. Appendix B: Statistical supplementary materials – Models.

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