Forest Ecology and Management 545 (2023) 121255

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Different triggers, different stories: Bark-beetle infestation patterns after storm and drought-induced outbreaks

S. Kärvemo [a,*], L. Huo [b], P. Öhrn [c], E. Lindberg [b], H.J. Persson [b]

[a] Swedish University of Agricultural Sciences, Department of Ecology, Box 7044, SE-750 07 Uppsala, Sweden
[b] Swedish University of Agricultural Sciences, Department of Forest Resource Management, SE-901 83 Umeå, Sweden
[c] SkogForsk (The Forestry Research Institute of Sweden), Uppsala Science Park, SE-751 83 Uppsala, Sweden

ABSTRACT

In the recent decades, Norway spruce forests (*Picea abies* Karst.) in Europe have been subject to large-scale tree mortality caused by the spruce bark beetle (*Ips typographus* L.). The outbreaks were induced by storm-felling events and periods of drought, which are becoming increasingly frequent due to climate change. Because storms and droughts spatially affect forests differently, the infestation patterns and configuration of the bark beetles might differ between storms and drought. In this study, we examined local and landscape factors associated with bark beetle-caused tree mortality after one storm (2005) and one drought-induced spruce bark beetle outbreak (2018), both occurring in southern Sweden. A total of 13,192 infested one-ha pixels after the storm and 6,425 one-ha pixels after the drought (in total 19,617) were compared regarding differences in infestation occurrence and size and associated forest structures and climate between the two different outbreaks, using a generalized linear model (GLM) approach. Based on our findings, we discovered that the allocation of infestation patch sizes (including four classes: 5–10, 11–25, 26–50 and >50 infested trees) for the two outbreaks were quite similar with a large proportion (>0.6) of small groups (≤10 trees).

However, the outcomes from this study demonstrate that the drivers behind the spatial configuration of bark beetle infestations can differ considerably between outbreaks triggered by storms and droughts, and the main cause seems to be linked to the spatial distribution of susceptible trees. The most consistent differences for both occurrence and infestation size were that storm-induced infestations increased more with spruce volumes and area of protected forests (nature reserves) in the landscape; whereas for the drought-induced infestations, occurrence and size increased more with clear-cuts in the landscape and spruce heights across spatial scales. Soil moisture and mean drought index (SPEI; May-July) were important for both outbreaks, but generally more important for the infestation sizes after droughts than after storms and may involve a time-lagged effect.

The reasoning behind the differences between storms and droughts may be that during storm-induced outbreaks, when the wind-felled trees are removed or not suitable anymore, bark beetles need to find specific susceptible standing trees, while after drought all trees are more or less stressed, which results in a selection of large trees in dry and warm landscapes as they have more resources and favorable reproduction conditions. Finally, we show that the previous infestation size influenced the later infestation size negatively within landscapes of 25 ha and this seems to be related to depletion of susceptible host trees.

These results are important for the assessment of more specific outbreak predictions, which should be integrated in future risk mapping of bark beetle outbreaks.

1. Introduction

Together with drought, wildfires and storms, tree-killing bark beetles are the most important biotic disturbances that affect temperate forests globally (Sommerfeld et al., 2018; Senf and Seidl, 2021). In western USA between 2002 and 2012, tree-killing bark beetles damaged more forests than wildfires, resulting in extensive carbon emissions (Berner et al., 2017). In Europe, the spruce bark beetle (*Ips typographus* L.) is the most important forest pest of Norway spruce (*Picea abies* Karst.) and outbreaks have increased vastly in recent years due to climate change (Hlásny et al., 2021a). Various tree stressors may provide the bark beetles with susceptible breeding material with weak defenses, which may cause eruptive population outbreaks resulting in increased colonization success. This positive feedback is enhanced by a substantial number of a new generation of beetles that increase the probability of overcoming the tree defense, thus causing extensive tree mortality across time and space. The stressors initiating the outbreak could have both abiotic (e.g. storms, droughts, fires, snow breakages, avalanches) and occasionally biotic origins (e.g. intensive thinning, clear-cutting, harvesting, and defoliation of other pests) (Wermelinger and Jakoby, 2022).

Drought and wind-felling are recognized as the two most important factors affecting spruce bark beetle outbreaks in Europe (Marini et al., 2017), which are both expected to increase with climate change (Haarsma et al., 2013; Seidl et al., 2017; Jactel et al., 2019).

Historically, most spruce bark beetle outbreaks in Europe have been triggered by storms, although drought-induced outbreaks have

* Corresponding author.
E-mail address: simon.karvemo@slu.se (S. Kärvemo).

https://doi.org/10.1016/j.foreco.2023.121255
Received 14 April 2023; Received in revised form 14 June 2023; Accepted 4 July 2023
Available online 18 July 2023

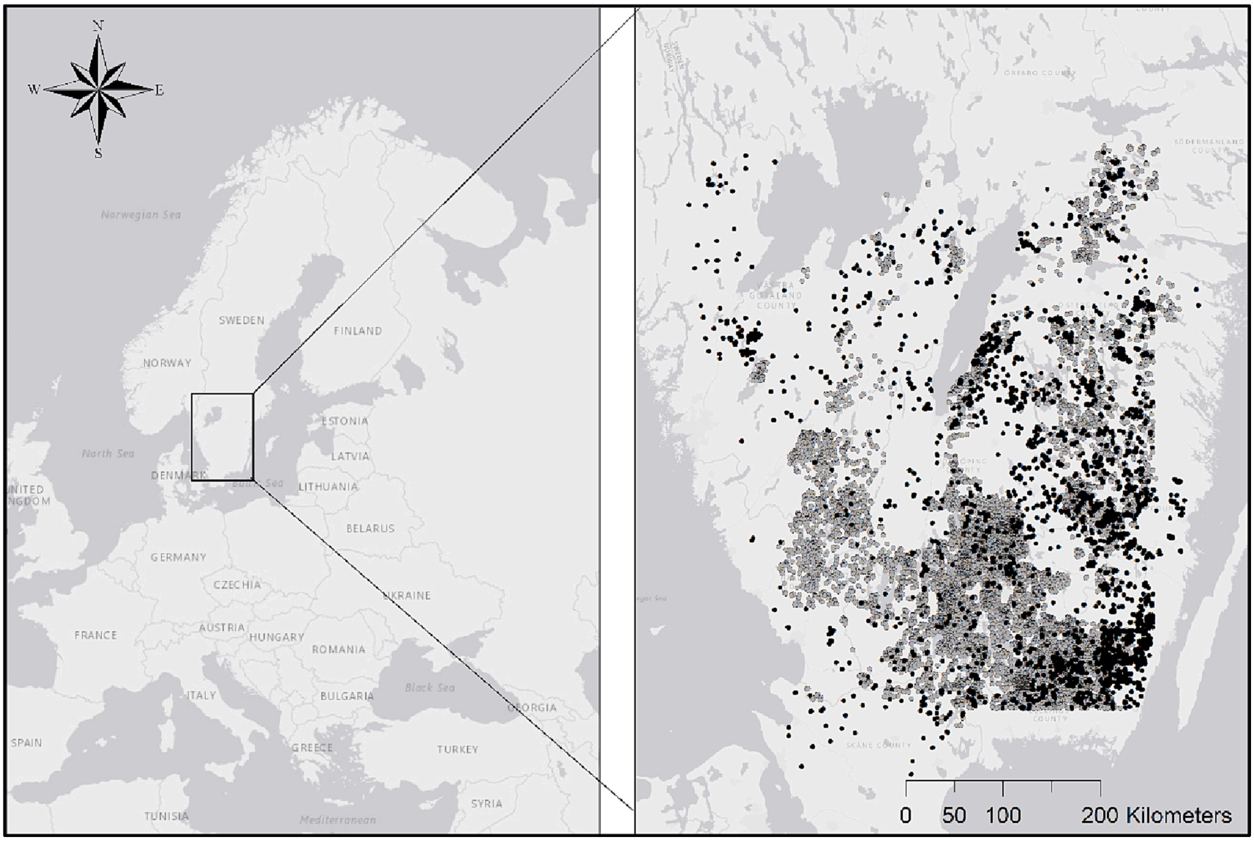

Fig. 1. The study area with infestation occurrences in southern Sweden, where gray dots represent data from the storm-induced outbreak (2006–2007) and black dots represent data from the drought-induced outbreak (2018–2019).

increased in recent years (Hlásny et al., 2021a; Hlásny et al., 2021b). For example, in 2018, an extensive drought - with warmer temperatures and lower rainfall - occurred across Europe, resulting in the largest spruce bark beetle outbreak ever recorded (Hlásny et al., 2021a). While droughts commonly affect host susceptibility and thus bark beetle outbreaks across large regional scales, storms generally operate in geographically smaller and more isolated areas (Seidl et al., 2016; Hlásny et al., 2021b; Wermelinger and Jakoby, 2022). To some extent storm-induced bark beetle infestations are more associated with the spatial distribution of the wind-felled trees (Hedgren el al., 2003), particularly at the early phase of the outbreaks (Kärvemo et al., 2014a; Økland et al., 2016; Schroeder, 2010) and when large amounts of the wind-felled trees have not been cleared from the forest due to logistical reasons (Schroeder et al., 2006; Marini et al., 2017; De Groot et al., 2021). In addition, since a much lower proportion of stressed standing trees are found during storm-induced outbreaks, at least at a landscape level, the bark beetles may be more associated with specific host trees with reduced resistance and areas with larger local bark-beetle populations. Consequently, indirect drivers of the spatial pattern of infestations may differ between storm and drought-induced outbreaks.

Previous landscape studies performed after storm-induced outbreaks have found that infestations are strongly associated with wind-felled spruces (Kärvemo et al., 2014a), host-tree volumes (Pasztor et al., 2014; Kärvemo et al., 2016), host age (Brůna et al., 2013), neighboring infestations (Stadelmann et al., 2014) and factors associated with aridity, such as slope, elevation, solar radiation (Netherer and Nopp-Mayr, 2005; Stadelmann et al., 2014; Sproull et al., 2017; Blomqvist et al., 2018), and temperature (Mezei et al., 2017). For drought-induced outbreaks, forest characteristics such as volume (Netherer et al., 2019), height (Müller et al., 2022) and age of the host tree (Overbeck and Schmidt, 2012), as well as neighboring infestations (Stereńczak et al., 2020) have been demonstrated to be important for infestation risks. As sanitation cuttings are conducted to a greater extent in managed forests compared to unmanaged forests, there might in some cases, be a higher population density in spruce dominated nature reserves due to migrations from the managed forests (Montano et al., 2016, but see Sommerfeld et al., 2018; Potterf et al., 2023). Even though the importance of some forest conditions may overlap between storm and drought-induced outbreaks, the general differences are poorly investigated.

Bark-beetle infestations are commonly spatially arranged in different-sized spots or patches of killed trees across landscapes and regions (e.g. Kärvemo et al., 2014b; Ayres et al., 2011). Previous studies have investigated how infestation patterns relate to forest characteristics between epidemics and endemics (e.g. Lausch et al., 2011; Stadelmann et al., 2014; De Groot et al., 2019) as well as forest resistance and differences between storms and droughts *per se* (e.g. Schlyter et al., 2006; Csilléry et al., 2017; Jactel et al., 2017). However, this is the first large-scale study to compare storm and drought-induced outbreak patterns across the same region. The aim of this study is to compare factors associated with the occurrence and infestation sizes between a storm (2005) and a drought-induced (2018) outbreak in southern Sweden. Kärvemo and Schroeder (2010) reported that the storm-induced outbreak resulted in just over 3 million m^3 of trees killed by the bark beetles. However, the more extensive outbreak caused by the drought has resulted in 32 million m^3 of bark-beetle killed trees so far (Swedish Forest Agency). This indicates that at a larger scale, there is only a minor interaction between the two outbreaks.

The specific research questions are: (i) does the importance of various forest characteristics differ between occurrences of storm and drought-induced infestations? (ii) How are infestation sizes influenced by the forest characteristics during the two different outbreaks? (iii) Is the local spatial configuration of infestation sizes from the recent outbreak influenced by the previous one?

Both storm intensities and elevated temperatures with subsequent

Table 1
Forest variable statistics for each of the studied outbreak areas 2006–2007 and 2018–2019 (of which 63% was overlapping), including units, modelled spatial scales - local (Lo) and landscape (La) - and in which models where the variable was evaluated, i.e., infestation occurrence model (Occ) or size (Size). SFM: SLU Forest Map; SFA: Swedish Forest Agency; LSS: Land Survey of Sweden; SMM: Soil Moisture Maps; CCKP: Climate Change Knowledge Portal.

Variables	Outbreak 06–07	Outbreak 18–19	Unit	Explanation	Scale	Models	Source
Spruce volume	79.8 (±60.1)	61.9 (±78.1)	m^3 ha^{-1}	mean (±SD)	Lo,La	Occ, Size	SFM
Spruce height	12.8 (±5.5)	11.1 (±6.6)	m	mean (±SD)	Lo,La	Occ, Size	SFM
Clear-cuts	6.4	5.8	%	area	Lo,La	Occ, Size	SFA
Nature reserves	1.4	2.1	%	area	La	Occ, Size	LSS
Soil moisture	34.5 (±25.7)	32.7 (±25.1)	index	mean (±SD)	Lo, La	Occ, Size	SMM
SPEI first year	−0.795	−1.738	index	drought	Lo	Size	CCKP
SPEI second year	0.955	0.009	index	drought	Lo	Size	CCKP

bark-beetle outbreaks have increased and will become more frequent in the future due to climate change (Venäläinen et al., 2020). A comparison of different drivers behind storm and drought-induced outbreaks will contribute to a more precise knowledge about the forest stands at highest risk of infestations. Current mapping of infestation risks is commonly based upon stand characteristics and climate data, including information from both storms and/or droughts, and this should be taken into consideration when applying indices to predict infestation risks. Therefore, it is important to gain an understanding of the differences in drivers between storm and drought-induced infestations to be better prepared in the future in order to mitigate any adverse effects on forest loss.

2. Material and methods

2.1. Study area

The two largest bark-beetle outbreaks recorded in Sweden erupted after a winter storm in January 2005 and a drought in 2018, both located in the southern parts of Sweden (Fig. 1). The mean elevation in the study area is 151.8 m with a standard deviation of ±68.2 (U.S. Geological Survey's EROS Data Center; https://databasin.org/). The storm in 2005 felled 50–75 million m^3 of forests (Kärvemo and Schroeder, 2010) and large management efforts were taken to salvage the wind-damaged trees before the spring swarming. However, such large volumes are impossible to remove within the first year (Økland et al., 2016) and tens of millions of wind-felled trees remained in the forest during the following summer, which provided the spruce bark beetle with a surplus of suitable breeding material. Consequently, due to the high population density emerging from the wind-felled trees, the spruce bark beetles were able to kill >3.2 million m^3 of healthy spruce trees during the next years; mostly in two counties in the west and central parts of southern Sweden. After the drought in 2018, an extensive bark beetle-induced spruce mortality occurred because of stressed trees with reduced defense capacity. So far (2018–2022), 32 million m^3 of Norway spruce has been killed across >10 counties in southern Sweden (Wulff and Roberge, 2021).

2.2. Outbreak data

In this study, we used infestation patch data from 2006 to 2007 and 2018 to 2019. This corresponds to a similar outbreak phase, i.e., the first–second year of attacks on healthy standing trees (Modlinger and Novotný, 2015, Schroeder and Lindelöw, 2002). Trees killed by the spruce bark beetle were surveyed by helicopter in September 2007 and categorized into one of four group size classes: 5–10, 11–25, 26–50 and >50 trees (cf. Kärvemo et al., 2014b, 2016). The helicopter data was validated from the ground in November 2007 (163 infested groups) and the result showed that of 1620 checked spruces, 1347 (83%) were confirmed to have been attacked by the spruce bark beetle in the same year (Kärvemo et al., 2016), indicating that a potential problem of false positives from the storm-induced outbreak is small in our data. The potential problem of false negatives should also be small because groups of killed trees are very apparent from helicopter at the low flying altitude and high density of transects used in the survey. We assume that a large proportion of the surveyed infestation patches were from 2006, as this was the peak year of the outbreak (Kärvemo and Schroeder, 2010). Data available from additional helicopter surveys in 2008 (~3 million ha) and 2009 (130,000 ha) were included when analyzing the dependencies of infestations between the storm and drought-induced outbreaks (see below). Data of individual bark beetle infested trees from 2019 were sampled from harvester machines equipped with global navigation systems (Södra skog; cf. Müller et al., 2022). Based on color changes in the infested tree crowns infested pixels-derived from satellite images (multi-temporal Sentinel-2) with a resolution of 10x10 m^2 – we can confirm an infestation patch accuracy of 79%, obtained from 126 infestation patches (Persson et al., 2022). As 34% of the infested trees were harvested before August 2019, when the majority of the trees had not yet changed crown color, we assume that these trees were infested in 2018. The infested trees from 2018 to 2019 were converted to equivalent infestation patch classes as the storm-induced outbreak. This was done via the *Aggregate points* function in ArcMap (ArcGIS 10; ESRI, Redland, California, USA), with a group distance limit of 10 m, to correspond to a similar visual separation and spatial accuracy of infestation patches from the helicopter data. For statistical modelling, the infestation patch classes from both outbreaks were converted to geometric means for the four classes (7.1, 16.6, 36.1 and 71.4, respectively), summed up in each of the 100x100 m pixels (see *Forest characteristics*). Geometric means were used because the distribution within each class was skewed toward small numbers (cf. Kärvemo et al., 2016). To ensure comparability with the harvest data exclusively collected from production forests, storm-induced infested pixels within nature reserves (1.5% of the total) were excluded from the data. The final number of infested pixels summed up to 13,192 pixels for the storm data and 6,425 for the drought data (Fig. 1.). The bark beetle infestation data from both outbreaks are distributed across 10 million hectares of land in Sweden. Of this, the 2007 helicopter data represents 6.7 million hectares and the 2019 harvesting data represents 9.2 million hectares, and 6.3 million ha overlaps spatially between the data of the two outbreaks.

2.3. Forest characteristics

The predictors for comparing infestation occurrence and magnitude from the two different outbreaks were six local variables and five landscape variables reflecting the forest composition in the surroundings. All predictor variables were aggregated by means for spruce volume and height and summed pixel area for clear-cuts and nature reserves (Table 1) to a resolution of 100x100 m^2, to facilitate data processing. The local variables were spruce volumes, spruce heights, areas with clear-cuts, soil moisture, and drought (standardized precipitation-evaporation index (SPEI)) from both the first and second year of standing tree mortality. Due to the strong correlation between forest age and height (r = 0.94), age was not evaluated. The forest predictors in the surrounding landscape (conducted with "moving windows" of 2x2 km^2 within the raster package (Hijmans, 2020)) were spruce volume, spruce height, clear-cut edges, nature reserves and soil

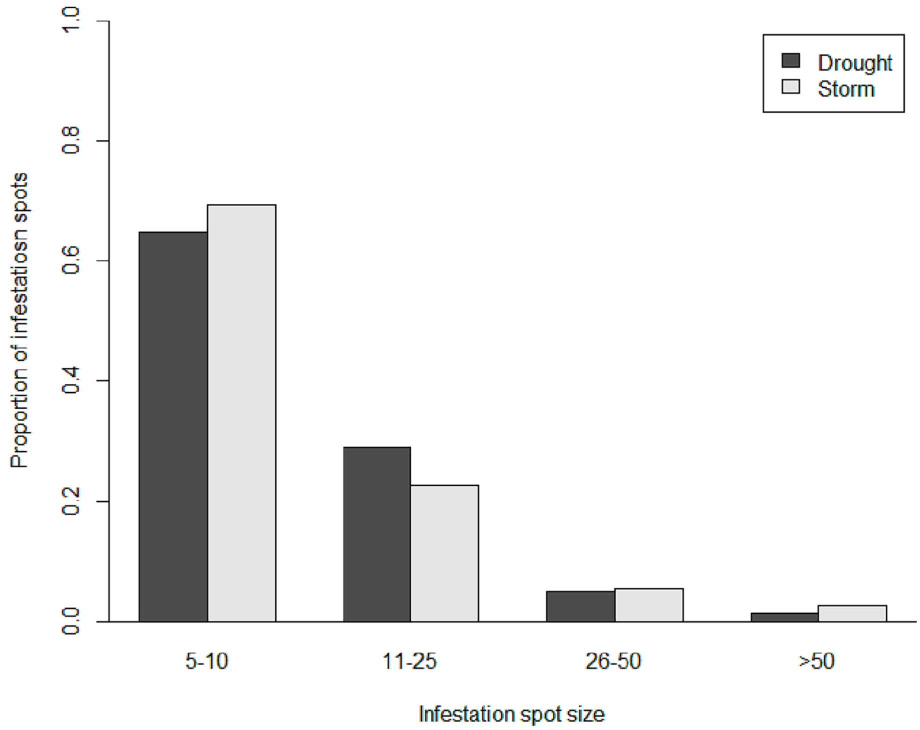

Fig. 2. The proportion of infestation patch sizes (classification of number of trees from original group size classes) between storm and drought-induced outbreak.

moisture. In addition, a distance-weight function was added to each landscape variable by applying a Gaussian kernel filter within the 2 × 2 km^2 "moving window" using the "focalWeight" function in the R package "raster"(Hijmans, 2020). A sigma value of 400 was chosen to correspond to a typical normal-distribution curve within the 4 km^2 window and was based on information of flight distances from previously reported studies, i.e., within 1000 m (Kautz et al., 2011; Kärvemo, 2015; Økland et al., 2016). Data of spruce volumes and heights were accessed from the 2005 and 2015 maps of forest land in Sweden (Reese et al., 2003). Spruce height was created by exclusively using forest height pixels with spruce (>100 m^3). As trees in newly exposed stand edges (facing fresh clear-cuts) experience an increased risk of infestations, clear-cut edges were assessed from satellite images of harvested forest conducted by the Swedish Forest Agency within the preceding five years for each outbreak, i.e., 2002–2006 and 2014–2018, respectively. Clear-cut polygons were rasterized and the number of pixels were summed in the landscape. The clear-cut layers were additionally used to mask out harvested pixels in 2005–2006 and 2014–2018, from the spruce volume and height 2005 and 2015. Vector data of all existing nature reserves as of 2007 and 2019 were derived from the Land Survey of Sweden (https://www.lantmateriet.se/en/) and converted to raster data. Mean soil moisture was extracted from a national-scale raster mapping (ranging from 0 to 100, 10-m resolution), based on digital terrain indices and ancillary environmental information (Ågren et al., 2021). Here, values > 98 were removed as they commonly indicate water bodies and thus non-forest. Historic reference climatic data for the SPEIs were assembled from the World Bank Climate Change Knowledge Portal (The World Bank, 2022) for the period 2000 to 2020. Annual mean temperatures and total precipitation were used for generating the SPEIs, conducted with the packages ncdf4 (Pierce, 2021), fields (Nychka et al., 2017) and raster (Hijmans, 2020) in program R. The monthly (May, June and July) SPEIs by Thornthwaite were calculated as the difference between precipitation and potential evapotranspiration. Mean May-July SPEI's from 2006 (first year) and 2007 (second year) were analyzed for the storm model, whereas mean May-July SPEIs' from 2018 (first year) and 2019 (second year) were analyzed for the drought model.

2.4. Statistical analyses

Analyses were performed with the statistical software R (ver. 4.0.3; R Core Team, 2020) and model assumptions were visually tested by comparing the standardized deviance residuals to the predicted counts. We confirmed that no explanatory variables correlated with each other using Pearson's correlation coefficients in a correlation matrix for each of the main models (Table 1), and all variables qualified with r < 0.7 (Dormann et al., 2013).

2.4.1. Occurrence of infestations

Differences in the occurrence of infestations and associated forest structures between storm and drought-induced outbreaks were statistically evaluated by generalized linear models (GLM) with binomial error distribution (Table 1). This means, given a specific condition, that there is either a higher probability to have a drought-induced or a storm-induced infestation. At both local and landscape scales, the forest variables considered in the analyses were spruce volume, spruce height and clear-cut edges. We analyzed the data with separate GLMs for local and landscape variables due to overfitted models, resulting in convergence issues. In addition, the areas of nature reserves were evaluated at the landscape scale. SPEIs were not included in the occurrence models due to complete separation, resulting in convergence issues (Albert and Anderson, 1984). Landscape variables were evaluated with non-weighted functions. All continuous variables were standardized to a mean of 0 and a standard deviation of 1, prior to the GLM analysis. However, odds ratios (odds that an outcome will occur given inclusion of the variable) were calculated from unstandardized variables to estimate true unit changes.

2.4.2. Infestation size

Evaluation of infestation sizes (sum of geometric means of infested trees per pixel) and associated forest structures were analyzed with separate GLMs for the storm- and drought- induced outbreaks (Table 1). Because of overdispersion when fitting the models with Poisson distributions, we modelled infestation frequencies using negative binomial error structures – function glm.nb from the MASS package in program R

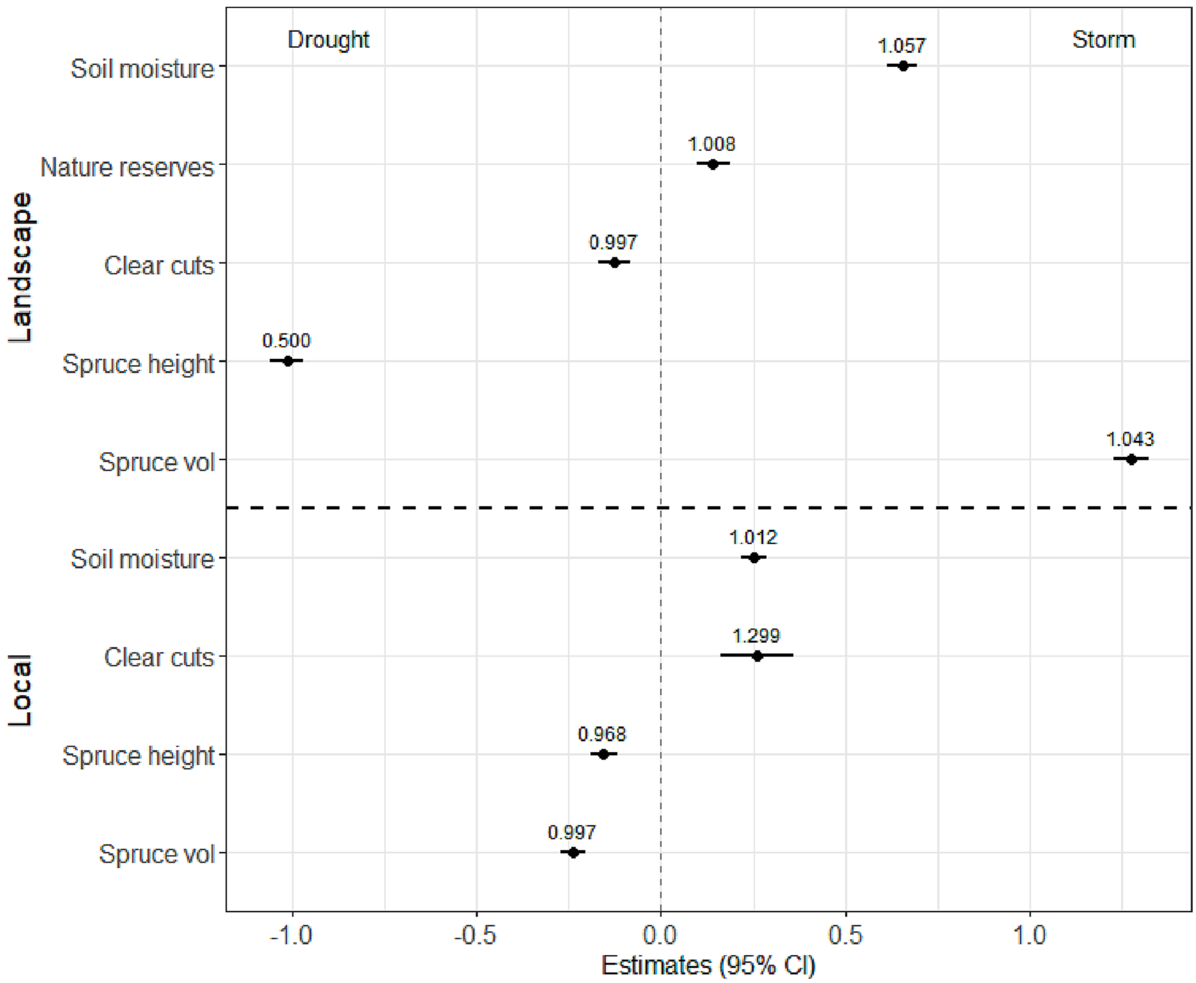

Fig. 3. Logistic regression results (GLM, by using drought and storm-induced infestation occurrence as a binary variable) from the local and landscape models, including estimates, confidence intervals and odds ratios above the point estimates, between the storm and drought-induced outbreak.

(Venables and Ripley, 2002). The best- fitted models were selected from AER::dispersiontest (Kleiber & Zeileis, 2008). As for the *Occurrence models,* local and landscape variables were analyzed separately including the same standardized variables, with the addition of SPEIs (drought index) representing the first and second year of the storm (2006 and 2007), and drought-outbreak models (2018 and 2019).

To evaluate the effects of distance-weight for the landscape variables, (i.e. when giving occupied pixels further away than the closer ones a lower weight) differences between AICs were evaluated by replacing the non-weighted variable one-by-one with the weighted variable. Due to collinearity, spruce height was not evaluated.

2.4.3. Dependencies between the outbreaks

Previous outbreak experience may involve dampening of infestation risks due to changes in forest conditions (Sommerfeld et al., 2021), or possibly a "vaccination" effect (Christiansen and Krokene, 1999). The association between infestation sizes from the storm-induced outbreak (data: 2007–2009) and the drought-induced outbreak was analyzed at different spatial scales by multiple GLMs with negative binomial error structures (MASS::glm.nb: Venables and Ripley, 2002). Five regressions between infestation sizes from both outbreaks within 300 to 1100 m moving-window side length (200 m stepwise) were modelled separately. This corresponds to summed infestation sizes from the two outbreaks within windows of 9, 25, 49, 81 and 121 ha, respectively. The sum of geometric means of infestation patch sizes from the drought-induced outbreak were the response variable, whereas the sum of geometric means of infestation patch sizes from the storm-induced outbreak were the explanatory variable. An additional set of models were run, where spruce volumes were added as an offset variable in the models, which resulted in a rate-dependent response, i.e., we controlled for spruce forest variations.

3. Results

Despite the different methods of collecting data for the two outbreaks, the results show relatively similar proportions with a higher frequency of small-sized infested patches, with > 80% of the patches containing<25 trees (Fig. 2).

The sum of patches within pixels indicated a higher patch density of the drought-induced outbreak compared to the storm-induced outbreak. For the drought data, more than one patch was found in 43% of the pixels, whereas for the storm data, only 4% of the pixels contained more than one patch.

3.1. Occurrence of infestations

The importance of forest conditions influencing the occurrence of infested patches differed considerably between the storm and drought-induced outbreak (Fig. 3; A1-A2). Except for large differences in SPEI where drought-induced infestations occurred at drier locations (Fig. A1d-f), the most important variables that differed between the outbreaks were spruce volume and tree heights in the landscape. Moreover, in comparison to the drought-induced outbreak, there was a higher probability of finding storm-induced infestations with increasing

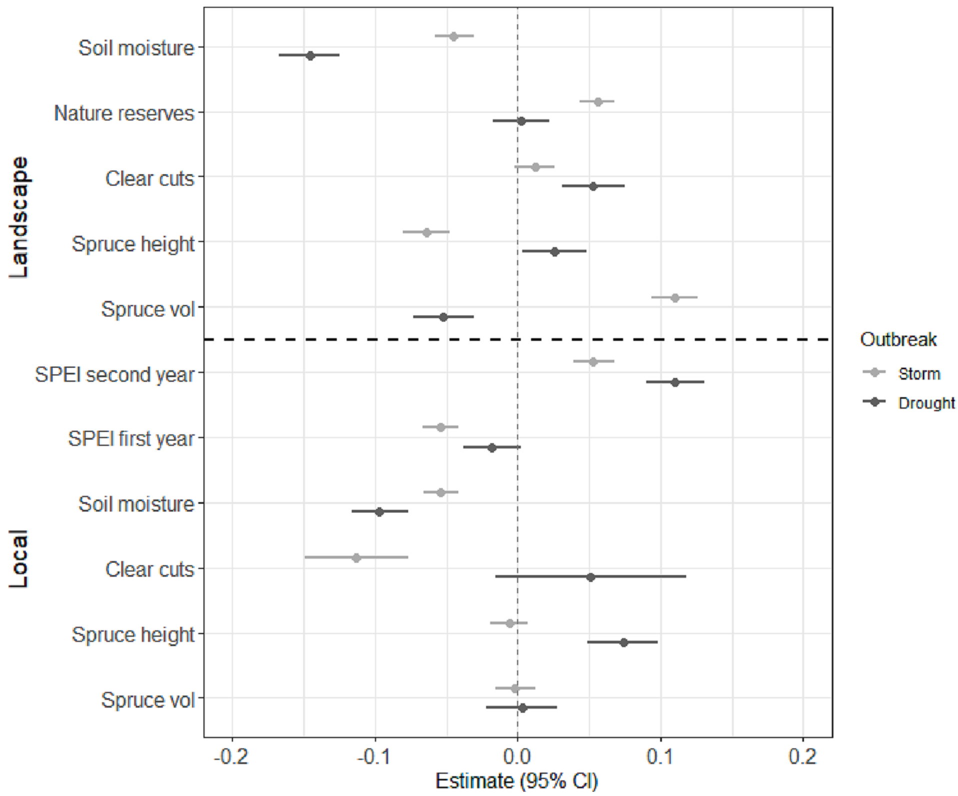

Fig. 4. Model estimates (95% confidence intervals) for infestation spot sizes after storm and drought-induced outbreak and associations with forest characteristic variables at different spatial scales. Black bold dashed line separates local and landscape variables while dashed grey line indicate zero threshold for significance.

areas of nature reserves and increasing soil moisture in the landscape. Clear-cuts in the landscape were more important for the drought-induced outbreak. However, if soil moisture was excluded from the model, clear-cuts were more important for the storm-induced outbreak (Estimate = 0.12; p=<0.001). This phenomenon, called Simpson's paradox is well known in statistics (Simpson, 1951) and may occur when variables are interacting, although the correlation coefficient (r) between clear-cuts and soil moisture was only 0.39. No other variable changed substantially if the variables were removed one-by-one from the models. The two most important local variables for the storm-induced outbreak were clear-cuts and soil moisture, while spruce height and volume were more important for the drought-induced outbreak.

3.2. Infestation size

The forest condition variables that influenced the sum of infestation patch sizes within one-ha pixels differed between storm and drought-induced outbreaks (Fig. 4). The models for each of the outbreaks indicate that clear-cuts in the landscape and drought (SPEI) in the first outbreak year increased infestation sizes. However, the clear-cuts for the storm-induced outbreak and the SPEI for the drought-induced outbreak were only marginally significant (p = 0.08, p = 0.09, respectively). Conversely, in the second year, areas with less drought (SPEI) were associated with increased infestation sizes. Moreover, increased soil moisture at both local and landscape scale seems to reduce infestation sizes. Spruce volumes and heights in the landscape models had a direct opposite relationship when comparing storm and drought-induced outbreaks. During the drought-induced outbreak, taller spruce trees were found to increase infestation sizes, while larger spruce volumes in the landscape were found to decrease infestation sizes. Conversely, storm-induced infestations sizes decreased with taller spruce trees and increased with spruce volumes in the landscape.

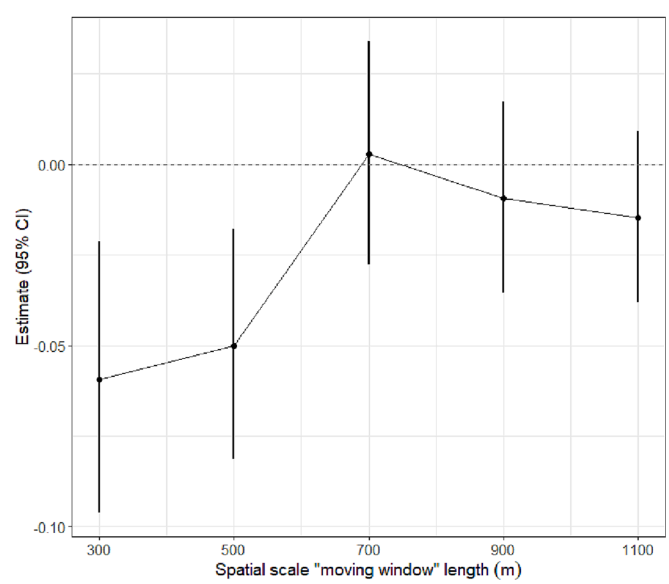

Fig. 5. Location-based coefficient outcomes (with confidence intervals) of infestation sizes between the drought-induced (response) and the storm-induced (predictor) outbreak across different spatial scales.

Another important landscape variable for the storm-induced outbreak, positively associated with infestation sizes, was area of nature reserves, whereas no effect of these was found for the drought-induced outbreak. Local spruce volumes were not significantly associated with infestation sizes for any of the outbreaks.

Distance effects for the landscape variables within moving-windows of 2x2 km^2 were exclusively important for clear-cuts. The inclusion of the distance-weight for this variable reduced the AIC by 9 and 10 for the storm and drought models respectively.

The main landscape model of the drought-induced outbreak was additionally performed by excluding all infestation data from the overlapping storm-outbreak area, indicating a situation where drought infestations were probably less affected by the storm-induced infestations. Considering the small sample size (N = 832; 13%), the results were comparable to those of the full model that included all infestations with no impact of nature reserves (Estimate = -0.007, p = 0.805), a positive estimate of height (Estimate = 0.0451, p = 0.15), a negative estimate of spruce volume (Estimate = -0.039, p = 0.20) and a positive estimate of clear-cuts (Estimate = 0.140, $p < 0.001$).

3.3. Dependencies between the outbreaks

The generalized regression models of infestation sizes from the two outbreaks were negative within the two smallest scales (Fig. 5), i.e., window lengths of 300 and 500 m (i.e. 9 and 25 ha), indicating lower risk of large drought-induced infestations where large storm-induced infestations occur. However, no correlations were found at larger scales. When spruce volume was included as an offset in the model (i.e. rate of attacks based on spruce availability), no negative correlations remained (Fig. A3). Instead, positive correlations between infestation sizes were found at the largest spatial scales, i.e., >700x700 m^2 (49 ha).

4. Discussion

Large forest disturbances such as storms, droughts and subsequent bark beetle outbreaks play major roles in forest ecosystems. Identification of bark beetle damage risks following different triggers and associated forest conditions are important to provide information needed for future development of bark-beetle outbreak prediction, risk indices of infestations and prioritization for forest management. We compared a storm and drought-induced outbreak after the second year of standing tree mortality, which corresponds to the second highest year of tree mortality across the phases of both outbreaks. The outcomes from this study demonstrate that the spatial configuration of bark beetle infestations after storms and droughts differs considerably and the main cause seems to be linked to the spatial distribution of susceptible trees. The storm-induced infestation probability (in relation to the drought-induced outbreak) and size increased more with spruce volumes and nature reserves in the landscape, whereas the drought-induced infestation probability (in relation to the storm-induced outbreak) and size increased more with clear-cuts in the landscape and spruce heights across spatial scales. We also demonstrate that infestation sizes of the second outbreak were locally negatively influenced by the infestation sizes of the first outbreak and that this phenomenon occurred within a landscape size of 25 ha (500x500 m^2). This negative relationship disappeared when controlling for spruce volumes and was therefore most likely influenced by a local depletion of susceptible host trees or an increased tree species diversity, which provided an important dampening feedback from the first outbreak (Sommerfeld et al., 2021). In addition, from the landscape infestation-size model, when removing areas apparently affected by both outbreaks, it appears that the forest variables that influenced the drought-induced outbreak were not considerably impacted by the previous outbreak caused by the storm.

The strong positive association between spruce volumes in the landscape, storm infestation occurrences (relative to drought) and infestation sizes may be caused by pure stands of Norway spruce, which increase the risk of storm-felling (Mezei et al., 2014; Roessiger et al., 2020). Thus, a higher population density of bark beetles occurs in these landscapes (Kärvemo et al., 2014b). The positive relationship between spruce volumes in the landscape and infestation risks after storm felling is supported by previous studies (Kärvemo et al., 2014a, 2016). The area of nature reserves in the landscape increased the infestation occurrence and size after the storm, whereas a relatively lower risk of occurrence and no difference in infestation size were found for nature reserves after the drought. In comparison with drought, when all trees are more or less affected by stress, trees retained after a storm may attract more bark beetles from the landscape and thus infested patches will increase in size due to relatively fewer susceptible trees in the landscape (Montano et al., 2016). This is additionally supported by large-scale removal of wind-felled spruce trees in the managed forest during the first year after the storm (Schroeder et al., 2006), while removal of trees in nature reserves was limited. In contrast, after the drought-induced outbreak, sanitary cutting may not be implemented to the same extent, mainly due to difficulties in locating infested trees showing almost no signs of infestations during spring and early summer. Furthermore, during the drought outbreak tree stress was affecting more trees across a larger region. This may have influenced the stronger impact of nature reserves in the landscape on storm-induced infestations compared to drought. It is important to note that the forest variables, such as spruce volume and height in the landscape, clear-cuts, drought index (SPEI) and soil moisture locally had a greater or similar effect on the occurrence and size of storm-induced infestations when compared to nature reserves, according to the models. Furthermore, it is crucial to consider the causative factors behind this relationship, as all types of nature reserves were incorporated into the models regardless of variables such as infestation rates and forest characteristics.

The association between infestation occurrence and clear-cuts at a local scale (and at the landscape scale when excluding soil moisture from the model) was relatively stronger for storm-induced outbreak compared to the drought and this may also be related a narrower range of host-tree choices. Clear-cuts at the landscape scale were more positively associated with infestation sizes after the drought. As the drought in 2018 started at the same time (May) as the first swarming period of the spruce bark beetle, these trees adjacent to clear-cuts may be the most susceptible due to a warmer microclimate (resulting in increased flight capacity, tree stress and volatile emissions), functioning as stepping-stones in the landscape for later attacks (Kautz et al., 2013). The reduction of AIC when including the distance-weight function revealed that distances closer to the clear cuts ($< \sim 1$ km) explained infestation size variation even better. This may be explained by the effect of the microclimatic functions at the edge of the clear-cuts (see above), linked to increased infestation risks and stepping stone functions.

In relation to storm-induced outbreak, local spruce heights for the drought-induced outbreak were more important for infestation occurrence and size. In general, the spruce bark beetle prefers to colonize larger (Jakuš et al., 2011; Mezei et al., 2014) or older trees (Overbeck and Schmidt, 2012; but see Hutchison and Reid, 2022) as they have a thicker phloem (food source) and a greater area for colonization. At the same time more beetles are needed to overcome the stronger defense from larger trees (Boone et al., 2011; Jakuš et al., 2011; Hutchison and Reid, 2022). As drought lowers vitality of the standing host trees at a larger scale than storms, greater amounts of taller trees are susceptible for bark beetle attacks after droughts where they also can reproduce more efficiently (Kärvemo, 2015). A relatively lower impact of local tree heights and a higher influence of spruce volumes for the storm-induced outbreak may be related to a higher discrimination of host trees due to a relatively lower number of large susceptible trees. Instead, variables related to reduced defenses such as clear-cut edges at a local scale and soil moisture across scales may be more important for the occurrence of infestation after storms, which is supported by the occurrence model results. However, when infestations are caused by drought, they tend to increase in size to a greater extent when the soil has low moisture levels and there are more clear-cuts in the surrounding landscape, as compared to when infestations occur due to storms.

Soil moisture reduced the occurrence of storm-induced infestation to a higher degree than drought-induced outbreak, whereas areas with more soil moisture reduced infestation sizes to a higher degree for the drought-induced infestations. The reason for a lower occurrence in wetter areas after the storm may be that the forests were not suffering from such an extreme drought as in 2018, which means that more water-

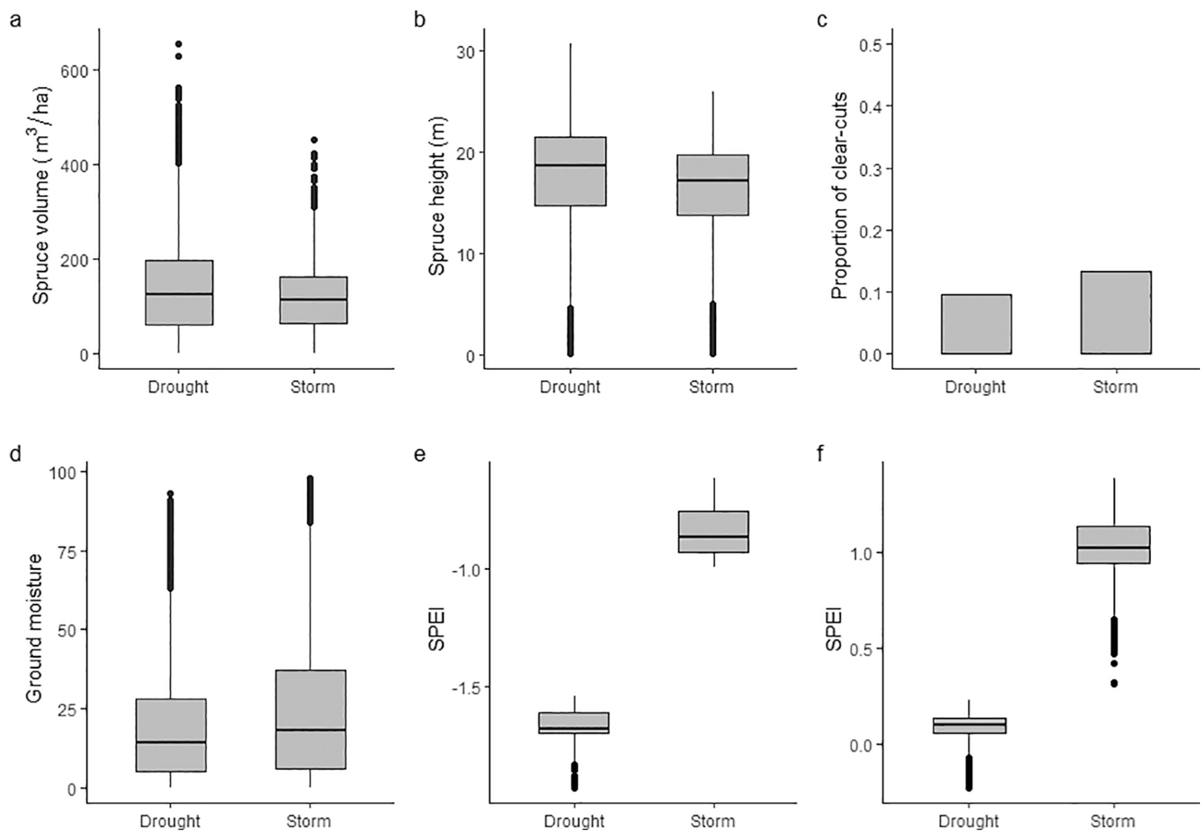

Fig. A1. Occurrence of bark-beetle infestation after drought and storm-induced outbreaks and associations with local variables, including (a) spruce volume, (b) spruce height, (c) proportion of pixels including clear-cut edges, (d) soil moisture and drought index (SPEI) during the (e) first and (f) second year of the outbreaks.

deficient spruce stands were at a relatively lower risk of colonization during the storm-induced outbreak. Commonly wetter areas were relatively drier after the drought in 2018, resulting in a more even and thus reduced influence of soil moisture on drought-induced infestation occurrences. This is in accordance with previous studies demonstrating relatively higher infestation risks at low elevation sites or mesic topographic positions after drought-induced outbreaks (Lausch et al., 2011; Harvey et al., 2021; Nardi et al., 2023). Still, compared to the storm, the drought-induced infestations were even more limited in size at these sites, possibly due to a higher probability of finding even better host trees in nearby stands.

For the drought-induced outbreak, the drought index (SPEI) data for both 2018 and 2019 were generally lower compared to the storm-induced outbreak 2006 and 2007 (Fig. A1e-f). The mean weather conditions in May-July 2006 and especially 2018 were drier than the long-term average (indicated by negative SPEI values) and drier sites had larger infestation sizes for both outbreaks. In contrast, the years 2007 and 2019 had a higher or similar drought index than the average, and surprisingly, the relatively wetter sites during those years were associated with larger infestation sizes. This may be a result of a mismatch between first and second infestation years and first and second-year SPEI data. In order to better understand this, the first and second-year harvest data of trees killed during the drought outbreak were analyzed separately (i.e. infestations harvested between Jan-July with the assumption that they were mainly infested in 2018, as spruce generally does not show signs of infestations until the autumn). Models from this filtered data (results not shown) revealed that the main results derived from the infestations in 2019 were similar, whereas infestations from 2018 were not significantly associated with SPEI 2018. A stronger impact of the drought year (i.e., SPEI 2018) on infestations in 2019 compared to 2018 indicates a strong lagged effect of drought. The main drought in 2018 started in May during the main swarming period, with a continuation in June and was particularly pronounced in July (Swedish Meteorological and Hydrological Institute); such a prolonged drought may have caused a strong lagged effect on the vitality of the Norway spruce in 2019 (Bigler et al., 2007). This theory is supported by previous studies demonstrating a time-lagged effect of drought on bark beetle-induced tree mortality (Lloret and Kitzberger, 2018; Müller et al., 2022). The significance of larger infestation sizes with less drought indicates that areas which have generally wetter conditions can be more sensitive to bark beetle attacks when experiencing extensive droughts (Nardi et al., 2023). The reason for this may be related to differing root lengths in different soil conditions. Spruce in wetter areas with less experience of drought develop shorter roots (Puhe, 2003), which makes them more susceptible to extreme droughts.

It is important to stress that the underlying data used in this study were intended for practical forest management planning. It was not sampled for scientific purposes and it is therefore exposed to some subjectivity, which in addition to errors from harvest or flight interpretation of infestations can lead to inconsistencies when linked together or summed up within pixels.

5. Conclusions

The results of the present study have implications for prediction of infestation risks of the spruce bark beetle. Bark beetle outbreaks are expected to increase with climate change, particularly those induced by drought. To predict high-risk areas, it is important to understand the differences between storm and drought-induced infestations. With the intense development of high-resolution satellite data of forest characteristics, technology and AI in the last decade, the number of risk index applications of bark beetle infestations is increasing rapidly. These predictions are commonly based on stand variables (e.g. spruce volume, age and size, soil moisture, terrain and stand densities) and climatic data

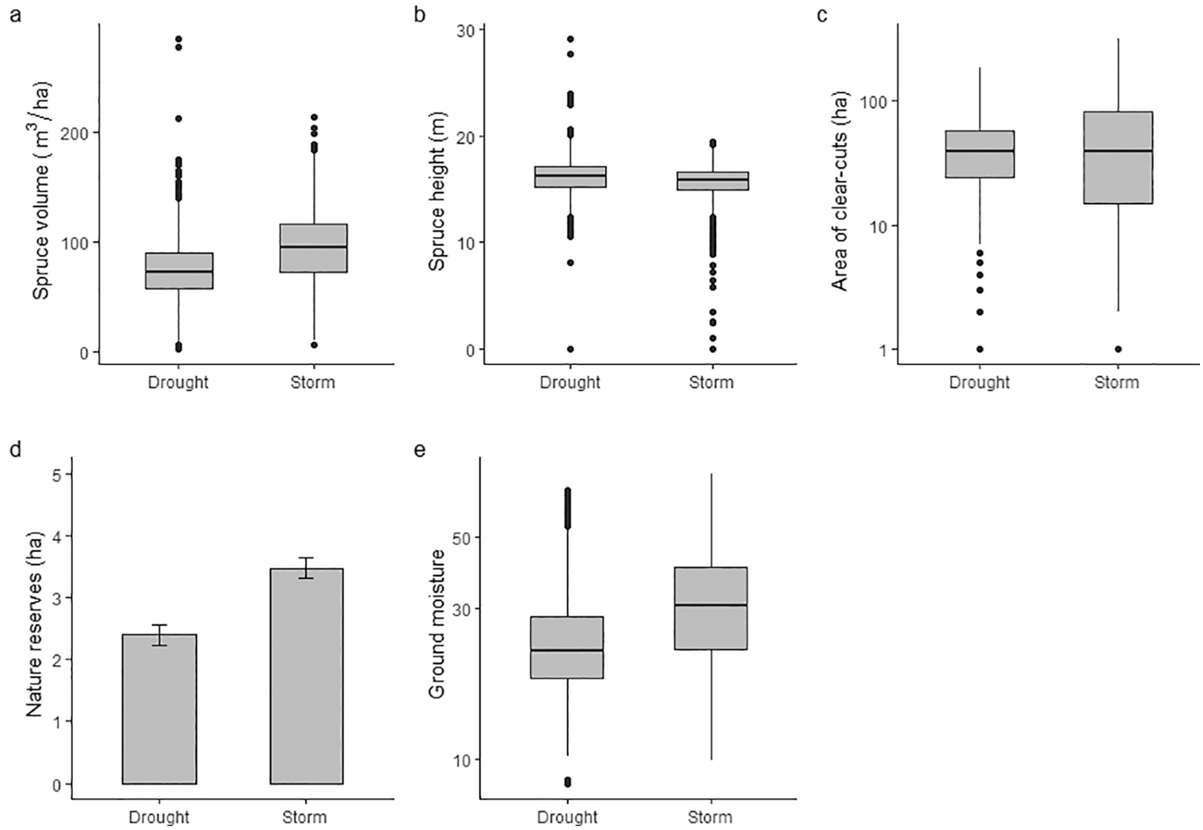

Fig. A2. Occurrence of bark-beetle infestations after drought and storm-induced outbreaks and associations with landscape variables within a 2x2 km "moving window" including, (a) means of spruce volume, (b) means of spruce height, (c) sums of clear-cut edge pixels, (d) mean hectares of nature reserves, and (e) mean soil moisture.

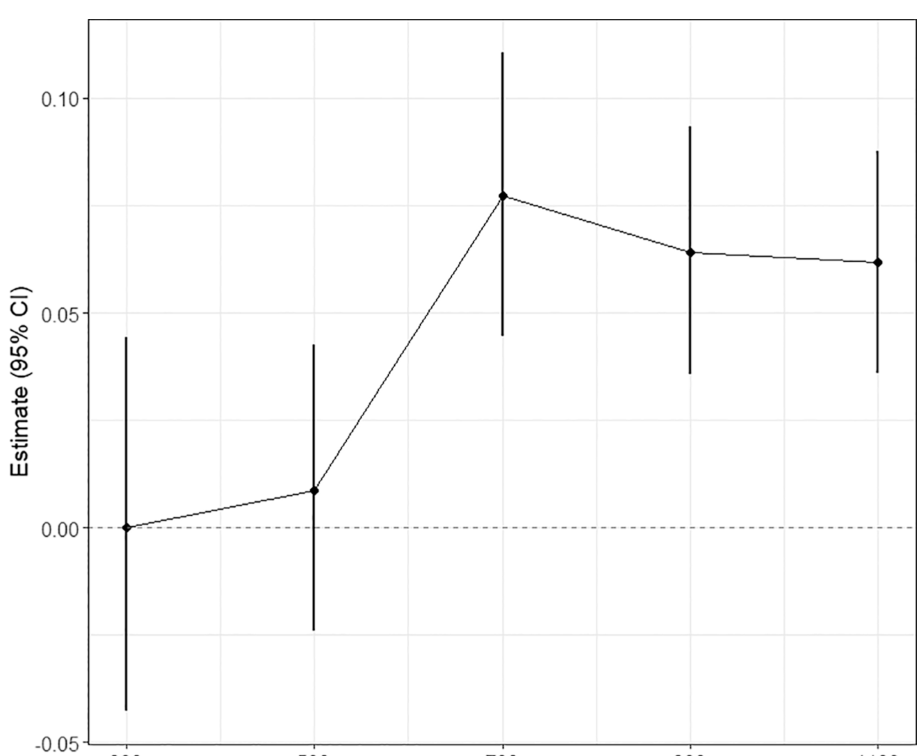

Fig. A3. Scale-based correlation outcomes of infestation spot sizes between the drought-induced (response) and the storm-induced (predictor) outbreak across different spatial scales, when controlling for spruce volumes as an offset in the models.

from empirical outbreak data triggered either from storms, droughts or a combination of these (Netherer and Nopp-Mayr, 2005; Yu et al., 2019; Nordkvist et al., 2023). However, the present study shows that forest stand variables and relationships with the occurrence and magnitude of infestations differ considerably between storms and drought. This must be taken into account in order to increase the precision of infestation prediction. The results indicate that areas with a high risk of large bark beetle infestation sizes following both storms and drought are typically located in dry areas and soils and with clear-cuts at a landscape scale. However, most variables included in this study differed considerably between storm and drought-induced outbreaks and the most consistent differences in risks for both infestation occurrence and size were spruce volumes, heights and nature reserves in the landscape. After the storm, spruce volume and nature reserves were positively associated with infestations size and occurrence (in relation to drought-induced outbreak). Nevertheless, due to the lack of certainty regarding the causation between nature reserves and infestations, these findings should be considered as a starting point, guiding future research to explore the mechanisms responsible for this relationship.

The results show that the underlying outbreak trigger and landscape factors, as well as drought levels and previous outbreak infestations locally, should be considered when applying indices to predict future infestation risks in time and space.

CRediT authorship contribution statement

S. Kärvemo: Conceptualization, Methodology, Writing – original draft. **L. Huo:** Writing – review & editing. **P. Öhrn:** Methodology, Writing – review & editing. **E. Lindberg:** Writing – review & editing. **H. Persson:** Writing – review & editing.

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.

Data availability

The authors do not have permission to share data.

Acknowledgements

Financial support was provided from Brattåsstiftelsen F20:02, Skogssällskapet 2020-774, Formas – a Swedish Research Council for Sustainable Development 2021-01610, the Stiftelsen Seydlitz MP bolagen Foundation, and the Stiftelsen Nils och Dorthi Troëdssons Foundation. We greatly appreciate the valuable feedback from Martin Schroeder and Sigrid Netherer on the study interpretation and design and Gerard Malsher and Mirjam Kärvemo for proof reading. We thank Södra skog (Henrik Holmberg) for the harvesting data of infestations from the drought outbreak and the Swedish Forest Agency who allowed us to use storm-induced outbreak data from their helicopter survey.

Appendix A

References

Ågren, A.M., Larson, J., Paul, S.S., Laudon, H., Lidberg, W., 2021. Use of multiple LIDAR-derived digital terrain indices and machine learning for high-resolution national-scale soil moisture mapping of the Swedish forest landscape. Geoderma 404, 115280.

Albert, A., Anderson, J.A., 1984. On the existence of maximum likelihood estimates in logistic regression models. Biometrika 71, 1–10.

Ayres, M.P., Martinson, S.J., Friedenberg, N.A., 2011. Southern pine beetle ecology: populations within stands. In: Coulson, R.N., Klepzig, K.D. (Eds.), Southern Pine Beetle II. Gen. Tech. Rep. SRS-140. US Department of Agriculture Forest Service, Southern Research Station, Asheville, NC, pp. 75–89.

Berner, L.T., Law, B.E., Meddens, A.J., Hicke, J.A., 2017. Tree mortality from fires, bark beetles, and timber harvest during a hot and dry decade in the western United States (2003–2012). Environ. Res. Lett. 12, 065005.

Bigler, C., Gavin, D.G., Gunning, C., Veblen, T.T., 2007. Drought induces lagged tree mortality in a subalpine forest in the Rocky Mountains. Oikos 116, 1983–1994.

Blomqvist, M., Kosunen, M., Starr, M., Kantola, T., Holopainen, M., Lyytikäinen-Saarenmaa, P., 2018. Modelling the predisposition of Norway spruce to *Ips typographus* L. infestation by means of environmental factors in southern Finland. Eur. J. For. Res. 137, 675–691.

Boone, C.K., Aukema, B.H., Bohlmann, J., Carroll, A.L., Raffa, K.F., 2011. Efficacy of tree defense physiology varies with bark beetle population density: a basis for positive feedback in eruptive species. Can. J. For. Res. 41, 1174–1188.

Brůna, J., Wild, J., Svoboda, M., Heurich, M., Müllerová, J., 2013. Impacts and underlying factors of landscape-scale, historical disturbance of mountain forest identified using archival documents. For. Ecol. Manag. 305, 294–306.

Christiansen, E., Krokene, P., 1999. Can Norway spruce trees be 'vaccinated'against attack by *Ips typographus*? Agric. For. Entomol. 1, 185–187.

Csilléry, K., Kunstler, G., Courbaud, B., Allard, D., Lassègues, P., Haslinger, K., Gardiner, B., 2017. Coupled effects of wind-storms and drought on tree mortality across 115 forest stands from the Western Alps and the Jura mountains. Glob. Change Biol. 23, 5092–5107.

De Groot, M., Diaci, J., Ogris, N., 2019. Forest management history is an important factor in bark beetle outbreaks: Lessons for the future. For. Ecol. Manag. 433, 467–474.

De Groot, M., Diaci, J., Kandare, K., Krajnc, N., Pisek, R., Ščap, Š., Stare, D., Ogris, N., 2021. Private forest owner characteristics affect european spruce bark beetle management under an extreme weather event and host tree density. Forests 12, 346.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36 (1), 27–46.

Haarsma, R.J., Hazeleger, W., Severijns, C., De Vries, H., Sterl, A., Bintanja, R., Van Oldenborgh, G.J., Van Den Brink, H.W., 2013. More hurricanes to hit western Europe due to global warming. Geophys. Res. Lett. 40, 1783–1788.

Harvey, B.J., Andrus, R.A., Battaglia, M.A., Negrón, J.F., Orrego, A., Veblen, T.T., 2021. Droughty times in mesic places: factors associated with forest mortality vary by scale in a temperate subalpine region. Ecosphere 12, e03318.

Hedgren, P.O., Schroeder, L.M., Weslien, J., 2003. Tree killing by *Ips typographus* (Coleoptera: Scolytidae) at stand edges with and without colonized felled spruce trees. Agric. For. Entomol. 5, 67–74.

Hijmans, R.J., 2020. raster: Geographic Data Analysis and Modeling. R package version 3.3-13. https://CRAN.R-project.org/package=raster.

Hlásny, T., König, L., Krokene, P., Lindner, M., Montagné-Huck, C., Müller, J., Qin, H., Raffa, K.F., Schelhaas, M.J., Svoboda, M., 2021a. Bark beetle outbreaks in Europe: State of knowledge and ways forward for management. Curr. For. Rep. 7, 138–165.

Hlásny, T., Zimová, S., Merganičová, K., Štěpánek, P., Modlinger, R., Turčáni, M., 2021b. Devastating outbreak of bark beetles in the Czech Republic: Drivers, impacts, and management implications. For. Ecol. Manag. 490, 119075.

Hutchison, I.K., Reid, M.L., 2022. Phloem and defence traits in relation to tree size and age: implications for host selection by bark beetles. For. Ecol. Manag. 513, 120183.

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, 223–243.

Jactel, H., Koricheva, J., Castagneyrol, B., 2019. Responses of forest insect pests to climate change: not so simple. Curr. Opin. Insect. Sci. 35, 103–108.

Jakuš, R., Edwards-Jonášová, M., Cudlín, P., Blaženec, M., Ježík, M., Havlíček, F., Moravec, I., 2011. Characteristics of Norway spruce trees (*Picea abies*) surviving a spruce bark beetle (*Ips typographus* L.) outbreak. Trees 25, 965–973.

Kärvemo, S., 2015. Outbreak dynamics of the spruce bark beetle *Ips typographus* in time and space. Doctoral dissertation Swedish University of Agricultural Sciences 2015 (27).

Kärvemo, S., Rogell, B., Schroeder, M., 2014a. Dynamics of spruce bark beetle infestation spots: Importance of local population size and landscape characteristics after a storm disturbance. For. Ecol. Manag. 334, 232–240.

Kärvemo, S., Schroeder, L.M., 2010. A comparison of outbreak dynamics of the spruce bark beetle in Sweden and the mountain pine beetle in Canada (Curculionidae: Scolytinae). Entomol. Tidskr. 131, 215–224.

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, e01257.

Kärvemo, S., Van Boeckel, T.P., Gilbert, M., Grégoire, J.-C., Schroeder, M., 2014b. Large-scale risk mapping of an eruptive bark beetle–importance of forest susceptibility and beetle pressure. For. Ecol. Manag. 318, 158–166.

Kautz, M., Dworschak, K., Gruppe, A., Schopf, R., 2011. Quantifying spatio-temporal dispersion of bark beetle infestations in epidemic and non-epidemic conditions. For. Ecol. Manag. 262, 598–608.

Kautz, M., Schopf, R., Ohser, J., 2013. The "sun-effect": microclimatic alterations predispose forest edges to bark beetle infestations. Eur. J. For. Res. 132 (3), 453–465.

Lausch, A., Fahse, L., Heurich, M., 2011. Factors affecting the spatio-temporal dispersion of *Ips typographus* (L.) in Bavarian Forest National Park: A long-term quantitative landscape-level analysis. For. Ecol. Manag. 261 (2), 233–245.

Lloret, F., Kitzberger, T., 2018. Historical and event-based bioclimatic suitability predicts regional forest vulnerability to compound effects of severe drought and bark beetle infestation. Glob. Chang. Biol. 24 (5), 1952–1964.

Marini, L., Økland, B., Jönsson, A.M., Bentz, B., Carroll, A., Forster, B., Grégoire, J.C., Hurling, R., Nageleisen, L.M., Netherer, S., 2017. Climate drivers of bark beetle outbreak dynamics in Norway spruce forests. Ecography 40, 1426–1435.

Mezei, P., Grodzki, W., Blaženec, M., Jakuš, R., 2014. Factors influencing the wind–bark beetles' disturbance system in the course of an *Ips typographus* outbreak in the Tatra Mountains. For. Ecol. Manag. 312, 67–77.

Mezei, P., Jakuš, R., Pennerstorfer, J., Havašová, M., Škvarenina, J., Ferenčík, J., Slivinský, J., Bičárová, S., Bilčík, D., Blaženec, M., Netherer, S., 2017. Storms, temperature maxima and the Eurasian spruce bark beetle *Ips typographus*—An infernal trio in Norway spruce forests of the Central European High Tatra Mountains. Agric. For. Meteorol. 242, 85–95.

Montano, V., Bertheau, C., Doležal, P., Krumböck, S., Okrouhlík, J., Stauffer, C., Moodley, Y., 2016. How differential management strategies affect *Ips typographus* L. dispersal. For. Ecol. Manag. 360, 195–204.

Müller, M., Olsson, P.-O., Eklundh, L., Jamali, S., Ardö, J., 2022. Features predisposing forest to bark beetle outbreaks and their dynamics during drought. For. Ecol. Manag. 523, 120480.

Nardi, D., Jactel, H., Pagot, E., Samalens, J.-C., Marini, L., 2023. Drought and stand susceptibility to attacks by the European spruce bark beetle: A remote sensing approach. Agric. For. Entomol. 25 (1), 119–129.

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. For. Ecol. Manag. 207 (1–2), 99–107.

Netherer, S., Panassiti, B., Pennerstorfer, J., Matthews, B., 2019. Acute drought is an important driver of bark beetle infestation in Austrian Norway spruce stands. Front. For. Glob. Change. 2, 39.

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.

Nychka, D., Furrer, R., John, P., Sain, S. 2017. fields: Tools for spatial data. R package version 12.3. https://github.com/NCAR/Fields.

Økland, B., Nikolov, C., Krokene, P., Vakula, J., 2016. Transition from windfall-to patch-driven outbreak dynamics of the spruce bark beetle *Ips typographus*. For. Ecol. Manag. 363, 63–73.

Overbeck, M., Schmidt, M., 2012. Modelling infestation risk of Norway spruce by *Ips typographus* (L.) in the Lower Saxon Harz Mountains (Germany). For. Ecol. Manag. 266, 115–125.

Pasztor, F., Matulla, C., Rammer, W., Lexer, M.J., 2014. Drivers of the bark beetle disturbance regime in Alpine forests in Austria. For. Ecol. Manag. 318, 349–358.

Persson, H., Kärvemo, S., Lindberg, E., Langning, H. 2022. Early detection and large-area mapping of spruce bark beetle damage in southern Sweden using Sentinel-2 images. Advances in new sensors and data processing development related to forest disturbance ecology. Horizon Europe. A workshop organized within the RESDINET project.

Pierce, D. 2021. ncdf4: Interface to Unidata netCDF (Version 4 or Earlier) Format Data Files. R package version 1.19. https://CRAN.R-project.org/package=ncdf4.

Potterf, M., Svitok, M., Mezei, P., Jarčuška, B., Jakuš, R., Blaženec, M., Hlásny, T., 2023. Contrasting Norway spruce disturbance dynamics in managed forests and strict forest reserves in Slovakia. Forestry 96, 387–398.

Puhe, J., 2003. Growth and development of the root system of Norway spruce (*Picea abies*) in forest stands—A review. For. Ecol. Manag. 175, 253–273.

R Core Team 2020 R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria*. Vienna, Austria.

Reese, H., Nilsson, M., Pahlén, T.G., Hagner, O., Joyce, S., Tingelöf, U., Egberth, M., Olsson, H., 2003. Countrywide estimates of forest variables using satellite data and field data from the national forest inventory. Ambio 32, 542–548.

Roessiger, J., Kulla, L., Sedliak, M., 2020. A high proportion of Norway spruce in mixed stands increases probability of stand failure. Cent. Eur. For. J. 66, 218–226.

Schlyter, P., Stjernquist, I., Bärring, L., Jönsson, A.M., Nilsson, C., 2006. Assessment of the impacts of climate change and weather extremes on boreal forests in northern Europe, focusing on Norway spruce. Clim. Res. 31, 75–84.

Schroeder, L.M., 2010. Colonization of storm gaps by the spruce bark beetle: influence of gap and landscape characteristics. Agric. For. Entomol. 12, 29–39.

Schroeder, L.M., Mitsell, N., Turesson, T. 2006. Granbarkborrens utnyttjande av vindfällen under första sommaren efter stormen Gudrun. (The spruce bark beetle in wind-felled trees in the first summer following the storm Gudrun). – Skogsstyrelsen, Rapport 15 (2006), Jönköping.

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, 530–540.

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., 2017. Forest disturbances under climate change. Nat. Clim. Change. 7, 395–402.

Senf, C., Seidl, R., 2021. Mapping the forest disturbance regimes of Europe. Nat. Sustain. 4, 63–70.

Simpson, E.H., 1951. The interpretation of interaction in contingency tables. J. R. Stat. Soc., B: Stat. Methodol. 13, 238–241.

Sommerfeld, A., Senf, C., Buma, B., D'Amato, A.W., Després, T., Díaz-Hormazábal, I., Fraver, S., Frelich, L.E., Gutiérrez, Á.G., Hart, S.J., 2018. Patterns and drivers of recent disturbances across the temperate forest biome. Nat. Commun. 9, 1–9.

Sommerfeld, A., Rammer, W., Heurich, M., Hilmers, T., Müller, J., Seidl, R., 2021. Do bark beetle outbreaks amplify or dampen future bark beetle disturbances in Central Europe? J. Ecol. 109, 737–749.

Sproull, G.J., Bukowski, M., Mcnutt, N., Zwijacz-Kozica, T., Szwagrzyk, J., 2017. Landscape-level spruce mortality patterns and topographic forecasters of bark beetle outbreaks in managed and unmanaged forests of the Tatra Mountains. Pol. J. Ecol. 65, 24–37.

Stadelmann, G., Bugmann, H., Wermelinger, B., Bigler, C., 2014. Spatial interactions between storm damage and subsequent infestations by the European spruce bark beetle. For. Ecol. Manag. 318, 167–174.

Stereńczak, K., Mielcarek, M., Kamińska, A., Kraszewski, B., Piasecka, Ż., Miścicki, S., Heurich, M., 2020. Influence of selected habitat and stand factors on bark beetle *Ips typographus* (L.) outbreak in the Białowieża Forest. For. Ecol. Manag. 459, 117826.

The World Bank. 2022. The Climate Change Knowledge Product. Available at: https://climateknowledgeportal.worldbank.org/.

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, Fourth Edition. Springer, New York.

Venäläinen, A., Lehtonen, I., Laapas, M., Ruosteenoja, K., Tikkanen, O.P., Viiri, H., Ikonen, V.P., Peltola, H., 2020. Climate change induces multiple risks to boreal forests and forestry in Finland: A literature review. Glob. Change Biol. 26, 4178–4196.

Wermelinger, B., Jakoby, O., 2022. Bark BeetlesWohlgemuth, T., Jentsch, A., Seidl, R. (Eds.), In: Disturbance Ecology. Springer, Cham, pp. 271–293.

Wulff, S., Roberge, C., 2021. Inventering av granbarkborreangrepp i Götaland och Svealand 2021. (Inventory of spruce bark beetle infestations in Götaland and Svealand 2021). Department of Forest Resource Management, Swedish Univeristy of Agricultural Sceinces, Report 534, Umeå.

Yu, Y., Chi, Z., Zhang, J., Sun, P., Wang, C., Pan, X., 2019. Assessing the invasive risk of bark beetles (Curculionidae: Scolytinae and Platypodinae). Ann. Entomol. Soc. Am. 112, 451–457.